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Mirror touch:

Electrophysiological and behavioural evidence on the effects of observing others' tactile sensations on somatosensory processing in the observer and possible links to trait empathy

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Abstract

Recent neuroimaging evidence suggests that the sight of somebody else being touched vicariously triggers activity in the secondary (SII) and possibly also the primary (SI) somatosensory cortex in the absence of any actual tactile stimulation on the onlooker’s own body. The present PhD thesis aimed to investigate electrophysiological and behavioural correlates of such shared neural representations for actually experienced and merely observed touch, importantly, not only in the context of observing somebody else being passively touched on their body but also in the context of witnessing somebody else perform actions with a tactile component (such as actively touching an object). In addition, the present thesis intended to explore possible links between variations in the strength of touch observation-related modulations in somatosensory processing and interindividual differences in dispositional empathy.

The obtained electrophysiological data indicated that, first of all, the sight of others’ *passive* tactile sensations modulated somatosensory activity relatively consistently at both early and late processing stages within the first 200 ms after tactile stimulus onset. These modulations occurred independently of whether the touch target was actually a human body or merely an inanimate object (Exp. 2.1). The perspective from which a body part was observed to be touched did differentially affect touch observation-related ERP modulations, but only during later-stage somatosensory processing (Exp. 2.2). The electrophysiological evidence further suggested that while the somatotopic organisation of vicarious somatosensory activations might not be fine-grained enough to represent which location *within* a given body part was seen to be touched (Exp. 2.3), it might nevertheless be sufficiently detailed (at least in SI) to code the touched location at the level of different body parts (Exp. 2.4). The sight of others’ *action-embedded* tactile sensations was, too, found to alter ongoing somatosensory activity but the pattern of modulations was rather complex and fragile (Exp.s 3.1-3.6), possibly in the context of movement observation-related vicarious somatosensory activity which might sometimes have obscured much subtler touch observation-related resonance responses, especially if participants were not sufficiently aware of the tactile component in the observed actions. Behaviourally, the sight of other’s (active) touch sensations was nevertheless associated with systematic shifts in tactile perception (Exp.s 4.1.3 and 4.1.5), even though the measurability of such changes appeared somewhat task-sensitive (Exp. 4.1.4).

Finally, a highly complex pattern of correlations between the strength of touch observation-related ERP modulations and interindividual differences in trait empathy associated the automatic sharing of others’ bodily states with complex emotional and cognitive empathy phenomena. How we respond to others’ somatic sensations thus appears to be fundamentally linked to how readily we respond emotionally to others’ mental and emotional states and how easily we can infer those states by intentionally putting ourselves into somebody else’s shoes. More research will be needed to shed more light on the intricate interplay between low-level resonance mechanisms and higher-order affective and cognitive processes in mediating the empathic understanding of others’ and the occurrence of appropriate other-related emotional responses.

Chapter 1

Vicarious somatosensory brain activity during the observation of others' passive and action-related tactile sensations

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1.1 Introduction

Humans have a remarkable capacity to intuitively and immediately understand what emotional or bodily state another person is in and to empathically share it, without first having to cognitively deduct what the other person might be feeling. Mirror-matching mechanisms in our brain are thought to be the neural basis of this ability to empathise with others so effortlessly (Gallese, 2007; Keysers & Gazzola, 2006). First discovered in the motor domain in the form of a remarkable overlap between motor areas active during both action execution and action observation (Rizzolatti & Craighero, 2004), it is now assumed that such mirror-matching mechanisms are a rather common phenomenon in the brain (Keysers & Gazzola, 2009): Be it an action (Rizzolatti & Craighero, 2004), a bodily sensation such as pain (see Lamm, Decety, & Singer, 2011, for a meta-analysis) or a basic emotion such as disgust (Wicker et al., 2003), the mere observation of these body states has been found to automatically trigger activity in cortical brain areas that were long thought of as being concerned exclusively with the actual execution or perception, respectively, of the observer's *own* actions, sensations and emotions. This vicarious brain activity is assumed to reflect the internal simulation of what it would be like for the observer to perform the same action or experience the same emotion or bodily sensation, allowing an immediate experiential understanding of what others do and feel (Gallese, 2003; 2007; Keysers & Gazzola, 2006; 2009).

Most current research on mirror-matching mechanisms actually focuses on shared neural representations for the execution and observation of *actions*, attempting to elucidate precisely where in motor-related brain areas action execution- and observation-related activity overlaps (e.g. Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008a; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Rizzolatti et al., 1996b; Shmuelof & Zohary, 2006) and how such vicarious motor activity might contribute to e.g. recognising other' actions (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996a), understanding their motor intentions (Blakemore & Decety, 2001; de Lange, Spronk, Willems, Toni, & Bekkering, 2008; Fogassi et al., 2005; Gallese & Goldman, 1998; Iacoboni et al., 2005b) and imitating their motor acts (e.g. Iacoboni, 2005a). Another main area of research interest concerns the shared neural representations for experienced and merely observed somatic pain and how the observer involuntarily simulates not only the affective dimension of the witnessed pain sensation (Botvinick et al., 2005; Jackson, Meltzoff, & Decety, 2005; Morrison, Lloyd, Di Pellegrino, &

Roberts, 2004; Saarela et al., 2007; Singer et al., 2004) but also its sensory (Bufalari, Aprile, Avenanti, Di Russo, & Aglioti, 2007; Cheng, Yang, Lin, Lee, & Decety, 2008; Valeriani et al., 2008) and motor components (Avenanti, Bueti, Galati, & Aglioti, 2005; Avenanti, Minio-Paluello, Bufalari, & Aglioti, 2006; Costantini, Galati, Romani, & Aglioti, 2008). The focus of the present thesis, however, is on the shared neural representations for both directly experienced touch on one's own body and the tactile sensations merely observed in the context of others' bodies, a domain of vicarious brain activity which has only recently attracted more research interest. Pain observation studies do often include the observation of non-noxious touch stimuli applied to others' body parts as control or baseline conditions (e.g. Avenanti et al., 2005; Costantini et al., 2008; Valeriani et al., 2008) but primarily so to expose the distinct neural response to both self- and other-related noxious versus non-noxious stimuli. The present thesis, on the other hand, will focus precisely on these purely tactile, non-painful events and how their observation on others' bodies recruits somatosensory brain areas also involved in processing self-experienced touch. Touch observation-related somatosensory brain activity is particularly fascinating as especially the sense of touch has long been regarded as an entirely private percept as people cannot slip into each other's skin to feel each other's tactile sensations (see Haggard, Taylor-Clarke & Kennett, 2003). Traditionally, the somatosensory cortices have indeed been associated with processing exclusively the tactile sensations from objects in contact with our own skin as well as the proprioceptive signals from our own muscles and joints (Burton & Sinclair, 1996; Kaas, 1990). The ensuing literature review will, however, present recent empirical evidence that both the secondary (SII) and presumably also the primary (SI) somatosensory cortex are also involved in the perception of *others'* tactile sensations. Such an involuntary "mirror touch response" in the form of vicarious somatosensory activity links the perception of others' touch sensations directly to one's own tactile experiences, thus allowing an intuitive interpersonal sharing of touch experiences on a subconscious level. Importantly, Chapter 1.2.1 of the following literature review will primarily focus on touch observation-related vicarious activity in response to the sight of others' being passively touched by e.g. an object (passive touch) while Chapter 1.2.2 will explore the possibility that the observation of others' touch sensations when these are embedded in others' actions and result e.g. from actively touching e.g. an object (active touch) might, too, evoke a distinct somatosensory resonance response, an aspect which has so far largely been neglected in both the touch observation and the action observation literature.

Even if rather uncommon and exceptionally, observing touch on another person's body can, interestingly enough, even elicit an actually felt tactile sensation on some individuals' own body as it is the case in people with mirror-touch synaesthesia (Banissy, Kadosh, Maus, Walsh, & Ward, 2009; Banissy & Ward, 2007). While the empirical work in the present thesis will exclusively concern how normal, non-synaesthetic individuals process others' touch experiences (be it from being touched or from actively touching something), it is nevertheless of great interest that mirror touch synaesthetes whose somatosensory cortex seems to respond particularly strongly to the sight of others' tactile sensations (Blakemore, Bristow, Bird, Frith, & Ward, 2005) have been found to be more empathic than non-synaesthetic controls (Banissy & Ward, 2007). And also for normal individuals, it has previously been suggested that the extent to which somatosensory areas are recruited during touch observation is linked to interindividual differences in dispositional empathy (Schaefer, Heinze, & Rotte, 2012). For this reason, the ensuing literature review will conclude with a brief section on the possible role of vicarious (somatosensory) brain activity in mediating empathy (chapter 1.3) and the associations with interindividual variations in empathic personality traits, followed by a summary of the specific research aims of this thesis (chapter 1.4) with respect to electrophysiological and behavioural correlates of the embodied simulation of others' passive and active touch sensations and possible empathy-related individual differences in how strongly the observer's own somatosensory system is involved in representing others' bodily states.

1.2 Mirror touch: Vicarious somatosensory activity during the observation of others' tactile sensations

1.2.1 Observing others' being touched

Being touched on one's own body evokes activity in a wide-spread cortical network, including primary somatosensory cortex (SI) in the postcentral gyrus, the secondary somatosensory cortex (SII) in the upper bank of the Sylvian fissure, the posterior-parietal cortex (PCC) and frontal regions (Del Gratta et al., 2002; Hari & Forss, 1999), as well as the supplementary motor area (SMA) and the insula (Burton, Videen, & Raichle, 1993; Korvenoja et al., 1999; Ostrowsky et al., 2002). Recent neuroimaging studies nevertheless suggest that the core structures of the somatosensory system, namely the immediate somatosensory cortex[1] consisting of SI and SII, might also respond to the mere sight of others' being touched, in the absence of any tactile stimulation on the observer's own body. Initial findings were, however, inconsistent as to whether observing others' tactile sensations recruits shared neural representations for both directly felt as well as merely observed touch sensations only in SII or also in SI: Keysers et al. (2004) found overlapping neural activity in left SII for when

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[1] For the remainder of this thesis, the term "somatosensory system" will be used to refer to the entire fronto-parietal network of somatosensitive brain areas in general while the term "somatosensory cortex/cortices" will be used to refer to both SI and SII in particular.

participants were tactually stimulated on their own legs (by repeatedly brushing over them with a washing glove) and when they passively observed somebody else’s lower legs being touched with a rod or a brush. SI did not show any such activation overlap for felt and experienced touch, even though there was a non-significant trend in this direction (as well as for right SII; note that during the direct experience of touch, SII is usually activated not only contralaterally, but bilaterally (Del Gratta et al., 2002; Hari & Forss, 1999)). This vicarious activity in SII was, in addition, not specific to observing a human body part being touched and occurred in equal measure for the sight of touch on somebody else’s legs as well for the sight of touch on inanimate paper rolls (Keysers et al., 2004). Blakemore et al. (2005), on the other hand, did reveal observation-induced SI activity which, in addition, showed a clear somatotopic organisation when comparing the activity patterns for touch observed on a neck versus a face and was lateralised. Furthermore, contrasting touch on a face or a neck, respectively, with touch on the corresponding part of an object (e.g. an electrical fan) resulted in significantly stronger activations in bilateral SII and SI, suggesting that mirror touch responses might after all be triggered preferentially by the sight of touch on a human body. Importantly, Ebisch et al. (2008) subsequently identified the perceived intentionality of the observed touch as a potential key for whether or not overlapping activity is found in primary somatosensory areas in particular: Participants observed touch that either occurred intentionally (human hand approaching and touching) or accidentally (wind-moved palm tree branch touching) and that was also directed either towards a human body part (hand) or an inanimate object (chair). In SII, the same overlapping activation between the actual experience of touch and the mere observation was found across all four touch observation conditions, suggesting in line with Keysers et al. (2004) that the tactile mirror-matching system might ultimately respond to an abstract notion of touch, irrespective of whether the observed touch occurs on a human body part or not. One particular region in the left primary somatosensory cortex (SI/Brodmann's area (BA) 2), however, showed a significant selectivity for intentional as opposed to accidental touch, i.e. overlapping activity for both experienced and observed touch in SI/BA 2 was restricted to those observational conditions in which a human hand (rather than a palm tree branch) actively touched either somebody else’s hand or a chair. Whether the touched target was a human body part or an inanimate object was yet again irrelevant. Importantly, such a scenario ultimately involves not one but two pieces of touch-related visual information: The passive touch on the target (be it a human hand or an object) – and the agent’s active motor act to reach and touch. The revealed vicarious activity in SI/BA 2 might actually not be triggered by the observed passive touch sensation but might in fact signifying a human tendency to resonate more with an intentionally acting biological touch agent rather than the passively touched target, reflecting the automatic simulation of the haptic combination of proprioceptive and tactile information associated with the touch agent’s hand movements and the tactile sensations resulting from the actual contact with the touch target (Keysers, Kaas, & Gazzola, 2010). Interestingly enough, SI/BA2 is a higher-order somatosensory area that plays a particularly crucial functional role during the haptic exploration or manipulation of objects, integrating afferent tactile and proprioceptive information from the body (as relayed through BA 3a, BA 3b and BA 1) before passing it on to SII (cf. Keysers et al., 2010). Pierno et al. (2009) demonstrated that SI/BA2 is also active during the observations of others' hand actions, more strongly so, however, when hands were seen to actually touch and manipulate an object as compared to merely pointing at it. Consequently, SI activation during touch observation might thus primarily reflect vicarious "active touch/haptics"-related BA 2 activity (see chapter 1.2.2) which is only found for observational conditions in which a human agent delivers touch and thus haptically interacts with a target (see Blakemore et al., 2005; Ebisch et al., 2008). If a body or object is merely touched by another object (e.g. a brush) in the absence of a (visible) human agent, only SII activations might result (Keysers et al., 2004; see, however, Schaefer, Xu, Flor, & Cohen, 2009). Interestingly, Keysers et al. (2010) speculate that it might actually have been the nearby somatosensory hand rather than the face representation in SI that was active during the observation of finger touching a face in Blakemore et al. (2005)'s study, in line with the interpretation that the resonant SI response is associated with the "touching body part" (hand) rather than with the "touched" one (face).

Overall, Keysers et al. (2010) conclude that resonant somatosensory activity in SI/BA 2 and SII might be functionally complementary during touch observation, with SI/BA2 being associated with vicariously representing the touch agent's proprioceptive and tactile sensations when delivering touch and SII activity being associated with the resonating with the passive tactile sensations of the touched target. This is in line with the notion that – within the somatosensory cortices – only BA 2 (within SI) and SII receive direct visual input (from e.g. the multisensory ventral intraparietal area (VIP); Lewis & Van Essen, 2000) that would allow a visually-induced vicarious somatosensory response to observed touching or touch (cf. Keysers et al., 2010). Any touch observation-related vicarious brain activity in BA3a, BA 3b and BA 1 would necessarily be weaker since it could only be mediated indirectly by back projections from BA 2 and SII (Keysers et al., 2010).

Alternatively, SI activity (for above mentioned reasons late- rather than early-stage activity in SI) might also be found during the observation of others' being passively touched by an object rather than a human as long as sufficient attention is drawn to the occurrence of touch. Schaefer et al. (2009), for instance, revealed systematic activations in both contralateral SI and ipsilateral SII during the observation of a paintbrush touching somebody else's hand while participants had to count the number of times the paintbrush stroked the seen hand vertically rather than horizontally (see also Schaefer et al., 2012). What is more, the pattern of activations in SI varied as a function of the viewing perspective: Viewing the hand being touched from an allocentric perspective resulted in stronger activity in SI/BA 2 while observing touch from an egocentric perspective preferentially triggered activity in SI/BA 3a and SI/BA 3b. Importantly, an egocentric perspective possibly facilitates incorporating the observed hand into one's own body schema which might explain why these primary-level somatosensory areas seemed to be recruited even though the viewed hand belonged to somebody else. In an earlier study, Schaefer, Heinze and Rotte (2005a) had demonstrated that observing touch on the thumb of a video hand while one's own hidden thumb is simultaneously touched lead to a (if small) shift of the cortical representation of the this digit along with an enhanced cortical activity in the corresponding SI area. Crucially, this SI modulation was only present when the observed and felt tactile stimulation occurred in synchrony rather than asynchrony with only the former evoking the feeling in the participants that the observed video hand was actually their own hand and the location of the felt tactile stimuli (Schaefer, Flor, Heinze, & Rotte, 2006). How easily an observed body part might be treated as part of one's own body might thus be another determining factor in whether or not passive touch observation results in SI activations or not.

Interestingly, recent neuropsychological studies that also (if indirectly) implement SI during passive touch observation do commonly depict somebody else's touched body part from an egocentric perspective while the tactile stimulation as such is delivered by an object (e.g. a brush or a stick) with no human agent being visible. Bufalari et al. (2007), for instance, analysed somatosensory-evoked potentials (SEPs) in response to electrical median nerve stimulation while participants observed a cotton bud touching a hand or a syringe penetrating it. Compared to a baseline condition (a static image of the isolated hand), the amplitude of the somatosensory P45 component was found to be significantly reduced by the observation of touch. This SEP component has been associated with late S1-processing, possibly originating from area 1 (Allison, McCarthy, & Wood, 1992). Note that the model's hand was presented from an egocentric perspective and that, in addition, participants were encouraged to concentrate on what the observed person might be feeling.

Wood, Gallese, and Cattaneo (2010), on the other hand, utilised the short-latency afferent inhibition effect (SAI) to highlight the possible role of SI during touch observation: SAI describes the phenomenon that somatosensory stimulation of the hand almost immediately decreases the excitability of the motor cortex which is reflected in a decrease in the amplitude of TMS-induced motor-evoked potentials (MEPs) in the stimulated hand (Tokimura et al., 2000). Wood et al. (2010) showed that the amount of SAI can be modulated by the concurrent observation of somebody else's hand being stroked on the index finger with a brush. Participants received TMS-stimulation to induce MEPs in one of the muscles of the hand contralateral to the stimulated hemisphere while they observed a brush that was either stroking the index finger of a right or left hand or was merely performing brushing movements on the surface next to the finger. An electrical stimulus to the respective hand shortly before the onset of the TMS impulse induced SAI which was found to be significantly increased when the presented congruent hand was observed to be touched as compared to be not touched by the brush. Wood et al. (2010) ascribed the demonstrated modulation effect of observing others' touch on SAI to an increased excitability in SI which, in turn, results in an increased inhibition of the motor cortex. It should, however, be noted that merely mapping the observed touch on the observer's own somatosensory system did not seem to be enough to directly induce SAI in the motor cortex since the amplitudes of TMS-induced MEPs in this study did not show any significant observation-related modulations whenever the TMS impulse was *not* preceded by an actual tactile stimulus. However, already present activity in primary somatosensory cortex triggered by an actual tactile stimulus was apparently modulated by the concurrent observation of others' touch in a way that also modulated the capacity of SI to inhibit the motor cortex. Yet again, the observed hand was shown from an egocentric point of view.

Pihko, Nangini, Jousmäki and Hari (2010) recorded somatosensory evoked fields (SEFs) using MEG while participants were first repeatedly touched on their right hand by the experimenter and then observed the experimenter touch her own hand. Directly experienced touch resulted in a strong activation of the contralateral, i.e. left SI 0-300 ms after touch onset along with a much weaker but still significant activation in ipsilateral SI. The latter continued in the subsequent 300-600 ms time window. Even though much less strong, merely observing touch also resulted in a significant activation of left SI. This activation was, however, delayed and occurred only 300-600 ms after the onset of the observed touch, thus reflecting the fact that processing and relaying the visual information from occipital areas to SI takes time.[2] It should, however, be noted that even though the authors concluded that observing somebody else *being touched* activates SI, it might actually have been the touch-related motor act of the experimenter that led to SI activation: Participants were initially touched on their right hand but later observed the experimenter touch her own *left* hand with her right index finger. According to Blakemore et al. (2005), cortical mirror-touch responses in SI are not only somatotopically organised but also lateralised which is why a right rather than a left SI activation could have been expected for the sight of touch on a left hand. The nevertheless revealed left SI activation might thus be due to an

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[2] At a first glance, a vicarious activation of SI with an delay of such an extent seems irreconcilable with earlier findings by Bufalari et al. (2007) that suggested a touch observation-related effect on somatosensory excitability as early as 45 ms after stimulus onset. Bufalari et al. (2007), however, investigated whether the sight of somebody else being touched *modulates ongoing* SI activity in response to median nerve simulation while Pihko et al. (2010) explored whether the sight of touch is capable of *inducing* measurable activity in SI in the absence of any concurrent tactile stimulation on the observer's own body. Touch observation-related modulations of existing somatosensory activity might be detectable much earlier than touch observation-related induction of somatosensory activity.

observed touch-related right-hand stimulus which suggests that it was actually the act of touching performed by the experimenter that was mirrored. Such an interpretation would be in line with the above discussed notion that SI (SI/BA 2 in particular) might have a tendency to preferentially resonate with the biological agent delivering touch rather than the passively touched target (Ebisch et al., 2008; Keysers et al., 2010). Regardless of whether the recorded SI activity in the observation condition was associated with the passive aspect of “being touched” or the active aspect of “touching”, Pihko et al. (2010) importantly demonstrate that observation-induced SI activity is not only less strong than the one during the actual experience of touch which might be important for an efficient self-other distinction; it is also less immediate, being measurable only 300 ms after observation onset the earliest (300-600 ms).

All in all, there is mounting evidence, especially from recent neurophysiological studies whose high temporal resolution allows the detection of very rapid modulations in somatosensory processing, that not only higher-order SII but also primary-level SI are active during the observation of (passive) touch. As far as the initial inconsistent neuroimaging evidence is concerned, SI activity might, on the one hand, simply be too subtle or to interindividually variable to be indentified reliably in fMRI group analyses, especially if touch is observed on body parts such as legs (Keysers et al., 2004) whose somatosensory representations are small as compared to hands (Ebisch et al., 2008; Schaefer et al., 2009) or faces (Blakemore et al., 2005) (note, though, that Keysers et al. (2004) did find a (non-significant) trend for SI activity). On the other hand, there are several factors which have been found to influence the mirror-touch responses in SI: The perspective from which the touch-related episode is viewed (egocentric vs. allocentric; Schaefer et al., 2009), determining how easily an viewed body part can be incorporated in the observer’s body schema, along with the type of task participants are asked to perform during observation (passive observation (Keysers et al., 2004) vs. touch-related tasks (Blakemore et al., 2005; Schaefer et al., 2012, 2009)) seems to modulate if and what areas within SI are triggered during touch observation. The presence of a human agent delivering touch also seems to facilitate the triggering of SI activity – in such scenarios, it might, however, no longer be the target’s passive touch sensation that is mirrored but the haptic experience of the touch agent, involving both the proprioceptive aspects of the observed movement and the tactile aspects of making contact with the target. In this context, it is important to note that the mere observation of others’ actions (irrespective of whether or not they contain a tactile component) has been found to trigger activity not only in SII but also in SI, due to the internal simulation of what it would proprioceptively feel like to perform the involved movements (e.g. Avenanti, Bolognini, Maravita, & Aglioti, 2007; Avikainen, Forss, & Hari, 2002; Gazzola & Keysers, 2009; Rossi et al., 2002). Whether it might be possible to effectively dissociate the touch observation-related vicarious somatosensory activity in the context of observing others' goal-directed actions (involving e.g. touching, grasping and manipulating objects or other people's body parts) from the movement observation-related vicarious somatosensory activity is an aspect which has so far barely been addressed, even though such a dissociation would provide insights into how fine-grained the embodied simulation of others' actions and bodily sensations might be. The ensuing chapter 1.2.2 will therefore take a closer look at "active touch" as an interface between action observation and touch observation to demonstrate that more research is needed on how we processes others' touch sensations when these are embedded in others' actions and thus inevitably involve the sight of movement.

1.2.1 Observing others' action-related tactile sensations

A substantial proportion of the instances in which we perceive touch on our skin does not result from an e.g. an object approach our body and passively touch it (passive touch) but from our own active interactions with objects and surfaces in our environment (active touch). When we, for example, impatiently thrum our fingers on the table, grasp a glass to take a sip of water or use a finger tip to push a key on a keyboard, our somatosensory system processes not only the proprioceptive feedback from the receptors in the muscles, joints and tendons involved in the actual movement, but also the afferent feedback from the cutaneous receptors in the skin that register which parts of our skin are in contact with the surface and what the haptic properties of the touched surface are (see Lederman & Klatzky, 2009, for a review on haptic perception). What has, however, barely been explicitly studied so far is if and how the somatosensory cortices might respond when we observe others' perform such actions and to what extent any vicariously triggered somatosensory activity might reflect specifically the presence of touch during those actions. Most research on action observation focuses primarily on how the motor aspects of the seen actions (be they object-directed or not) are mapped onto the observer's own motor system, after initial studies on monkeys revealed that certain neurons in area F5 of the ventral premotor cortex as well as in the inferior parietal lobule (IPL) of the macaque brain discharged not only when the monkeys performed a given goal-directed hand movement but also when they observed the experimenter perform a similar action (Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008). With this fronto-parietal "mirror neuron network" quickly being assumed to be crucial in mediating action recognition and action understanding (Fogassi et al., 2005; Keysers et al., 2003; Kohler et al., 2002; Rizzolatti, Ferrari, Rozzi, & Fogassi, 2006; Umiltà et al., 2001; see, however, Dinstein, Thomas, Behrmann, & Heeger, 2008, and Hickok, 2009, for a criticism), an overwhelming amount of research has ever since been dedicated to revealing similarly shared neural representations for executed and observed actions in the motor areas of the human cortex (albeit at the level of common brain regions rather than single neurons). The fronto-parietal network of motor areas active during both the execution and the observation of others' actions identified by neuroimaging studies (fMRI, PET) appears indeed similar to the mirror neuron network in monkeys, comprising the inferior frontal gyrus (IFG) – more specifically the ventral premotor cortex (BA6) and BA44/45 (Broca's area) – and the intraparietal cortex, including the inferior parietal lobule (IPL) (Chong et al., 2008a; Grafton et al., 1996; Kilner et al., 2009; Rizzolatti et al., 1996b; Shmuelof & Zohary, 2006).[3] In contrast to monkeys, the shared neural motor circuits for executed and merely observed actions in humans, however, possibly includes also the primary motor cortex (MI) (Hari et al., 1998; Holz, Doppelmayr, Klimesch, & Sauseng, 2008; see Raos, Evangeliou, & Savaki, 2004; Raos, Evangeliou, & Savaki, 2007 and Tkach, Reimer, & Hatsopoulos, 2007, for evidence on MI involvement during action observation also in monkeys) and the SMA (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011; Holz et al., 2008; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010).

Only relatively few studies, on the other hand, address the possible involvement of the somatosensory cortices in action simulation at all, despite the fact that somatosensory regions play an important role during the actual preparation and execution of movements. The existing empirical evidence does indeed clearly implicate also non-motor somatosensory areas (mainly SI/BA2 and to a lesser extent SII) in the automatic internal replication of an observed motor act (Arnstein et al., 2011; Avikainen et al., 2002; Gazzola & Keysers, 2009; Hari et al., 1998; Möttönen, Järveläinen, Sams, & Hari, 2005; Oouchida et al., 2004; Rossi et al., 2002; Voisin et al., 2011b), presumably due to the supplementary internal simulation of the proprioceptive features of the seen movement. In the light of recent findings that suggest that the somatosensory cortices respond to touch merely observed on others' bodies (Blakemore et al., 2005; Bufalari et al., 2007; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012, 2009; Wood et al., 2010); see chapter 1.2.1), it seems, however, important to note that, since studies on the somatosensory effects of observing others' actions do often involve the

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[3] It is, however, important to bear in mind that revealing shared voxels for executed and merely observed actions in an fMRI study is not equivalent to demonstrating that these voxels contain motor mirror neurons. The measured activity in a given voxel averages the activity of many different subpopulations of neurons and even if there were to be mirror neurons, their neural response would be inseparably intermingled with that of many other neurons with different response properties (see Dinstein et al., 2008). FMRI approaches that study the selectivity of fMRI adaption phenomena (also referred to as repetition suppression; Grill-Spector & Malach, 2001) in the context of executed as well as merely observed actions allow more clearly to dissociate (still at the level of neural populations rather than single neurons) whether a neural response in a certain brain area (or even within a voxel (Grill-Spector & Malach, 2001)) reflects the activity of a specific neuron population that does indeed respond to both observed and executed actions or the activity of distinct but overlapping populations of exclusively visual and motor neurons (see e.g. Chong et al., 2008a; see, however, Lingnau, Gesierich, & Caramazza, 2009).

sight of somebody else either grasp (e.g. Arnstein et al., 2011; Gazzola & Keysers, 2009) or manipulate an object (e.g. Avikainen et al., 2002; Hari et al., 1998), it cannot be ruled out that the observed somatosensory activity actually reflected, at least in parts, a somatosensory resonance response to the observed active touch component. Some studies contrasted the somatosensory activity during the observation of somebody else manipulating or grasping an object directly with the effect of the actual execution of the observed object-directed movements but did not include a condition in which somatosensory activity was probed when participants observed similar movements in the absence of an object (Avikainen et al., 2002; Gazzola & Keysers, 2009; Hari et al., 1998), rendering it unclear whether the recorded modulations in somatosensory activity were exclusively due to the sight of movements or whether the sight of touch might also have contributed. The lack of a comparison condition in which similar but touch-free movements were observed did not allow to distinguish whether the action observation-related activation of a subarea of SI (BA 2) by the sight of a human agent intentionally touch a target rather than the sight of an wind-driven palm tree accidentally do the same found by Ebisch et al. (2008) was indeed only related to the simulation of the proprioceptive properties of human movements, as suggested by the authors, or whether the occurrence of touch might also have played a role. Two recent fMRI studies did show that SI/BA 2 responded more strongly to the observation of a hand grasp or manipulate an object rather than merely move next to it (Arnstein et al., 2011) or point at the object (Pierno et al., 2009), possibly implicating SI in the internal simulation of the others' active touch sensations, but the kinematic differences between the object-directed and the non-object-directed movements in these studies might have confounded this contrast. Turella, Tubaldi, Erb, Grodd, and Castiello (2012), on the other hand, compared activity in SI/BA 2 when participants observed somebody else either grasp a (partly hidden) object or mimic exactly the same grasping movement when participants had to assume that the object was not present. With the movement kinematics of the observed hand actions being controlled in this way (such as which muscles and joints were involved), the revealed preferential response of SI/BA 2 to the sight of an actual interaction of the hand with the object thus strongly indicated that somatosensory activity in SI during action observation was specifically related to the simulation of the tactile properties of the observed grasping action, i.e. of what it tactually feels like to make contact with the object with the fingers and the palms. Importantly, BA 2 is an area in SI that plays a vital role in processing and integrating tactile as well as proprioceptive information during haptic exploration before passing this information on to SII (cf. Keysers et al., 2010), rendering BA 2 a likely candidate for simulating also others' haptic experiences.

All in all, the current evidence that it might be possible to dissociate touch observation-related somatosensory activity from movement-related somatosensory activity in SI (Turella et al., 2012) is, however, somewhat scarce. As for SII which has reliably been found to be involved in resonating with others' passive touch sensations (Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Schaefer et al., 2012, 2009), it is, on the other hand, still entirely unclear to what extent vicarious activity in this higher-order somatosensory area during action observation (Avikainen et al., 2002; Gazzola & Keysers, 2009) might not also entail a somatosensory resonance response to tactile sensations embedded in others' actions that is, importantly, distinct from any movement observation-related vicarious somatosensory activity. Shedding more light on the involvement of SI in the simulation of others' action-related touch sensations and clarifying whether also SII might contribute to the internal representation of others' active touch sensations will thus be one of the research aims in this thesis (see chapter 1.4).

Functionally, the proposed shared neural networks for actually felt and merely observed touch (be it passive or active) might allow the observer to obtain an implicit and intuitive understanding of others' tactile sensations, through an automatic link to the observer's own experiences of being touched and touching, respectively (Keysers et al., 2004). Importantly, individuals have, however, been found to show a certain interindividual variability in how strongly they recruit their own somatosensory system to resonate with the tactile sensations they observe in others (Schaefer et al., 2012). Most notably, individual differences in empathy-related personality dispositions seem to be associated with variations in the strength of not only vicarious somatosensory activity during touch observation in particular, but also of vicarious brain activity during the observation of others' actions and somatic sensations in general, corroborating the notion that mirror-matching mechanisms might constitute a sensorimotor basis of empathy (Gallese, 2003;2007; Gallese, Keysers, & Rizzolatti, 2004; Keysers & Gazzola, 2006). The subsequent chapter 1.3 will thus provide a definition of empathy, clarify what aspects of empathy in particular mirror-matching mechanisms might underpin and briefly review empirical findings that link (albeit indirectly) the recruitment of shared neural representation for self and other with interindividual differences in trait empathy.

1.3 Vicarious (somatosensory) brain activity and its possible role in empathy

Empathy is a complex, multidimensional psychological construct that describes the human ability to "tune into how someone else is feeling, *or* what they might be thinking." (Baron-Cohen & Wheelwright, 2004, p. 163, highlighting added). This brief definition already highlights that empathy is considered to comprise both cognitive as well as affective components which might at the same time engage different neural networks. The cognitive side of empathy refers to high-level cognitive processes such as deliberately taking somebody else's perspective and inferring their mental states such as beliefs, desires and intentions (cf. Gallagher & Frith, 2003). Often termed “theory of mind (ToM)”, “mentalising” or “mind-reading”, these complex reasoning processes are commonly associated with activity in e.g. the medial prefrontal cortex (mPFC), the temporo-parietal junction (TPJ), the (posterior) STS and the temporal poles (Carrington & Bailey, 2009; Frith & Frith, 2003; Gallagher & Frith, 2003; Van Overwalle, 2009), that is with activity in brain regions that are quite different from the sensorimotor ones mentioned so far in the context of shared neural representations for self and other. The affective side of empathy[4], on the other hand, reflects the intuitive and immediate sharing of what others are feeling, be it an emotion or, as more recently suggested (Keysers & Gazzola, 2009), a bodily sensation such as pain or touch. Importantly, automatically triggered and stimulus-driven mirror-matching mechanisms are thought to be the neural basis of this immediate and experiential insight into what another individual feels: The embodied simulation of others’ emotions (Bastiaansen, Thioux, & Keysers, 2009; Jabbi & Keysers, 2008; Jabbi, Swart, & Keysers, 2007; Wicker et al., 2003) and somatic sensations (e.g. Bufalari et al., 2007; Ebisch et al., 2008; Jackson et al., 2005; Keysers et al., 2004; Singer et al., 2004) in the very same brain areas that would also be active if the observer were to directly experience a given emotion or bodily sensation translates the observed emotional and bodily states effortlessly and immediately into the corresponding states in the observer (Gallese, 2003; 2007; Gallese et al., 2004; Keysers & Gazzola, 2006). It is those more basic, low-level mirror mechanisms that rely on shared neural representations for self and other in the aforedescribed frontoparietal network of motor areas as well as somatosensory (see chapters 1.2.1 and 1.2.2) and (para)limbic structures such as the anterior insula (AI) and the anterior cingulate cortex (ACC) (e.g. Jackson et al., 2005; Morrison et al., 2004; Wicker et al., 2003). Perceiving, for instance, others’ emotional facial expressions (i.e. an observable motor act) has been associated with activity in motor-related areas such as the IFG and the ventral premotor cortex (vPMC) (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Gorno-Tempini et al., 2001; Hennenlotter et al., 2005; Leslie, Johnson-Frey, & Grafton, 2004; Van der Gaag, Minderaa, & Keysers, 2007) as well as in the somatosensory cortices (Hennenlotter et al., 2005; Winston, O’Doherty, & Dolan, 2003), suggesting an involuntary simulation of the motor component of the observed facial expression and of what it would proprioceptively feel like to produce the underlying muscle contractions. That viewing emotionally expressive faces reliably and very quickly (if to a lesser extent) induces the displayed affective state in the onlooker (Hess & Blairy, 2001; Wild, Erb, & Bartels,

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[4] Importantly, the aforementioned ToM processes do not only involve the attribution of mental states to others, but also include reflecting on others’ emotional states. It is important to differentiate between such deliberate cognitive inferences about others’ emotions (“affective ToM”) and the involuntary experiential sharing of others’ emotional states, termed “emotional empathy” or “emotional contagion” (cf. Shamay-Tsoory, 2011).

2001) – a phenomenon called "(primitive) emotional contagion" (Hatfield, Cacioppo, & Rapson, 1993) – is thought to be mediated by these automatically triggered simulation processes, possibly with the insula as a crucial relay station interfacing between simulation-involved sensorimotor areas and limbic regions (Carr et al., 2003; Jabbi & Keysers, 2008). While the relative contributions of covert motor (Carr et al., 2003; Jabbi & Keysers, 2008) and somatosensory simulations (Goldman & Sripada, 2005) in emotional contagion as well as recognising and understanding others' emotions are still quite unclear as is how exactly these sensorimotor mirroring mechanisms might bring about the corresponding affective state in the observer, lesion studies indicate that both the motor and the somatosensory component might in any case be crucial: Lesions in IFG, for instance, are associated with general deficits in emotional empathy (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009) while lesion in the (right) somatosensory cortex seem to be specifically linked to impairments in recognising emotions from facial expressions (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000) as well as from full-body movements (Heberlein, Adolphs, Tranel, & Damasio, 2004), highlighting the importance of being able to create sensorimotor representations of what we observe in others for how we understand others and empathise with them.

Correlations between the strength of activations in shared neural networks during the observation of others' actions, emotions and somatic sensations and individual levels of self-reported trait empathy further corroborate the notion that mirror-matching mechanisms might be fundamentally linked with empathy. Mirror activity in shared neural networks for e.g. felt and observed pain as well as for executed and heard actions has been shown to be stronger in participants scoring higher on standard empathy scales (Gazzola, Aziz-Zadeh, & Keysers, 2006; Lamm, Batson, & Decety, 2007; Saarela et al., 2007; Singer et al., 2004). Similarly, the suppression of TMS-induced MEP-amplitudes (Avenanti, Minio-Paluello, Bufalari, & Aglioti, 2009) as well as the suppression of SI-related oscillatory activity during the observation of others' pain (Cheng et al., 2008) has been found to be more pronounced in participants with high trait empathy. Dispositionally empathic individuals also seem to exhibit a stronger tendency to mimic others' postures, mannerisms and facial expressions (Chartrand & Bargh, 1999; Sonnby–Borgström, 2002), involuntary resonance behaviours which have been associated with the activation of sensorimotor mirroring areas. With respect to shared neural representations for felt and merely observed touch in particular, it has recently been found that highly empathic individuals tend to show stronger SI activations during the observation of somebody else's body being passively touched (Schaefer et al., 2012). Mirror touch synaesthetes who actually feel the passive touch they observe on somebody else's body on their own body (Banissy et al., 2009), presumably due to an overactivity in their tactile mirror system (Blakemore et al., 2005), also score significantly higher on an (emotional) empathy scale than non-synaesthetic controls (Banissy & Ward, 2007), suggesting a positive link between the amount of mirror activity particularly in somatosensory brain areas and the tendency to respond emotionally to others. In this context, it is, however, important to note that the standard empathy questionnaires used in the aforementioned studies usually comprise different empathy-related subscales that tap into either the cognitive or the affective dimension of empathy and that the revealed links between differences in the extent with which shared neural representations are recruited in a given situation and interindividual variations in trait empathy involve often exclusively the cognitive but not the affective component of empathy: The strength of vicarious activity in somatosensory areas during the passive observation of others' touch or pain sensations or in response to the sight of others' movements, for instance, seems to be primarily associated with interindividual differences in individuals' (self-reported) capability to cognitively adopt other people's perspective (Avenanti et al., 2009; Cheng et al., 2008; Gazzola et al., 2006; Schaefer et al., 2012) rather than their tendency to respond emotionally to what they observe in others. Also in more complex social scenes in which participants had to decode changes in others' mental and emotional states, activity in somatosensory areas correlated positively with individuals' cognitive empathic skills (Hooker, Verosky, Germine, Knight, & D'Esposito, 2010), suggesting that individuals who are adept in mentally projecting themselves into other people's shoes are also more likely to use their own somatosensory system to simulate and understand others' emotional states. In the light of the aforementioned dissociation between the neutral networks that support mentalising processes such as perspective-taking and thus cognitive empathy and those with shared neural representations for self and other which are thought to underpin the automatic sharing of what others are feeling (be it an emotion or a bodily state) and thus affective empathy, one might have expected vicarious brain activity to be primarily linked to individuals' *emotional* empathic traits instead (cf. Hooker et al., 2010). While such a seemingly discrepant pattern of correlations (see, however, e.g. Schulte-Rüther, Markowitsch, Fink, & Piefke, 2007, for a correlation of IFG activity with an emotional empathy scale during a task that involved the perception of emotional faces) might indicate that the spontaneous recruitment of motor as well as somatosensory brain areas during the observation of others' actions and somatic sensations simultaneously contributes to affective as well as cognitive components of empathy (most real life situation are likely to involve both dimensions anyway), it should also be noted that at least some of the studies that revealed variations in the strength of mirror activity in sensorimotor areas as a function of interindividual differences in *cognitive* empathy skills are fMRI studies (e.g. Gazzola et al., 2006; Hooker et al., 2010; Schaefer et al., 2012). Due to the low temporal resolution of this neuroimaging technique, it can thus not be ruled out that the strength of rapid and/or short-lived modulation in e.g. vicarious somatosensory processing during the sight of somebody else's touch sensations might be found to be linked to individual differences in *emotional* empathy after all as long as they are assessed with a sufficiently temporally resolved neuroscientific method. The use of EEG in a majority of the experiments in the present thesis provided the opportunity to test precisely this possibility (see below).

1.4 Research aims and overview of the experiments in this thesis

The empirical evidence that has been outlined in this chapter shows that observing others being passively touched on their body is not a purely visual process but involves (in parts) the very same somatosensory brain areas, namely SII and most likely also SI (Blakemore et al., 2005; Bufalari et al., 2007; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012; 2009; Wood et al., 2010), that are also involved in processing our own experience of being touched. In addition, empirical findings indicate that also observing others' action-embedded touch sensations (such as when we observe somebody else actively reach out and touch an object) might be associated with a distinct somatosensory resonance response that is dissociable from vicarious somatosensory activity due to the sight of movements (Arnstein et al., 2011; Pierno et al., 2009; Turella et al., 2012). The aim of the present thesis was to shed more light on certain aspects of such an involuntary sharing of others' tactile sensations and to complement and extend existing fMRI-based evidence on the embodied simulation of observed touch by means of EEG, a neuroscientific technique that allows to study (electrical) brain activity with a temporal resolution much higher than that of fMRI approaches. To this purpose, mechanical tactile stimuli were presented to participants' hands to activate the somatosensory cortices and to evoke and record somatosensory event-related potentials (ERPs) associated with the processing of these stimuli while participants observed either a cotton bud touch a model's hand rather than the empty space next to it (passive touch; chapter 2) or a model's hand actively perform finger movements that did or did not involve a tactile component from making contact with a surface (active touch; chapter 3). Therefore, rather than showing that the mere observation of others' touch sensations directly triggers activations in the somatosensory cortices that overlap (in parts) with the activations during the actual experience of touch (e.g. Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012; 2009), shared somatosensory representations for observed and felt touch were to be investigated more indirectly by testing whether *ongoing* somatosensory processing of tactile stimuli is altered by the concurrent sight of touch (see also Bufalari et al., 2007). Touch observation-related modulations in the electrical brain activity associated with processing tactile stimuli strongly suggest that merely observing and actually feeling touch recruit indeed the same neural structures. Importantly, mechanical tactile stimulation evokes a characteristic sequence of positive and negative ERP components within the first 200 ms after tactile stimulus onset (P50-N80-P100-N140; see chapter 1.5 for a brief introduction of these components) which are commonly associated with somatosensory processing in SI or SII (Allison et al., 1992; Hämäläinen, Kekoni, Sams, Reinikainen, & Näätänen, 1990; Tarkka, Micheloyannis, & Stokić, 1996; Valeriani, Pera, & Tonali, 2001b). Systematically analysing touch observation-related ERP amplitude differences for short time epochs that overlap with the latencies of these different components thus allowed to pinpoint if and to what extent the sight of touch modulates either early (SI), late (SII) or both stages of somatosensory processing.

In the light of the notion that vicarious brain activity in general constitutes the neural basis of empathy (Gallese, 2003; 2007; Gallese et al., 2004; Keysers & Gazzola, 2006) and fMRI-based empirical evidence that variations in the strength of vicarious somatosensory brain activity in particular during not only the sight of others' touch sensations (Schaefer et al., 2012) but also their actions and pain sensations (Cheng et al., 2008; Gazzola et al., 2006) are associated with interindividual differences in certain aspects of dispositional empathy, the present thesis also aimed to investigate the role of such individual differences in the context of highly temporally resolved electrophysiological correlates of resonating with others' tactile experiences. Finally, the present thesis also intended to provide behavioural evidence for shared neural representations for felt and merely observed (active) touch, investigating how observing others' haptic sensations might influence tactile perception, an aspect that has so far barely been addressed.

Importantly, the empirical work of this thesis will subsequently be presented in three separate chapters: Chapter 2 focuses on a series of four ERP studies in which SEPs in response to tactile stimuli presented to participants' hand(s) were used to analyse whether the sight of somebody else being passively touched modulated the electrical brain activity associated with processing these tactile stimuli. Due to the high temporal resolution of ERP measures, this approach allowed to pinpoint exactly which stages of somatosensory processing (early-stage SI activity or later-stage somatosensory activity in e.g. SII) were altered by the touch-related visual information. This was of particular importance given that fMRI-based evidence on whether only SII (Ebisch et al., 2008; Keysers et al., 2004) or also SI (Blakemore et al., 2005; Schaefer et al., 2012; 2009) are involved in the internal simulation of others' passive touch sensations is still somewhat inconsistent. Since it is, however, conceivable that touch observation-related vicarious activity in SI might simply be too subtle to be detected reliably by fMRI, electrophysiological data on the effects of the sight of touch especially on early stages of *ongoing* somatosensory processing might thus prove very valuable (see also Bufalari et al., 2007) in clarifying the possible role of SI during touch observation. Similarly, also slight variations in vicarious SII activity as a function of e.g. the animacy of the touch target or the viewing perspective, two factors for which fMRI currently suggests an insensitivity of touch observation-related SII activity (Ebisch et al., 2008; Keysers et al., 2004; Schaefer et al., 2008;

see, however, Blakemore et al., 2005), might be too subtle or short-lived to be picked up by fMRI. For this reason, the first two studies in chapter 2 re-investigated both the role of the animacy of the touch target (Exp. 2.1) and the viewing perspective (Exp. 2.2) in the context of somatosensory-related ERPs, focussing on whether or not early-latency ERPs (associated with SI activity) would be affected by touch-related visual information at all and whether any touch observation-related modulations of mid- and long-latency ERPs (associated with SII activity) might after all appear to be influenced by the type of touch target and the viewing perspective. In the light of previous findings that indicate that vicarious brain responses during the observation of others' actions as well as their pain and touch sensations can be quite somatotopically organised (Blakemore et al., 2005; Buccino et al., 2001; Voisin, Marcoux, Canizales, Mercier, & Jackson, 2011a), two additional ERP studies aimed to explore how clearly vicarious somatosensory activity might represent which skin area within a given body part (Exp. 2.3) or at least which body part (Exp. 2.4) was observed to be touched.

Chapter 3, on the other hand, presents a series of six ERP studies (Exp. 3.1 – 3.6) in which it was attempted to clarify whether the sight of others' *active* touch sensations modulates ongoing somatosensory in the observer which would suggest that the observation of others' haptic sensations elicits a distinct somatosensory resonance response. With the scarce previous (fMRI-based) evidence on vicarious somatosensory activity triggered specifically by the tactile component of others' actions pointing primarily to a role of SI(/BA2) in the internal simulation of others' action-embedded touch sensations (Arnstein et al., 2011; Pierno et al., 2009; Turella et al., 2012), it was of particular interest whether a temporally more sensitive EEG approach might not also reveal an involvement of higher-order somatosensory areas such as SII. In addition, almost all studies in chapter 3 (Exp. 3.2-3.6) also investigated to what extent touch observation-related modulations in somatosensory processing might be finger-specific, given the close interconnectivity between motor and somatosensory areas (cf. Gazzola & Keysers, 2009) and the fact that at least the motor component of the observed touch actions was likely to be mapped onto the observer's own motor system in a highly effector-specific way (Avenanti et al., 2007; Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006).

For almost all studies in chapter 2 and 3, the strength of any touch observation-related ERP modulations for which the main analysis indicated statistical significance was correlated with self-report measures of both affective and cognitive trait empathy (see chapter 1.5 for a brief introduction of the two used empathy questionnaires) to test whether variations in how strongly individuals' somatosensory system was involved in processing others' touch sensations was associated with interindividual differences in dispositional empathy. Again, the high temporal resolution of the electrophysiological data might allow to detect links which fMRI-based approaches might not have been able to detect, especially with respect to the question as to whether vicarious somatosensory activity is indeed primarily associated with cognitive rather than affective dimensions of empathy (see Cheng et al., 2008; Gazzola et al., 2006; Hooker et al., 2010; Schaefer et al., 2012).

Finally, chapter 4 reports a series of experiments which aimed to investigate possible behavioural effects of observing others' haptic (Exp. 4.1.1-4.1.5) but also passive touch sensations (Exp. 4.2.1) based on a range of different tactile tasks since behavioural consequences of resonating with others' tactile experiences for the perception of concurrent tactile stimuli on the observer's own body have so far barely been investigated (see, however, Serino, Pizzoferrato, & Làdavas, 2008b).

Prior to reporting the experimental results of this thesis in the subsequent chapters 2, 3 and 4, the final section 1.5 of the present chapter contains a brief introduction to SEPs as well as to the used standard measures of dispositional empathy to clarify the general methodological approach in chapter 2 and 3 in particular.

1.5 Brief introduction to SEPs and the trait empathy measures used in the experiments of this thesis

In the ERP studies subsequently reported in chapters 2 and 3 of this thesis, SEPs[5] in response to tactile stimuli presented to participants' hands (see Exp. 2.4 for an exception) were used to investigate whether the sight of touch modulates the electrical brain activity associated with processing these stimuli. Importantly, mechanical tactile stimulation elicits a characteristic sequence of positive and negative voltage deflections in the scalp-recorded EEG signal within the first 200 ms after stimulus onset which are presumed to be linked to different processing stages in the somatosensory cortex. More precisely, the earliest reliable deflection evoked by mechanical stimuli is usually a positive peak at around 50 ms post-stimulus (P50) at centro-posterior electrode sites over the hemisphere contralateral to the stimulated hand which tends to reverse its polarity to negative at more anterior recording sites. Ipsilaterally, the deflection at this latency is usually negative with an anterior amplitude maximum (Hämäläinen et al., 1990). The P50 is followed by a negative peak at 70-80 ms (N80) that tends to be largest at central and posterior electrode sites over the contralateral hemisphere (Hämäläinen et al., 1990), followed

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[5] The ERP measures obtained in the EEG experiments of this thesis were time-locked to the onset of the tactile stimulation and are thus continuously referred to as "somatosensory ERPs" or "SEPs". Due to the fact that the tactile stimuli were always presented simultaneously with continuous task-irrelevant visual stimuli, it can, however, not be ruled out entirely that that the recorded ERP waveforms included, to some extent, also visual ERP responses as well as multisensory superadditive and subadditive effects.

by a bilateral positive peak at approximately 100 ms post-stimulus (P100), again with a contralateral-posterior amplitude maximum (Hämäläinen et al., 1990). Finally, mechanical tactile stimulation commonly elicits a contralateral-posteriorly quite pronounced negative deflection at a latency of around 140 ms (N140) with often a relatively broad peak (Hämäläinen et al., 1990). Importantly, the described somatosensory P50 and N80 components are thought to arise from SI (Allison et al., 1992; Hämäläinen et al., 1990) where primary stages of somatosensory processing take place, such as encoding basic sensory properties such as the type, intensity and location of tactile stimuli. The P100 and N140 components[6], on the other hand, are presumed to be generated in SII (Tarkka et al., 1996; Hämäläinen et al., 1990; Valeriani et al., 2001a), a secondary somatosensitive cortical region which is concerned with higher-order functions such as the integration of sensory input from both sides of the body as well as of tactile and proprioceptive information in the context of sensorimotor integration (Keysers et al., 2010). By identifying which of the aforedescribed SEP components are sensitive to the sight of touch, it is thus possible to determine whether touch-related visual information affects exclusively higher-order (SII) or also primary (SI) levels of somatosensory processing.

As described in chapter 1.4, in addition to investigating which stages of somatosensory processing might be modulated by the concurrent sight of touch, the EEG experiments in chapter 2 and 3 of this thesis also aimed to explore possible links between the strength of touch observation-related SEP modulations and individual differences in trait empathy. To this end, participants were asked to complete two standard self-report empathy questionnaires at the end of each testing session, namely the *Empathy Quotient (EQ)* by Baron-Cohen and Wheelwright (2004) as well as the *Interpersonal Reactivity Index (IRI)* by Davis (1983). The EQ consists of 40 empathy-related items and 20 unrelated distractor items. For each item, participants are required to indicate on a four-point rating scale how well the statement describes them. In addition to the computation of a total EQ score based on the sum of the test scores for the 40 critical empathy items, supplementary scores for three separate but interrelated subscales, namely the *cognitive empathy* (11-item subscale), *emotional reactivity* (11-item subscale) and *social skills* (6-item subscale) subscale, can be calculated (Lawrence, Shaw, Baker, Baron-Cohen, and David 2004). The former subscale assesses individuals' tendency to appreciate and comprehend mental states in others whereas the latter two measure the tendency to respond emotionally to others' states and the capability, respectively, to spontaneously use social skills

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[6] The classification of the described SEP components as "early" or "late" varies in the literature, mostly depending on what overall latency range is investigated in a given SEP study. In accordance with Schubert et al. (2008), the SI-generated somatosensory P50 and N80 components will be labelled "early-" or "short-latency" in this thesis. The SII-associated P100 component will be termed "mid-latency while the subsequent N140 component will be referred to as a "long"-or "late-latency" component.

and to intuitively understand social situations (Lawrence et al., 2004). The IRI (Davis, 1983), on the other hand, comprises four 7-item scales (*perspective-taking*, *fantasy*, *empathic concern* and *personal distress* scale) for whose items participants indicate on a five-point rating scale how well an item describes them. The first two subscales tap cognitive dimensions of empathy and assess the tendency to spontaneously adopt others' perspective and to readily identify oneself with fictional characters in e.g. books or movies, respectively (Davis, 1983). The remaining two subscales, on the other hand, tap emotional aspects of empathy and measure the tendency to respond with feelings of compassion and concern or, respectively, with feelings of anxiety and discomfort to witnessing others' negative experiences (Davis, 1983). Since these subscales have been found to be mostly uncorrelated with each other (Davis, 1983), it is not recommended to calculate a total test score as the sum of the subscale scores for the IRI.

Both the EQ and the subscales of the IRI have a reasonably good test-retest reliability (EQ: $r = .835$; Lawrence et al., 2004; IRI: $r \geq .061 \leq .81$, depending on subscale and gender; Davis, 1983) and have previously been used successfully to investigate possible links between the strength of vicarious brain activity and interindividual differences in empathic dispositions (e.g. Cheng et al., 2008; Costantini et al., 2008; Gazzola et al., 2006; Hooker et al., 2010; Lamm et al., 2007; Perry, Troje, & Bentin, 2012; Saarela et al., 2007; Schaefer et al., 2012; Singer et al., 2004). Importantly, only some EQ measurements (such as the total EQ score and the *emotional reactivity* subscale score) have been found to correlate positively with certain IRI subscales (such as *empathic concern* and *perspective-taking*; Lawrence et al., 2004). Therefore, it appears that the EQ and the IRI assess, at least in parts, slightly different aspects of dispositional empathic behaviour. For this reason, both questionnaires were usually administered in the EEG studies of chapter 2 and 3 of this thesis.

Chapter 2

ERP investigations on the effects of observing others' passive touch sensations on somatosensory processing in the observer

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Recent neuroimaging evidence suggests that observing somebody else's body being touched is not a purely visual process but activates also the onlooker's somatosensory system, just as if their own body was being touched (Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Schaefer et al., 2012; 2009). Corroborating the notion of shared neural representations for merely observed and actually felt touch further, the sight of others' touch has been found to alter, both at a behavioural and a neural level, ongoing somatosensory processing in the observer (Bufalari et al., 2007; Serino et al., 2008b; Wood et al., 2010).

The present chapter will report a series of four studies which investigated such interfering effects of the sight of touch on concurrent somatosensory processing by means of EEG to further characterise the properties of visuotactile mirror-matching mechanisms: Exp. 2.1 addressed the question to what extent shared neural representations for observed and felt touch might also be triggered by the sight of touch on inanimate objects while Exp. 2.2 studied the possible effects of changes in the viewing perspective from which the touch on somebody else's body is observed. Exp.s 2.3, on the other hand, looked into the degree to which vicarious somatosensory activity represents the precise location within a given observed-to-be touched body part while the final Exp. 2.4. tested the body part specificity of mirror touch responses. In addition, all four studies explored possible links between interindividual differences in dispositional empathy and the strength with which the observer's own somatosensory system is recruited during the observation of others' touch sensations.

Experiment 2.1

Modulations in somatosensory processing as a function of observing touch on a body part or an inanimate object

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2.1.1 Introduction

Observing somebody else being touched on their body activates the observer's somatosensory system just as if they were touched on their own body (Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Schaefer et al., 2012; Schaefer et al., 2009). This mirror-like activation of somatosensory cortical areas matches the witnessed tactile sensation with representations of the observer's own touch experiences, allowing an immediate intuitive understanding of what the other person is feeling on their body ("visuotactile empathy"; Wood et al., 2010). It is, however, unclear whether the tactile mirror system is indeed exclusively tuned to the sight of touch on other human bodies or whether it might not actually respond quite unspecifically to *any* kind of observed touch, even between inanimate objects. Touch observation-induced *SII* activations have previously, in fact, been found to occur rather unspecifically to any form of seen touch, be it touch on a human body part or an inanimate object such as paper rolls (Keysers et al., 2004) or a chair (Ebisch et al., 2008). Blakemore et al. (2005), on the other hand, demonstrated somatosensory activations in both SII and SI (among others areas) that were significantly stronger when a human face or neck was observed to be touched as compared to when the seen touch occurred on the equivalent regions of an object (e.g. a fan), indicating that the tactile mirror system might after all have a preference for biological targets of touch. The sight of touch on the sensitive face and neck area as particularly salient and socially-relevant body stimuli might, however, have triggered particularly strong vicarious somatosensory activations as compared to those in response to the sight of touch on other, less prominent body parts or even inanimate objects which could explain the contradictory findings between Blakemore et al. (2005)'s study and the aforementioned two fMRI experiments by Keysers et al. (2004) and Ebisch et al. (2008). Specifically with respect to mirror touch responses in SI, it should also be noted that Keysers et al. (2004), in a ROI-interest approach, did not further analyse touch observation-related SI activity as to whether or not it might differentiate between animate and non-animate touch targets after SI activity was initially found only as a non-significant trend. Ebisch et al. (2008), on the other hand, found that activity in SI/BA2 during touch observation was primarily sensitive to whether or not the "touching agent" was biological but not to whether or not the target of the touch was biological. The revealed vicarious SI activity seemed to be related to the observed *act of touching* performed by a human agent rather than to the sight of *touch* as such, leaving the question open as to whether

SI would be involved at all when the observed passive touch occurs between inanimate objects in the absence of a human agent.

The current fMRI-based evidence is thus somewhat unclear as to whether also the observation of touch on inanimate objects recruits the somatosensory cortex in a similar way as the observation of touch on somebody else’s body does, especially with respect to touch observation-related vicarious activations in SI. FMRI allows to identify which neural structures are activated during the observation of touch and where overlapping activations for felt and observed touch occur. The temporal resolution of this method is, however, low which means that very rapidly occurring and/or short-lived modulations in brain activity in response to the sight of touch might not be detected. For the same reason, fMRI measures do also not allow to distinguish whether e.g. seemingly body-specific SI activations (Blakemore et al., 2005) reflect an early modulatory effect that takes place during initial SI signal processing or whether it might actually occur somewhat later during SI processing as a result of feedback projections from e.g. SII or other higher-order cortical regions (cf. Schubert et al., 2008). The aim of the present study was therefore to take advantage of the high temporal resolution of the EEG technique to investigate whether the early stages of somatosensory processing (up to 200ms post-stimulus) associated with activity in SI and SII are modulated by the sight of touch and whether this modulation varies as a function of whether the observed touch is applied to somebody else’s body part or an inanimate object. Somatosensory-evoked potentials (SEPs) in response to non-painful tactile stimuli presented to participants’ left index finger were recorded while participants observed a cotton bud touch or merely approach either somebody else’s hand or a wooden box. The inclusion of a “no touch”-condition did not only allow to control for unspecific effects of the presence of visual stimuli, including the sight of a body part and the movement of the cotton bud in proximity to that body part, but, more importantly, to also consider the effects of observing touch (rather than no touch) for both body and non-body touch targets independently: The previous conclusion by Blakemore et al. (2005) that the sight of touch on a body activates both SI and SII more strongly than the sight of touch on an object was based on a direct contrast between both observational conditions, which does, however, not necessarily mean that observing an object being touched as such does not elicit any somatosensory activity in the somatosensory cortices at all; the induced activity might just be weaker yet still significant. The design of the observational conditions in the present study allowed to address this possibility.

In addition, the present study aimed to investigate possible links between the extent of touch observation-related modulations in somatosensory processing and empathic dispositions. Mirror activity in shared neural networks for e.g. felt and observed somatic sensations (touch/pain) as well as for executed and heard actions has previously been shown to be stronger in participants scoring higher on standard empathy scales (Avenanti et al., 2009; Cheng et al., 2008; Gazzola et al., 2006; Saarela et al., 2007; Schaefer et al., 2012; Singer et al., 2004). Furthermore, mirror touch synaesthetes who actually feel the passive touch they observe on somebody else's body on their own body show a strong over-activity in their tactile mirror system (Blakemore et al., 2005) and also score significantly higher on the "emotional reactivity"-subscale of a general empathy questionnaire than non-synaesthetic controls (Banissy & Ward, 2007), suggesting a positive link between the amount of mirror activity in relevant brain areas and empathic skills in the tactile domain. In the present study thus aimed to investigate whether the tendency to map others' tactile sensations onto one's own somatosensory system might covary with empathic skills also within a sample of non-synaesthetic individuals. For this purpose, participants were asked to complete two standard trait empathy questionnaires at the end of the experiment.

2.1.2 Methods

Participants. 20 neurologically healthy volunteers (10 females, 10 males) aged between 16 and 37 years (mean age: 25.75 years; SD = 6.06 years) took part in the experiment. The 16-year old participant was a work-experience student visiting City University's psychology department who took part with special permission and parental consent. All participants were naive as to the purpose of the experiment and gave informed consent to participate after a detailed explanation of the involved procedures. All participants were right-handed and all had normal or corrected-to-normal vision by self-report. Participants were paid £ 7/h for their participation in the study. The procedures were approved by the local ethics committee.

Stimuli. The task-irrelevant visual stimuli consisted of a set of colour images showing either a left hand in palmar view and as seen from a first-person perspective or a wooden box, superimposed on a blue background (see Fig. 2.1.a). Using a rubber hand as an inanimate touch target would have had the advantage of more closely matching a human hand with respect to size, shape and colour. However, it has repeatedly been found that rubber hands are quite readily incorporated in the onlooker's body schema, especially when presented from an egocentric perspective and repeatedly being seen to be touched in synchrony with the observer's real hand (so-called rubber hand illusion; Botvinick, & Cohen, 1998), which, after all, would be the case in 50 % of the trials in this experiment. For this reason, an inanimate object (a wooden box) was chosen that was clearly not reminiscent of a body part.

A cotton bud was presented in three different positions (see Fig. 2.1.a): In a neutral starting position (neutral), in a position closer to the finger or the top right corner of the box, respectively, (approach) and in an end position in which the cotton bud either touched the hand on the index finger/the object on its top right corner (touch) or merely the empty space next to it (no touch). By presenting a rapid sequence of these images in chronological order (see Fig. 2.1.a for presentation times), the impression was created that the cotton bud approached the hand/object, briefly either touched the index finger/object or the empty space next to it, then retracted and resumed its neutral starting position. When producing the images, the box was aligned with the hand such that the actual touch (or no touch) in both conditions occurred in the same spatial location.

The images deliberately did not depict a human agent holding and moving the cotton bud since the mere observation of somebody else's actions in itself might already modulate activity not only in motor, but also in somatosensory brain areas (Avenanti et al., 2007; Avikainen et al., 2002; Rossi et al., 2002). For the same reason, the images also did not depict a human agent touching the model hand or the object directly with their own finger (see e.g. Blakemore et al., 2005; Pihko et al., 2010). Such a "social" scenario might have been more salient (Blakemore et al., 2005) but it would also have been difficult to differentiate to what extent any somatosensory mirror response then reflects resonance with the observed tactile sensation of "being touched", "touching" (especially SI might preferentially resonate with the act of touching; Ebisch et al., 2008) or a combination of both. Unlike in Bufalari et al. (2007)'s study in which the modulatory effect of the sight of touch on a hand on somatosensory processing was compared with somatosensory processing during the sight of a static hand, the visual stimuli in the present study also contrasted two dynamic visual conditions that both involved an object (cotton bud) approach a hand and eventually either touch it or not. Ishida, Nakajima, Inase and Murata (2010) demonstrated that some bimodal visuotactile neurons in parietal cortex whose receptive fields were anchored to specific body parts of monkeys responded also to visual stimuli moving (but not touching) in the immediate peripersonal space around the corresponding body part of an experimenter, i.e. the observation of actual touch was not necessary to elicit a response in those neurons. Involving the dynamics of a moving object in both visual conditions in the present study thus did not only control overall visual similarity between the visual stimuli but also took into account that already the observation of an object approaching a body, thus entering peripersonal space, might have a modulating effect on somatosensory processing, irrespective of whether it ultimately touches the body or not. The perceived speed of the observed cotton bud movements was identical while movement trajectory and angle were kept as comparable as possible across the two observational conditions. The hand/object images subtended approximately 14.7° x 11.2° of visual angle and were presented on a black background.

To induce somatosensory-evoked potentials (SEPs), task-irrelevant tactile stimuli were presented for 200 ms to participants' left index finger tip using a 12-volt solenoid which was tapped to the stimulated finger and drove a plastic rod with a blunt conical tip against the participants' skin whenever a current was passed through it. To mask any sounds made by the tactile stimulator, continuous white noise (65 dB SPL) was played through headphones.

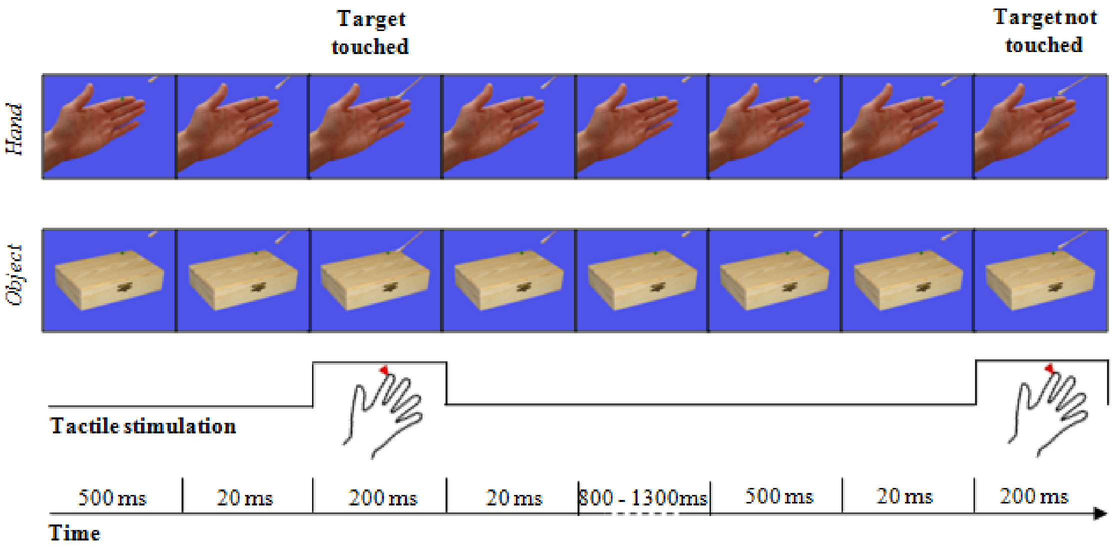


Fig. 2.1.a. Schematic representation of the typical sequence of visual and tactile events in touch and no touch trials, respectively. The finger tip tactually stimulated was anatomically congruent with the observed-to-be-touched finger tip (left index finger tip).

Procedure. Participants sat in a dimly lit sound-attenuated experimental chamber resting both arms at a distance of approximately 30 cm on a table in front of the them, such that their hands were in a similar position to the observed hand, i.e. with their forearms slightly turned inwards toward the midline and their palms facing towards their body. A wooden panel ensured that participants could not see their hands since the mere sight of one's own body has previously been found to modulate somatosensory processing not only at a behavioural level (Kennett, Taylor-Clarke, & Haggard, 2001) but also at a neural level (Longo, Pernigo, & Haggard, 2011; Taylor-Clarke, Kennett, & Haggard, 2002). The visual stimuli were presented on a computer screen located approximately 75 cm in front of the participants using E-Prime, Version 1.1.

Participants were instructed to continuously fixate on a green fixation cross that was superimposed on the viewed touch target, approximately equidistant from the end positions of the cotton bud in the *touch* and *no touch* condition.

Each trial started with a presentation of the touch target (hand vs. object) with the cotton bud in a neutral position for 500 ms which was followed by a brief 20 ms presentation of an image showing the cotton bud halfway between its initial and its final position on or next to the touch target, which was subsequently shown for a total of 200 ms (see Fig. 2.1.a). The onset of this latter, critical stimulus image was simultaneous with the presentation of a tactile stimulus for 200 ms. To create the impression of a smooth backwards movement, the cotton bud was then once more shown in its slightly retracted position for 20 ms and finally for a variable duration between 800 and 1300 ms back in its neutral starting position to complete the trial.

Within each block, the trajectory of the cotton bud and thus the observed tactile feedback was manipulated on a trial-by-trial basis. Each experimental block consisted of 62 trials presented in random order. In 25 trials each, the cotton bud approached the touch target and then either touched the target or the empty space next to it, respectively. In 12 trials of each block (approx. 19 %), the approach of the cotton bud was accompanied by a colour change of the fixation cross from green to red and participants were instructed to report each colour change by saying “pa!” as quickly as possible. This task was to ensure that participants paid close attention to the visual display and to evade contamination of the ERP with eye movement artifacts. Participants were instructed to entirely focus on this task and to ignore the presented hand images and the tactile stimuli delivered to their finger tips. The duration of the image of the cotton bud back in its neutral position at the end of each trial was prolonged by 500 ms for all trials in which a correct or incorrect (false alarm) vocal response occurred to avoid any contamination of ERPs with response-related artifacts. Vocal responses were recorded with a free-standing microphone. Participants were encouraged to take breaks to relax and move between the blocks to counteract tiredness and the associated increase in ERP contaminating alpha waves.

The type of presented touch target was manipulated block-wise. Participants observed the cotton bud touch or merely approach the model’s hand or the object, respectively, for four consecutive blocks each, resulting in 8 experimental blocks in total. The presentation order was counterbalanced: 50 % of the participants observed the human hand first, 50 % the object.

Prior to the experimental blocks of each visual condition, a short demo (6 trials only) of the upcoming visual stimuli of the respective condition was shown to the participants. Following this demo, participants were gently touched twice with a cotton bud on their left index finger tip to demonstrate the different tactile consequences associated with the observed events on the screen. This was followed by a short practice block consisting of 22 trials (6 catch trials) to familiarise participants with the colour change detection task at hand. Since participants usually had no problems at all with performing this task, only the four blocks of the starting condition (hand vs. object) were preceded by such a practice block.

At the end of the experiment, participants completed the 60-item *Empathy Quotient* (EQ) questionnaire (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) as well as the 28-item *Interpersonal Reactivity Index* (IRI) by Davis (1983). The order in which the two questionnaires were administered was counterbalanced across participants.

Recording and data. Continuous EEG was recorded with Ag-AgCl electrodes from 28 scalp sites following the 10-20 international system (midline electrodes: Fz, Fcz, Cz, Pz; electrodes over the right hemisphere: Fp2, F4, F8, Fc2, Fc6, C4, T8, Cp2, Cp6, P4, P8, O2 and the homologous electrode sites over the left hemisphere) using a Brain Vision 32 channel system. The horizontal electrooculogram (HEOG) was recorded bipolarly from two electrodes placed at the outer canthi of both eyes to detect horizontal eye movements. The vertical electrooculogram (VEOG) was recorded bipolarly from an electrode placed under the right eye and Fp2 above the right eye. All scalp electrodes were referenced to an electrode on the right ear lobe and re-referenced off-line to an average of both ear lobes for analysis. Electrode impedances were kept below 5 KΩ or 2 KΩ, respectively, for the reference electrodes. The impedance of the earlobe electrodes was kept as equal as possible.

EEG and EOG were sampled at a digitisation rate of 1000 Hz with a bandpass filter of 0.016 to 100 Hz and subsequently filtered off-line with a low pass filter of 30 Hz.

EEG data were analyzed using Brain Vision Analyzer software (version 1.05; Brain Products GmBH, Gilching, Germany). EEG, HEOG and VEOG were segmented off-line into 500 ms epochs starting 100 ms before the onset of the tactile stimulus until 400 ms thereafter, epoched separately for all four combinations of observed tactile feedback (touch vs. no touch) and touch target (hand vs. object). Trials with horizontal eye movements (EOG exceeding ± 30 μV relative to the 100 ms pre-stimulus baseline), eye blinks or other artifacts (voltage exceeding ±60 μV at any electrode relative to baseline) measured in this epoch were excluded from analysis. Trials in which a (correct or incorrect) vocal response occurred were also excluded. For the remaining trials, ERPs for tactile stimuli were averaged relative to a 100 ms pre-stimulus baseline for all four combinations of observed tactile feedback and touch target. Scalp maps to visualise the topographic distribution of the ERP amplitude difference as a function of the observed tactile feedback in a given time epoch were plotted using EEGLAB, version 9.0.3.4b.

Data analysis. The statistical analyses involved posterior as well as anterior electrodes over both hemispheres, grouped into four clusters (see Fig. 2.1.b): Ipsilateral-anterior (Fp1, F3, F5, Fc1, Fc5), ipsilateral-posterior (C3, Cp1, Cp5, P3, P7), contralateral-anterior (Fp2, F4, F8, Fc2, Fc6) and contralateral-posterior (C4, Cp2, Cp6, P4, P8).

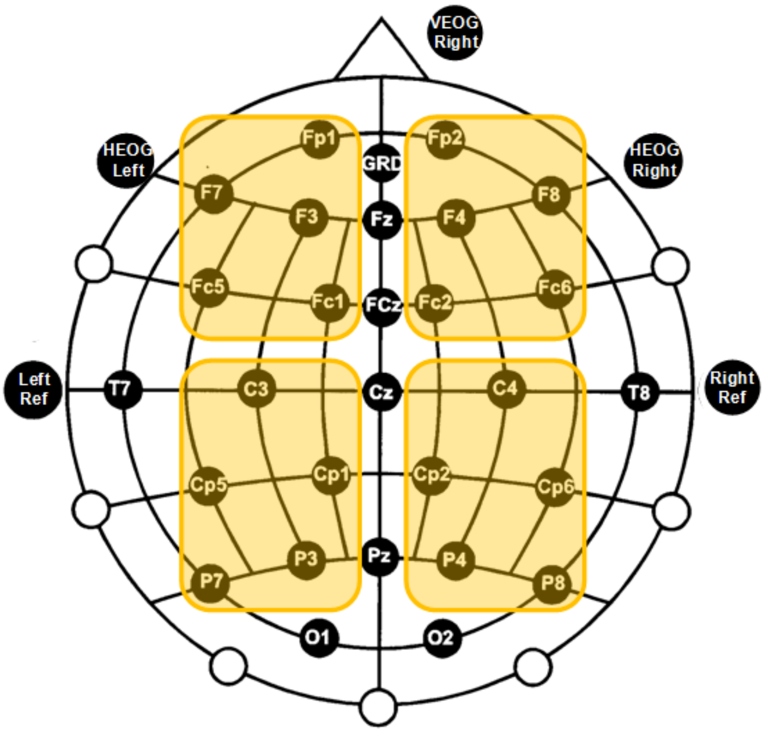


Fig. 2.1.b. Arrangement of the 32 electrodes following the 10-20 international system, with the electrode clusters used in the statistical analysis indicated in orange. All scalp electrodes were referenced to the electrode on the right earlobe and re-referenced offline to an average of both earlobes for analysis. The HEOG was recorded bipolarly from two electrodes placed at the outer canthi of both eyes to detect horizontal eye movements while the VEOG was recorded bipolarly from an electrode placed under the right eye and Fp2.

ERP mean amplitudes were computed for successive latency windows centred on the peak amplitudes of early somatosensory ERP components typically observed in response to tactile stimulation: P50 (40-60 ms post-stimulus onset), N80 (60-80 ms post-stimulus onset), P100 (90-110 ms post-stimulus onset) and N140 (110-150 ms post-stimulus onset). The choice of the time epochs was based on visual inspection of the grand average ERP components elicited by tactile stimuli averaged across all four experimental conditions over contralateral somatosensory cortex at C4, Cp2 and Cp6 where SEPs in response to tactile stimuli to the hand are usually clearest.

To investigate whether the observation of somebody else’s passive touch sensations modulates somatosensory processing of a concurrently delivered tactile stimulus and whether any such modulation might be contingent upon whether the touch target is animate or not, 5-way repeated measures ANOVAs with the within-subject factors *hemisphere* (ipsilateral vs. contralateral), *anterior-posterior* (anterior vs. posterior), *touch target* (hand vs. object), *observed tactile feedback* (touch vs. no touch) and *electrode site* were conducted on the mean ERP amplitudes for a given latency window. When an interaction including the factor *observed tactile feedback* was found to be significant, further ANOVAs were conducted to analyse the effect of observing either touch or non-touch separately for each factor level of the interacting factors. For instance, a *hemisphere* by *observed tactile feedback*-interaction was followed-up by running a 4-way ANOVA with the factors *anterior-posterior*, *touch target*, *observed tactile feedback* and *electrode site* separately for each of the two hemispheres. A significant *hemisphere* by *anterior-posterior* by *observed tactile feedback*-interaction, on the other hand, was followed up by conducting separate 3-way ANOVAs with the factors *touch target*, *observed tactile feedback* and *electrode site* for the four different electrode clusters (i.e. the ipsilateral-anterior, ipsilateral-posterior, contralateral-anterior and contralateral-posterior cluster). Interactions including the factor *touch target* (but not also the factor *observed tactile feedback*) were further analysed in the same way. Any significant interactions for the two factors of interest (*observed tactile feedback* and *touch target*) involving the factor *electrode site* were not followed-up and thus also not reported. Trivial effects such as main effects of *hemispher*e, *anterior-posterior* and *electrode site* as well as interactions between the three are also not reported. Greenhouse-Geisser adjustments to obtained p-values were applied where appropriate. An alpha level of .05 was used for all statistical tests.

To investigate whether the ERP modulation contingent upon the observation of others' passive touch experiences is linked to trait empathy, a standard correlational analysis was carried out. For a given time window (with a significant effect), an index of the strength of the observed SEP modulations was computed as the difference between the mean ERP amplitudes for both observation conditions (mean $\text{amplitude}_{\text{touch}}$ – mean $\text{amplitude}_{\text{notouch}}$) and correlated with the *Empathy Quotient* (EQ) and its three subscales (*cognitive empathy*, *emotional reactivity*, *social skills*; Baron-Cohen & Wheelwright, 2004; Lawrence et al. 2004) as well with the *perspective-taking*, *empathic concern*, *personal distress* and *fantasy* scales of the *Interpersonal Reactivity Index* (IRI; Davis, 1983) using Spearman's rank correlation coefficients. The correlation analyses were conducted non-parametrically since the empathy scores on some of the scales were found to be somewhat skewed.

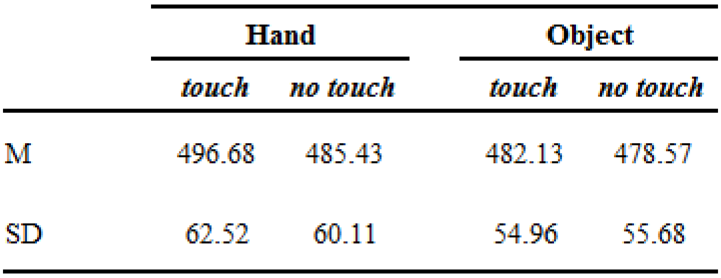
2.1.3 Results

Behavioural performance

The mean accuracy rate in the colour change detection task was 99.2 % with only very few false alarms (1.5 %), indicating that participants paid close attention to the visual display. Overall, participants were somewhat slower in detecting a colour change of the fixation cross (see Table 2.1.a) when they concurrently observed the cotton bud actually touch rather than merely approach the touch target ($F(1,19) = 5.947$, $p = .025$, $\eta^2_p = .238$). Whether the observed touch target was a hand or an object did, however, not modulate this effect ($F(1,19) = 1.365$, p =

.257, η^2_p = .067) nor did it significantly affect response times in itself (F(1,19) = 2.863, p = .107, η^2_p = .131).

Table 2.1.a. Means and standard deviations of response times in colour change detection task (in ms) as a function of *observed touch target* and *observed tactile feedback*



	Hand		**Object**	
	touch	***no touch***	***touch***	***no touch***
M	496.68	485.43	482.13	478.57
SD	62.52	60.11	54.96	55.68

Electrophysiological data

Touch observation-induced modulations of somatosensory cortical processing

Visually-induced effects of observing either somebody else's hand or an inanimate object being touched on somatosensory processing were determined by comparing ERPs obtained when tactile stimulation was accompanied by observing a cotton bud either touch the index finger tip of a left hand/a wooden box or the empty space next to it. Figures 2.1.c and 2.1.d contrast the obtained SEP waveforms for the two types of observed tactile feedback at all analysed electrode sites for the two different touch targets, separately for anterior and posterior electrode sites. Note that the somatosensory P50 and N80 components are often observable only at electrode sites contralateral to the site of tactile stimulation and that the P50 component tends to reverse to a negative-going peak at more anterior electrode sites (see, for instance, the waveforms at Fc2c; Hämäläinen et al., 1990).

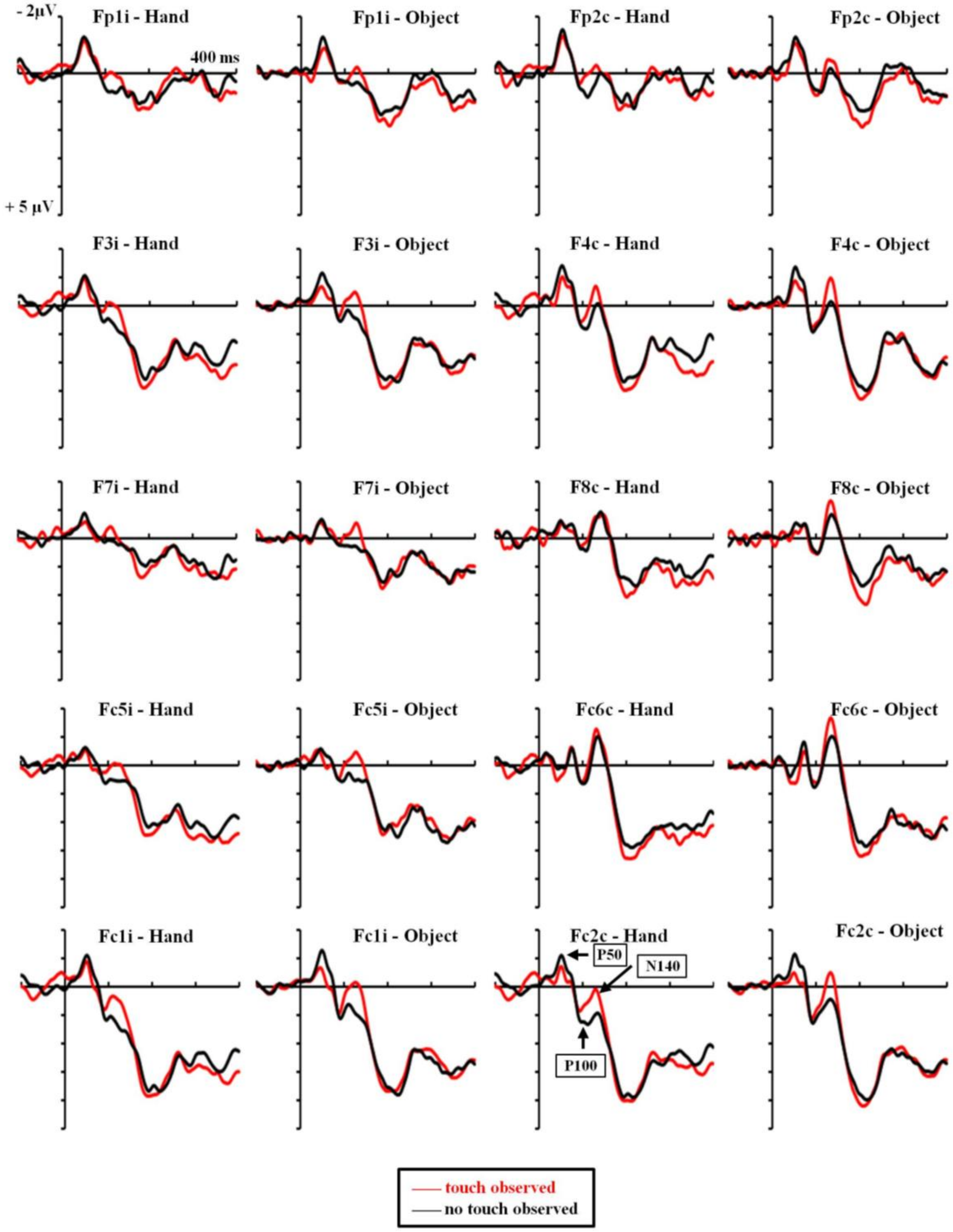


Fig. 2.1.c. Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the left index finger tip during the observation of touch (red) or no touch (black) on somebody else’s hand or an object. Shown are all anterior electrode sites included in the analysis, both ipsi- and contralateral (indicted by the electrode name ending in an i and c, respectively) to the tactile stimulation.

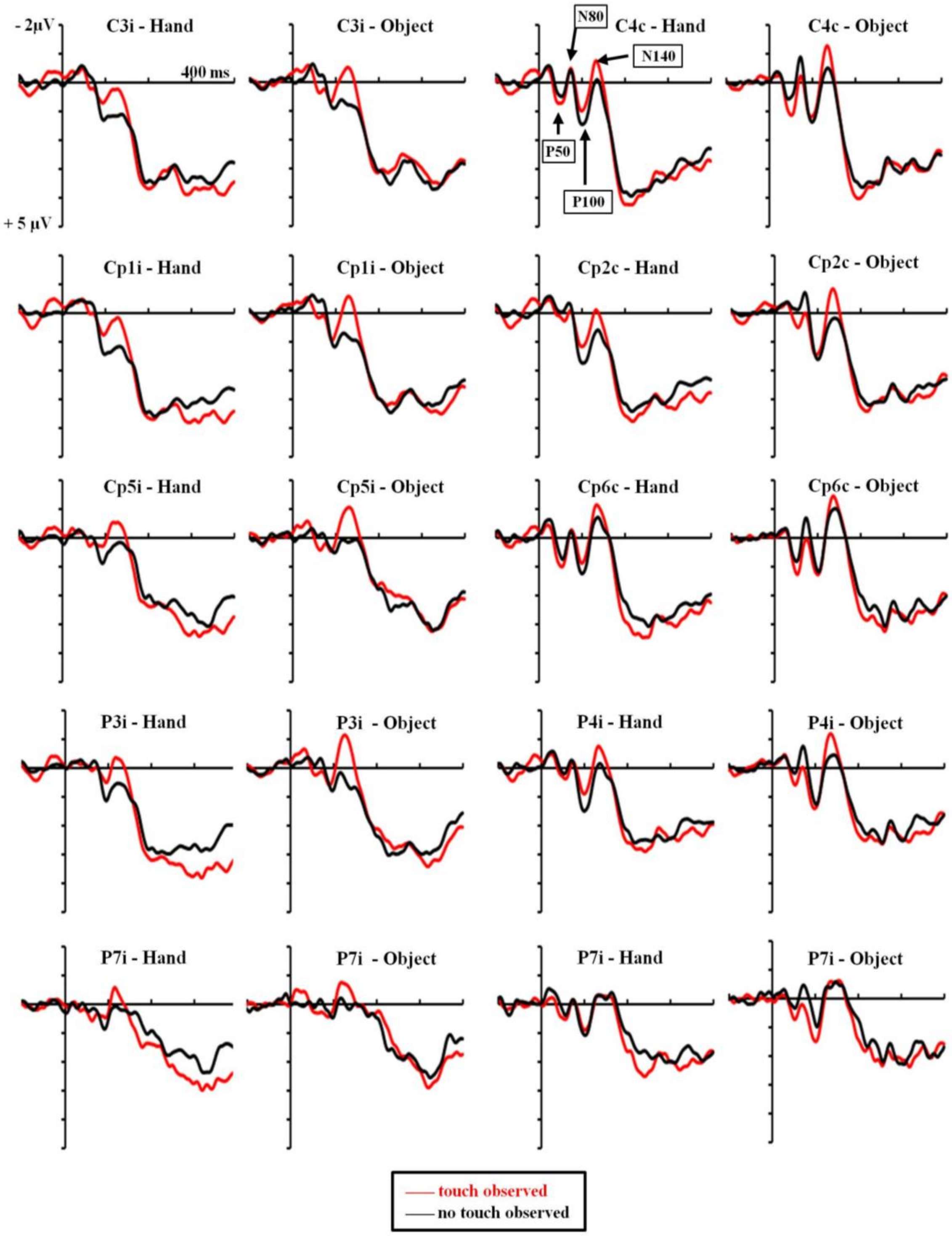


Fig. 2.1.d. Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the left index finger tip during the observation of touch (red) or no touch (black) on somebody else’s hand or an object. Shown are all posterior electrode sites included in the analysis, both ipsi- and contralateral to the tactile stimulation. The four analysed SEP components are indicated at C4c-Hand

Looking at a body part rather than in inanimate object in the same spatial location can modulate somatosensory cortical processing (Longo et al., 2011; Taylor-Clarke et al., 2002). The conducted 5-way repeated measures ANOVAs did, however, not indicate for any of the analysed SEP components here that mean SEP amplitudes were reliably altered as a function of the type of observed touch target per se: For the somatosensory P100 component, there was a marginally significant *hemisphere* by *touch target*-interaction ($F(1,19) = 4.242$, $p = .053$, $\eta^2_p = .183$) but follow-up analyses did not confirm any differences in somatosensory cortical processing as a function of the observed touch target for either hemisphere (both $p \geq .050$).

As far as the effect of observing touch was concerned, it was found that the sight of touch did not have any reliable effects on somatosensory processing in the N80 and P100 latency range, irrespective of what kind of touch target was presented: Main effects of the factor *observed tactile feedback* in these time epochs were not significant ($F \leq 3.97$, $p \geq .061$) and follow-up analyses of any revealed significant interactions involving this factor did also not yield any significant results (all $p > .05$).

Touch-related visual information did, however, significantly modulate somatosensory processing during an early time epoch of 40-60 ms (P50) right after tactile stimulus onset as well as during a later time epoch of 110-150 ms (N140) after tactile stimulus onset. For the somatosensory P50 component, a small but significant main effect of the *observed tactile feedback* was revealed ($F(1,19) = 5.765$, $p = .027$, $\eta^2_p = .233$). The mean amplitude of this component was significantly more positive-going when the cotton bud was observed to actually touch rather than merely approach the touch target. Crucially, this observation-induced SEP modulation did not depend on the type of observed touch target (all $F(1,19) \leq .227$, $p \geq .639$, $\eta^2_p \leq .012$ for interactions involving both *observed tactile feedback* and *observed touch target*), even though a visual comparison of the obtained SEP waveforms for the two touch targets seemed to suggest that the P50 modulations were actually somewhat stronger for touch observed on an inanimate object (compare, for instance, panels a) and b) in Fig. 2.1.e).[7]

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[7] Especially with respect to the somatosensory P50 component, a close visual inspection of Figures 2.1.c and 2.1.d cast some doubts on whether the observation of touch did indeed modulate somatosensory cortical processing in this time window in a similar fashion for animate as well as inanimate touch targets as suggested by the absence of a significant interaction with the factor *observed touch target*. Instead, the sight of touch on the wooden box appeared to have a much more pronounced and wide-spread effect on the mean SEP amplitude of this component than the sight of touch on a human hand. To clarify if the initial analysis might have lacked the power to detect a respective interaction, especially in the light of strong modulations in the “touch on object”-condition, the conducted ANOVAs were re-run on an exploratory basis for the two touch targets separately. The results clearly indicated the P50 modulations were only present when an object was seen to be touched (main effect of *observed tactile feedback*: $F(1,19) = 6.944$, $p = .016$, $\eta^2_p = .268$). Seeing a hand being touched did not elicit any modulations at all in this time window (all $F(1,19) \leq .993$, $p \geq .332$, $\eta^2_p \leq .050$, for main effect and interactions with the factor *observed tactile feedback*). For the N140 component, on the other hand, the re-analysis confirmed the

The mean amplitude of the late N140 component was also found to be enhanced during the observation of touch, with the sight of touch resulting in a significantly more negative-going N140 amplitude than the sight of no touch (F(1,15) = 15.828, p = .001, η^2_p = .454). Post hoc comparisons following-up a significant *hemisphere* by *anterior-posterior* by *observed tactile feedback*-interaction (F(1,19) = 5.153, p = .035) confirmed that this observation-induced effect was present across all four electrode clusters but most pronounced over posterior electrode sites ipsilateral to the stimulated hand (ipsilateral-anterior: F(1,19) = 14.825, p = .001, η^2_p = .438 ; ipsilateral-posterior: F(1,19) = 19.57, p < .001, η^2_p = .507; contralateral-anterior: F(1,19) = 7.070, p = .015, η^2_p = .271; contralateral-posterior: F(1,19) = 4.825, p = .041, η^2_p = .203). Again, the absence of any significant interactions involving both the *observed tactile feedback* and *observed touch target* suggested that concurrent somatosensory processing was modulated in a similar fashion for the sight of touch on a human hand as well as on an inanimate object (all F(1,19) ≤ 1.402, p ≥ .251, η^2_p ≤ .069). Figures 2.1.e and 2.1.f show the ERP waveforms at an representative electrode each for the observation of touch on a hand, an object and when collapsed across the two types of touch target, along with the topographic distribution of the mean difference in SEP amplitude for observed touch and observed no touch in the P50 and N140 latency range, respectively, when averaged across the two touch targets.

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presence of a similar pattern of touch observation-induced modulations for both touch targets (main effect of *observed tactile feedback* for hand: F(1,19) = 5.537, p = .030, η^2_p = .226; main effect of *observed tactile feedback* for object: F(1,19) = 6.139, p = .023, η^2_p = .244; following-up a significant *hemisphere* by *anterior-posterior* by *observed tactile feedback*-interaction (F(1,19) = 6.511, p = .019) with separate *observed tactile feedback* (2) by *electrode site* (5)-ANOVAs for the four different electrode clusters suggested, however, that the touch observation-induced SEP effect for the sight of touch on an object was actually more reliable over the ipsilateral hemisphere, especially at posterior electrode sites (ipsilateral-anterior: F(1,19) = 5.154, p = .035, η2p = .213; ipsilateral-posterior: F(1,19) = 11.578, p = .003, η^2_p = .379).

For the somatosensory P50 component, for which the separate explorative analysis suggested a modulation effect for the sight of touch on an object only, an additional explorative analysis was conducted to establish whether this early modulation might have been contingent on a carry-over effect from having seen a human hand being touched before. Based on two separate ANOVAs (*hemisphere* (2) by *anterior-posterior* (2) by *observed tactile feedback* (2) by *electrode site* (5)) for each presentation order, it was indeed found that this modulation tended to occur only when the object condition was run *after* the hand condition (F(1,18) = 9.075, p = .007, η^2_p = .335 for hand first, F(1,18) = .713, p = .410, η^2_p = .038 for object first), which might indicate that the sight of touch on an object triggers vicarious somatosensory activity in SI only when the observed-to-be-touched location on the object can be matched to a location of the observer’s body.

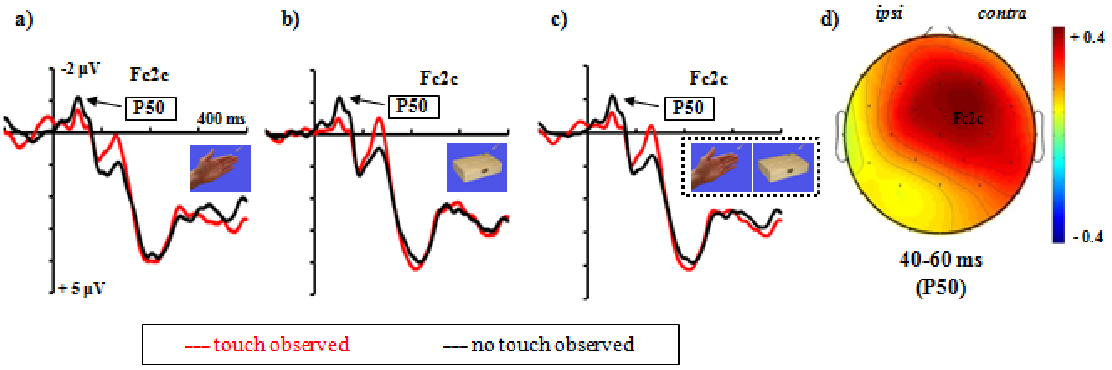

Fig. 2.1.e. ***A-c)*** Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the hand during the observation of touch (red line) or no touch (black line) on somebody else's hand ***(a)*** or an object ***(b)*** or when collapsing across the two different touch targets ***(c)***, at a representative electrode (Fc2c). Note that the somatosensory P50 amplitude tends to reverse its polarity at anterior electrodes sites (Hämäläinen et al., (1990). ***(d)*** Topographic distribution of the difference in mean SEP amplitude for the observation of touch and no touch (= mean amplitude$_{touch}$ – mean amplitude$_{notouch}$) in the 40-60 ms post-stimulus (P50) time window (collapsed across touch targets). Note that a positive difference indicates an increased P50 amplitude for the sight of touch.

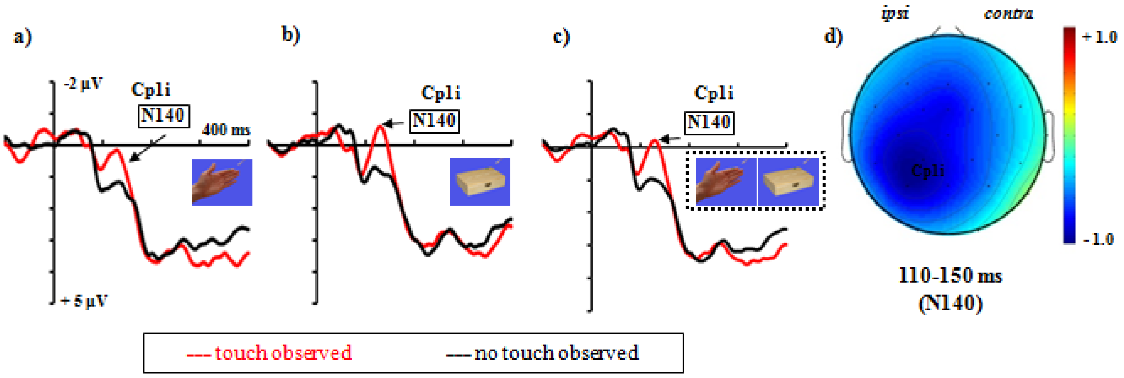

Fig. 2.1.f. ***A-c)*** Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the hand during the observation of touch (red line) or no touch (black line) on somebody else's hand ***(a)*** or an object ***(b)*** or when collapsing across the two different touch targets ***(c)***, at a representative electrode (Cp1i). ***(d)*** Topographic distribution of the difference in mean SEP amplitude for the observation of touch and no touch (= mean amplitude$_{touch}$ – mean amplitude$_{notouch}$) in the 110-150 ms post-stimulus (N140) time window (collapsed across touch targets). Note that a negative difference indicates an increased N140 amplitude for the sight of touch.

Empathy correlations

Table 2.1.b shows the trait empathy measures obtained with the two standard empathy questionnaires EQ (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) and the IRI (Davis, 1983) at the end of the experiment.

Table 2.1.b. Mean scores and standard deviations for the self-report measures of dispositional empathy.

	Empathy Quotient (EQ)				**Interpersonal Reactivity Index (IRI)**			
	Total	CE	ER	SS	PT	FS	EC	PD
Sample (N=20)	48.80	14.60	14.45	6.65	20.05	19.15	21.65	12.95
	(10.06)	*(4.68)*	*(4.35)*	*(2.85)*	*(4.02)*	*(5.49)*	*(3.86)*	*(3.76)*
Normative data[a]	46.20	n/a	n/a	n/a	17.37	n/a	20.36	10.87
	(10.60)	n/a	n/a	n/a	*(4.79)*	n/a	*(4.02)*	*(4.78)*

[a)] Normative data are derived from: Lawrence et al., 2004 (EQ) and Bellini, Baime, and Shea (2002) (IRI).

EQ: CE = Cognitive Empathy ER = Emotional reactivity SS = Social skills

IRI: PT = Perspective taking FS = Fantasy scale EC = Empathic concern PD = Personal distress

Maximal scores: Total score of EQ = 80; Cognitive empathy (EQ) = 22, Emotional reactivity (EQ) = 22, Social skills (EQ) = 12; each subscale of the IRI = 28.

In comparison to normative data (Bellini et al., 2002; Lawrence et al., 2004; see Table 2.1.b), participants in the present sample scored generally somewhat higher on the empathy (sub)scales but the obtained EQ and IRI scores were still quite comparable.

To investigate whether the strength of the touch observation-induced P50 and N140 modulations was linked to individual trait empathy levels, the difference between the mean ERP amplitudes for both observation conditions (mean $\text{amplitude}_{\text{touch}}$ – mean $\text{amplitude}_{\text{notouch}}$) was computed as an index of the strength of the observed SEP modulations for all electrode sites included in the main analysis[8] and then correlated with the obtained EQ and IRI scores. Empathy-related correlations are only reported below if they were found at clusters of at least three electrodes in topographic proximity, i.e. correlations at isolated electrodes sites are subsequently omitted.

For a small subset of posterior electrodes over the hemisphere contralateral to the tactually stimulated hand, a systematic pattern of correlations between the strength of the visually-induced amplitude modulations and two separate measures of emotional empathy were found for both somatosensory components: In the P50 time epoch 40 to 60 ms after tactile stimulus onset, the correlational analysis suggested that it was in fact the participants who tended to score lower on either the *empathic concern* subscale of the IRI and/or the *emotional reactivity* subscale of the EQ that showed an enhanced P50 amplitude when observing touch rather than no touch (*empathic concern*: C4: $r_s(20) = -.626$; Cp2: $r_s(20) = -.547$; Cp6: $r_s(20) = -$

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[8] Correlational analyses were thus not conducted on midline electrodes, T7/T8 and O1/O2 since those electrode sides were not included in the ANOVAs reported earlier.

.696; P4: $r_s(20) = -.646$; P8: $r_s(20) = -.498$; all $p \leq .05$; in addition, one topographically close electrode showed a marginally significant correlation in the same direction: Fc2: $r_s(20) = -.431$, $p = .058$; *emotional reactivity*: Fc6: $r_s(20) = -.498$; C4: $r_s(20) = -.459$; Cp6: $r_s(20) = -.517$; all $p \leq .05$). Participants with a disposition for strong *empathic concern*/*emotional reactivity* towards others, on the other hand, seemed more likely to show only small P50 modulations. For the N140 component, this relationship was reversed for participants' tendency to show *empathic concern* for others: High scores on this subscale were associated with stronger modulations of the N140 mean amplitude (C4: $r_s(20) = -.522$; Cp2: $r_s(20) = -.479$; Cp6: $r_s(20) = -.512$; all $p \leq .05$; P4 showed a marginally significant correlation in the same direction: P4: $r_s(20) = -.433$, $p = .057$). Unlike for the P50 effect, no such relationship between the strength to the N140 effect and the *emotional reactivity* subscale was found, even though *empathic concern* (IRI) and *emotional reactivity* (EQ) as such were positively correlated ($r_s(20) = .608$; $p = .004$), suggesting that the two subscales might measure related components of empathy. Fig. 2.1.g visualises the revealed empathy correlations for the touch observation-related ERP modulations in the P50 and N140 latency range at two representative contralateral electrodes (Cp6 and C4, respectively).

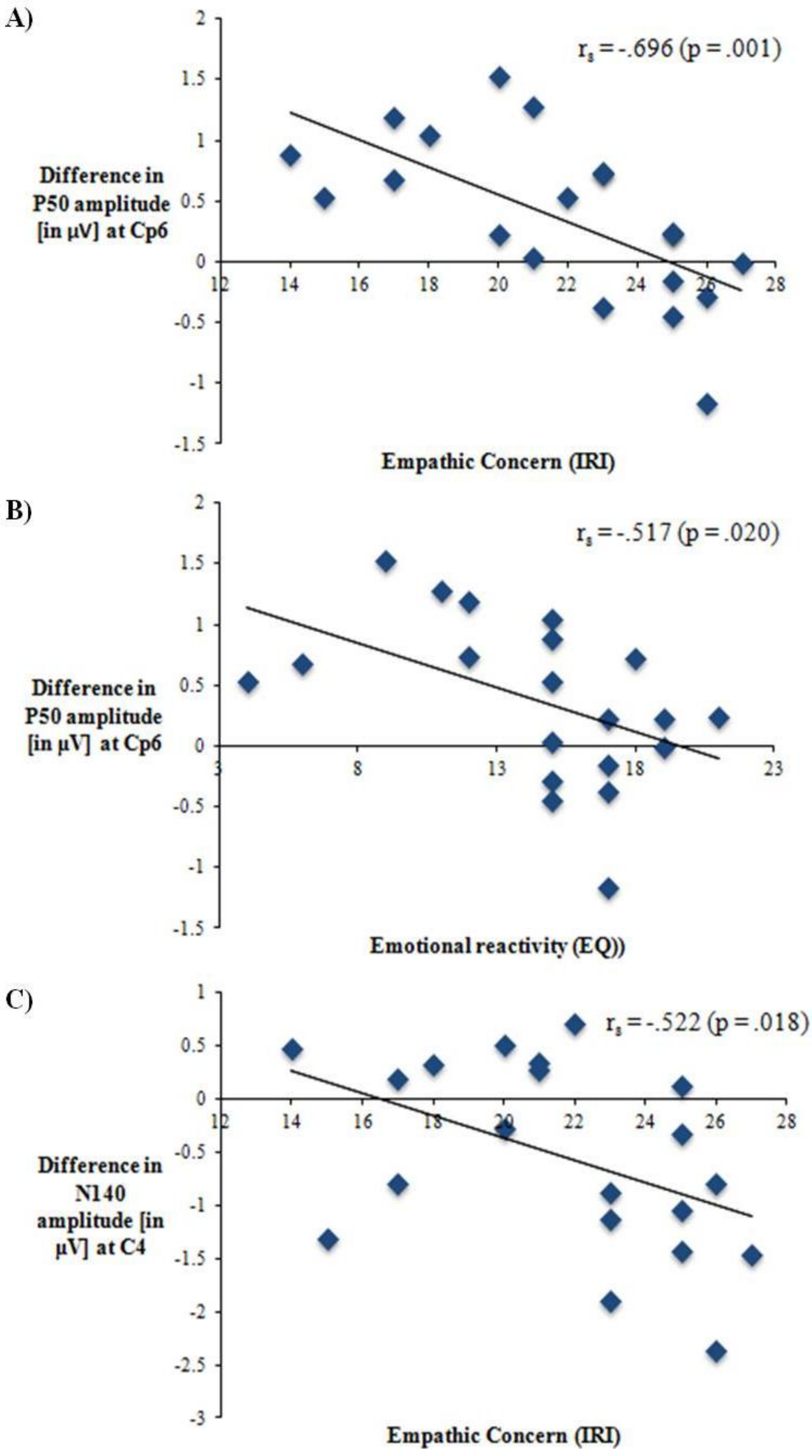

Fig. 2.1.g. Mean difference in SEP amplitude (averaged across both touch targets) for observing touch vs. no touch as a function of self-reported levels of *empathic concern* (IRI) and *emotional reactivity* (EQ) for the somatosensory P50 **(A, B)** and N140 **(C)** component, at a representative electrode that showed the strongest correlations for a given latency range and empathy subscale (Cp6c and C4c, respectively).

2.1.4 Discussion

The present ERP study was designed to investigate whether the observation of touch modulates somatosensory processing of concurrently delivered tactile stimuli to the observer's own hand and whether any such modulations are specific to the sight of touch on somebody else's body or whether they can also be found when touch is observed on an inanimate object. Participants were presented with non-painful stimuli to their index finger tip while they simultaneously observed a cotton bud either touch a model's hand on the corresponding index finger or merely the empty space next to it. Alternatively, the cotton bud was seen to either touch the top right corner of a wooden box in the same position as the hand or merely move through the empty space next to the box.

Modulations in early somatosensory processing during the observation of touch

The cortical response to the presented tactile stimuli was found to be modulated by the touch-related visual information for two of the analysed somatosensory components, namely the late-latency N140 component, assumed to be associated (at least in parts) with activity in SII (Tarkka et al., 1996; Valeriani, Fraioli, Ranghi, & Giaquinto, 2001a), and the early-latency P50 component which is thought to indicate SI activity (Allison et al., 1992; Hämäläinen et al., 1990). Crucially, the mean amplitudes of both components were increased during the sight of touch, regardless of whether the observed touch was directed at a hand or an object.

The N140 component is associated with higher-order somatosensory processing, such as contributing to the conscious perception of presented tactile stimuli (Schubert, Blankenburg, Lemm, Villringer, & Curio, 2006), and is presumably generated in bilateral SII (Tarkka et al., 1996; Valeriani et al., 2001a; see, however, Allison et al., 1992; Ku et al., 2007 and Tomberg, 1999, for another major source of the N140 in the bilateral frontal lobes, most likely activated by cortico-cortical connections with higher-order somatosensory areas in the posterior-parietal cortex, such as area 7b (Tomberg, 1999)). The significant increase in N140 amplitude when the cotton bud was observed to touch a hand but also when it was seen to make contact with an object suggests that the sight of touch vicariously activated SII regardless of the animacy of touch target, in line with previous findings by Ebisch et al. (2008) and Keysers et al. (2004) that suggest that SII might actually respond to *any* sight of touch irrespective of whether that touch occurs on somebody else's body or an inanimate object. Statistically, there was no indication that the sight of a hand being touched resulted in stronger modulations in SII-related somatosensory processing than the sight of an object being touched, in contrast with Blakemore et al. (2005)'s finding that vicarious touch observation-related activity in SII (and also SI) was much stronger for the sight of touch on a human face rather than on an equivalent location on an object. The body-related touch observed in Blakemore et al. (2005)'s fMRI study was, however, seen to be directed at a face as a possibly particularly salient body part might have biased the detected strong vicarious SII activity in favour of particularly strong somatosensory mirror response as compared to the sight of touch on an object. Whether the target-unspecific N140 modulation in the context of assumed SII activity revealed in the present study might still not be sensitive to the animacy of the touch target if the biological touch target involved a face rather than a hand should be tested in future studies.

Importantly, the sight of touch, regardless of whether a hand or an object was touched, did, however, not only result in the just described modulations of the N140 component. In addition, also the early-latency P50 component was affected, in a similarly target-unspecific fashion. The somatosensory P50 component is thought to originate from contralateral SI (Allison et al., 1992; Hämäläinen et al., 1990) and thus reflects early-stage sensory processing of a presented tactile information. The significant increase in P50 amplitude during the observation of touch as compared to no touch thus suggested that the mere sight of touch, too, activates SI, in line with previous findings (Blakemore et al., 2005; Bufalari et al., 2007; Pihko et al., 2010; Schaefer et al., 2012; 2009; Wood et al., 2010). Notably, the statistical analysis indicated that the touch observation-related P50 SEP modulations did not depend on the type of observed touch target, i.e. on whether the observed touch was directed at somebody else's hand or an inanimate wooden box, suggesting that not only SII (Ebisch et al., 2008; Keysers et al., 2004) but also SI might resonate with an "abstract notion of touch", extending current knowledge on the characteristics of mirror touch responses in SI. Previous (fMRI) studies were unclear as to whether or not SI is involved in representing observed touch between inanimate objects: Keysers et al. (2004) did not further analyse the specificity of touch observation-related SI activity in a ROI-approach after SI failed to show more than a (non-significant) trend for an overlap during the sight and experience of touch on the legs while Ebisch et al. (2008)'s results pointed to a particular role of SI/BA2 in resonating with the observed *act of touching* rather than with the sight of somebody (or something) *being touched*. Blakemore et al. (2005), on the other, concluded that SI (and SII) preferentially respond to the sight of touch on a face rather than an object but the use of faces as body touch targets might have unduly biased the respective comparison in favour of body-related touch (see above). The conducted contrast ($\text{body}_{\text{touch}}$ vs. $\text{object}_{\text{touch}}$) also did not allow to dissociate whether the sight of touch on objects did not induce any vicarious somatosensory activity (be it in SI or SII) at all or whether it might just be weaker but still significant. The present ERP study suggests that the sight of touch on an inanimate object might vicariously engage SI in a similar way as the sight of touch on a (non-face) body part.

The target-unspecificity of the P50 modulations revealed in the present study should nonetheless be interpreted with caution: While the statistical main analysis clearly indicated that there was no significant interaction between the observed tactile feedback and the concurrently observed touch target in this latency range, there were all the same indications that the sight of touch on either touch target did not only affect somatosensory processing differently but did so in a quite unexpected fashion: Surprisingly enough, separate (explorative) analyses for the two touch targets indicated that the P50 effect was actually driven by the observation of touch on the inanimate object rather than on the hand. One possible explanation might be that the sight of a cotton bud making contact with box was perceived as somewhat artificial and unusual, rendering the observed touch more salient. Another possible explanation might, however, be that the touch on the object was perceived as more intense as touch on a hand due to the hard wooden surface that was being touched. Interestingly, Bufalari et al. (2007) found that the strength of the revealed P50 (P45) effect during the observation of touch (on a hand) in their study correlated positively with subjective ratings of the intensity of the touch experienced by the model: The more intense participants rated the observed touch intensity, the more pronounced was the difference in P50 amplitude. This might point to the importance of ensuring in future studies that the inanimate touch targets used for comparison sufficiently resemble a body part in e.g. its softness, allowing a cotton bud to slightly indent the surface as it would when touching skin and flesh (see, for instance, Avenanti et al., 2005: tomato).

An additional explorative analysis of the P50 modulation in the context of observing touch on an inanimate box, however, indicated at the same time that the strong object-related P50 effect tended to be present only when the object condition was run *after* the hand condition. The increase in P50 amplitude elicited by observing the cotton bud touch the object rather than merely the empty space next to it thus appeared to depend somewhat on having seen a hand in the same spatial location being touched first (carry-over effect). Blakemore et al. (2005) demonstrated that mirror touch activations in SI are somatotopically organised and lateralised, raising the question if and how touch observed on an *object* would be matched to a specific part of the observer’s body to result in a similarly specific activation in SI. The minority of mirror touch synaesthetes who do report tactile sensations when observing objects being touched show no consistent anatomical re-mapping between the touched part of the object and the part of their own body where they feel the mirror touch sensation (Banissy et al., 2009). It could thus have been the case that having seen a hand being touched before predisposed participants to match the observed touch on an object to a specific location on their own body, namely their hand, facilitating a more somatotopically defined activation in SI.

It is, however, important to note with respect to the P50 enhancement during the sight of touch that the main analysis nevertheless did suggest that the SEP modulations in this early latency range were sufficiently similar between the two touch targets since there was no significant interaction between the observed tactile feedback and the touch target to suggest otherwise. The described deviations were apparently not grave enough to result in such a statistically significant interaction. Their implications are, however, most certainly useful for the design of other future studies, regarding the selection of appropriate inanimate touch targets for comparison and possible carry-over effects. While the possible order effect in the context of the revealed P50 modulations during the "touch on object"-condition in the present could at best be considered a weak trend, given that the respective analysis was explorative and based on only a small number of participants, it nevertheless points to the possibility that vicarious SI activity (unlike SII[9]) might depend on being able to somehow match the object-related touch to a specific location on one's own body. Further research with larger samples is needed to elucidate this more reliably.

Not only with respect to the somatosensory P50 modulations but also with respect to the aforedescribed N140 effect, it should also be mentioned that both components have previously been found to be sensitive to changes in spatial as well as non-spatial tactile attention (Forster & Eimer, 2004; 2005; García-Larrea, Lukaszewicz, & Mauguière, 1995; Schubert et al., 2008). It seems, however, unlikely that the revealed increase in P50/N140 mean amplitude in response to the sight of touch rather than non-touch merely reflect an unspecific attention effect: There were no instructions at all for participants to attend to any particular features, be it spatial or non-spatial, of the presented stimuli. Instead, they were explicitly told to completely ignore both the tactile and the visual stimuli and to focus entirely on the colour change detection task. Behaviourally, participants did tend to be somewhat slower in detecting a colour change of the fixation cross when it was accompanied by the sight of the cotton bud touch the touch target rather than merely the empty space next to it which could be interpreted as an indication that participants spontaneously directed more attention to the condition where the cotton bud "missed" the touch target (e.g. because this appeared, for instance, less goal-directed or more accidental than actually touching the target which might have increased the salience of the non-touch stimuli) which might, in turn, also have resulted in an increase of attention to the concurrently presented tactile stimuli (e.g. because the deviation between feeling touch but not seeing it was more salient). This difference in response latencies was, however, very small (only

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[9] Vicarious touch observation-related SII activity, on the other hand, might depend less on being able to match the observed touch to a specific body part: Keysers et al. (2004) found an overlap in observed and experienced touch during the sight of touch on inanimate objects even though the "touch on object"-condition was run *before* the "touch on legs"-condition and before the "experience touch on legs"-condition.

approx. 10 ms) and is unlikely to reflect a reliable attentional difference.[10] Albeit indirectly, the finding that the strength of the revealed P50 and N140 modulation correlated with participants' empathic dispositions (see below) also corroborates the notion that the observed SEP modulations were associated with visuotactile mirror-matching mechanism rather than with an unspecific attention effect.

Variations in touch observation-related modulations in somatosensory processing as a function of interindividual differences in trait empathy

For both the P50 and the N140 component, the strength of the touch observation-related amplitude increase (regardless of whether the touch was directed at a body part or an object) was correlated with participants' self-reported empathic dispositions. For the N140 component (indexing vicarious SII activity), it was found that the touch observation-related increase in ERP amplitude was more pronounced for participants who scored high on the IRI's *empathic concern* subscale. This scales consists of seven items and measures the tendency to respond with "feelings of warmth, compassion and concern to others undergoing negative experiences" (Davis, 1983, p. 6), thus tapping the tendency to react emotionally to others' misfortunes. Exemplary items are "I often have tender, concerned feelings for people less fortunate than me." or "When I see someone being taken advantage of, I feel kind of protective towards them.". Interestingly, mirror touch synaesthetes whose synaesthetic experience seems to be associated with an atypically strong activation of their tactile mirror system during the sight of touch (Blakemore et al., 2005), have also been found to score higher on an empathy scale that, too, assesses emotional responses to others' (affective) states (Banissy & Ward, 2007), indirectly linking the strength of neural mirror touch responses to individual differences in emotion-related trait empathy.

For the earlier P50 modulations (indexing vicarious SI activity), it was also found that their strength covaried with interindividual differences regarding emotional empathy-related personality traits, namely, again, *empathic concern* (see above) and *emotional reactivity*. Similar to the *empathic concern* subscale described above, the EQ's *emotional reactivity*

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[10] Interestingly enough, Wood et al. (2010) demonstrated that the sight of touch increases the inhibitory effect of somatosensory stimuli on the motor cortex (short-latency afferent inhibition effect (SAI); see chapter 1.2.1) which might explain the observed increase in reaction times when the colour change of the fixation cross coincided with seeing the target being touched. Apart from the fact that the response time difference in the present study was based on a very small number of catch trials, it should, however, also be noted that Wood et al. (2010)'s findings suggested a certain specificity of the inhibitory effect for the observed-to-be-touched body part. Given that present study involved the sight of touch on a hand while responses were made vocally rather than via e.g. a button press with a finger of the observed-to-be-touched hand, such a SAI-based explanation is thus highly speculative.

subscale also taps the self-reported tendency to react emotionally to others' states, with items such as "Seeing people cry does not really upset me". A moderate correlation between the two scales (see also Lawrence et al., 2004) suggested that both scales measure similar, yet distinct aspects of emotion-related empathy. What was however, unexpected, was the nature of the revealed relationship between individual differences in both empathy measures and the extent to which the P50 amplitude was found to be modulated: Surprisingly enough, it were the participants who scored *low* on both scales who showed the strongest P50 modulations. Most studies in which positive correlations between the strength with which shared neural networks are activated during the observations of other's actions, emotions and somatic sensations and the individuals' empathic dispositions are shown (e.g. Gazzola et al., 2006; Saarela et al., 2007; Schaefer et al., 2012; Singer et al., 2004) are fMRI studies in which neural activity in certain structures is lumped together over several seconds. It is thus conceivable that the high temporal resolution of EEG might thus have allowed to pick up on a possibly short-lived reversed relationship between the strength mirror touch responses and empathic skills in a very short and specific time window during somatosensory processing which might no longer be detectable when considering vicarious SI activity over a more extended time range. It is nevertheless unclear what mechanisms could bring about such a counterintuitive finding of a reduced SI responsiveness to observed touch for high empathy participants. This will be discussed in more detail in chapter 2.5. It should also be noted that this negative relationship was found based on the difference in P50 amplitude as a function of the observed tactile feedback, averaged across both touch targets, even though there was some indication that type of touch target did after all somewhat influence the touch observation-related modulation of somatosensory processing in this early latency range. The empathy-related correlations in the P50 latency range should thus be interpreted with some caution.

Conclusions

All in all, the results of the present ERP study suggest that SII (as indexed by a systematic modulation of the somatosensory N140 component) is vicariously activated by the sight of touch on a human body part but also on an inanimate object, suggesting, in line with previous fMRI evidence (Ebisch et al., 2008; Keysers et al., 2004), that SII represents a more "abstract notion of touch" (Ebisch et al., 2008; p. 1611). The fact that SII generally exhibits a less fine-grained somatotopic organisation than SI (Hari et al., 1993; Maeda, Kakigi, Hoshiyama, & Koyama, 1999) might render this area in the somatosensory cortex particularly suited to resonate with observed touch, irrespective of whether it occurs on somebody else's body or an inanimate object: Neurons in SII have rather large receptive fields, possibly allowing SII to convey a simulation of the experiential quality of the observed touch without representing the exact body location the observed touch was directed at (Keysers et al., 2010), which, in turn, might allow SII to also resonate with touch on a non-body object without a clear anatomical mapping to a specific body part of the observer. Touch observation-related vicarious SI activity (as indexed by a systematic modulation of the somatosensory P50 component) might, however, also have a tendency to respond to the sight of *any* form of touch but there are possibly indications that vicarious SI activity in response to the sight of touch on an object might somewhat depend on being able to relate the seen touch to a specific body location. Further research is, however, needed to clarify the latter in more detail. In addition, it was found that the electrophysiological correlates of mirror touch in both the P50 and the N140 latency range were linked to interindividual differences in *emotional* trait empathy, however, in a complex and partly unexpected fashion.

Experiment 2.2

Modulations in somatosensory processing as a function of observing touch on somebody else's body from an egocentric or an allocentric viewing perspective

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2.2.1 Introduction

An ever increasing body of evidence suggests that we map the passive touch we observe on others' bodies onto our own somatosensory system: In the absence of any actual tactile stimulation, observing somebody else being passively touched activates both primary and secondary somatosensory cortices just as if we were touched ourselves (e.g. Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012; Wood et al., 2010). What has barely been address so far in studies on touch observation-related somatosensory activations is, however, the role of the viewing perspective from which the touched body parts are observed. Most studies on mirror touch presented participants either exclusively with egocentric (Bufalari et al., 2007; Pihko et al., 2010; Schaefer et al., 2012; Wood et al., 2010) or allocentric (Ebisch et al., 2008; 2011) body images. Studies in which touch is observed to occur on other people's faces (Blakemore et al., 2005; Cardini et al., 2011; Serino, Giovagnoli, & Làdavas, 2009; Serino et al., 2008b) are inherently restricted to an allocentric viewing perspective. The perspective from which a presented body part is viewed is, however, crucial for how readily the seen limb can be attributed to one's own body. When it comes to the observing touch on somebody else's body, the vicarious mirror touch response on the onlooker's own somatosensory system during in an egocentric viewing perspective might thus be more influenced by (voluntary or involuntary) self-attribution processes (making the observed touch more "one's own touch" than somebody else's) than the vicarious mirror touch response during an allocentric viewing perspective.

To date, only two fMRI studies have investigated to what extent vicarious somatosensory activity might indeed be modulated by the viewing perspective: Findings by Keysers et al. (2004) indicated that activity in (left) SII significantly overlapped during the experience and observation of touch to the legs but did not differ as a function of whether the touch was observed from a ego- or an allocentric perspective. Showing hands instead of legs being touched, Schaefer et al. (2009) found visually-induced activations in both bilateral SII and contralateral SI, irrespective of the viewing perspective. A direct contrast of the two viewing perspectives, however, revealed significant activation differences *within* SI: Observing touch on a hand presented from an egocentric perspective lead to stronger activations in anterior parts of SI (BA 3a, 3b) while observing touch on a hand presented from an allocentric perspective triggered stronger responses in posterior parts of SI (BA 2). This points to SI as one of the crucial neural structures involved in discriminating whether observed touch is more likely to be related to one's own body or somebody else's, possibly in the context of a more general role in distinguishing whether a seen body part belongs to the self or somebody else (Saxe, Jamal, & Powell, 2006). The fact that Keysers et al. (2004) did not find such an differentiating effect of viewing perspective might be due to fact that their SI activation during touch observation was only an insignificant trend which was not followed up for perspective-related differences in the context of an region-of-interest analysis.

Taking advantage of the high temporal resolution of the EEG technique, the present study was designed to investigate whether also electrophysiological correlates of mirror touch might be sensitive to the viewing perspective from which touch on somebody else's body is observed and if so, which stages of somatosensory processing might be affected. Somatosensory-related ERPs were recorded in response to tactile stimulation of participants' index finger tip while they observed somebody else's index finger being touched or merely approached by a cotton bud. Crucially, the observed hand was presented in either a self-consistent first-person perspective or self-inconsistent third person perspective. In the context of Schaefer et al. (2009)'s findings, it was of particular interest whether somatosensory ERP components that index activity in SI (i.e. P50/N80) might show viewing perspective-related differentiations, were they to be found to be modulated by the sight of touch, and whether the use of EEG might possibly also allow to reveal differential effects of the viewing perspective for SII activity, as indexed by somatosensory-related ERP components such as the P100 and the N140. Different outcomes with respect to possible modulations of mirror touch responses as a function of the viewing perspective were conceivable: Mirror touch responses (as indexed by touch observation-related ERP amplitude modulations) might be more pronounced and/or occur earlier when the viewing perspective allows the observer to attribute the observed hand to their own body, since the observed tactile sensation might gain in relevance. Alternatively, if the putative tactile mirror system's function is to represent touch sensations of others, its response might be stronger and/or occur at earlier processing stages if the viewing perspective strongly suggests that the observed body part indeed belongs to somebody else. Especially later-stage mirror touch responses might, however, show no perspective-related modulations at all (Keysers et al., 2004; Schaefer et al., 2009).

2.2.2 Methods

Participants. 16 neurologically normal volunteers took part in the experiment (8 males and 8 females), aged between 20 and 33 years (mean age: 25.56 years; SD = 4.23 years).

Participants were naive as to the purpose of the experiment and gave informed consent to participate after a detailed explanation of the involved procedures. Two participants were left-handed and all had normal or corrected-to-normal vision by self-report. Participants were paid £ 7/h for their participation in the study. The procedures were approved by the local ethics committee.

Stimuli. The task-irrelevant visual stimuli consisted of a set of colour images showing a left hand in palmar view superimposed on a blue background, either presented from an egocentric or an allocentric perspective. The allocentric hand images were obtained by flipping the egocentric images first vertically and then horizontally. For each viewing perspective, a cotton bud was presented in three different positions (see Fig. 2.2.a): In a neutral starting position (neutral), in a position closer to the finger (approach) and in an end position in which the cotton bud either touched the hand on the index finger (touch) or merely the empty space next to it (no touch). By presenting a rapid sequence of these images in chronological order, the impression was created that the cotton bud approached the hand, briefly either touched the index finger or the empty space next to it, then retracted and resumed its neutral starting position. Like in Exp. 2.1, the images deliberately did not depict a human agent holding and moving the cotton bud since the mere observation of somebody else's actions in itself might already modulate activity not only in motor, but also in somatosensory brain areas (Avenanti et al., 2007; Avikainen et al., 2002; Rossi et al., 2002). The perceived speed of the observed cotton bud movements was the same while movement trajectory and angle were kept as comparable as possible across all observational conditions.

The hand images "subtended" approximately 8.1° x 11.5° of visual angle and were presented on a black background.

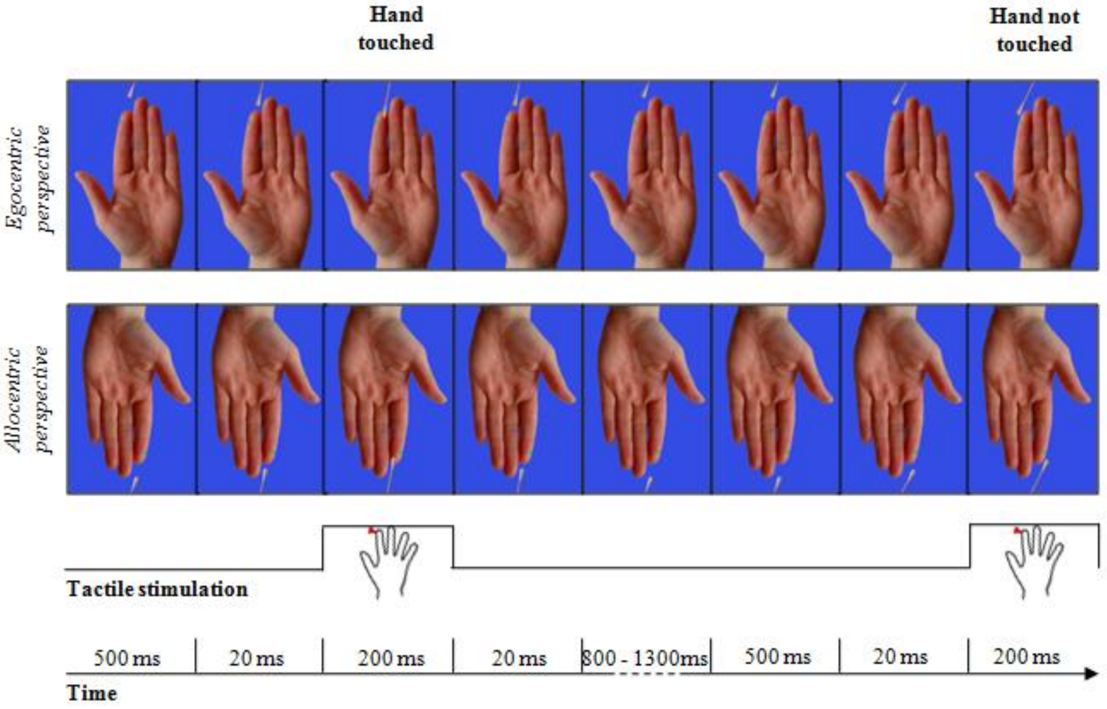


Fig. 2.2.a. Schematic representation of the typical sequence of visual and tactile events in *touch* and *no touch* trials, respectively. Tactile stimuli were presented to participants' left index finger tip. Viewing perspective was manipulated block-wise for four consecutive blocks each. On infrequent catch trials, a brief colour change of the cotton bud's tip (not shown here) required a vocal response.

On approximately 14 % of the trials, the colour of the tip of the cotton bud (rather than the fixation dot, see Exp. 2.1) briefly changed from white to purple and participants were instructed to report each colour change by saying "pa!" as quickly as possible. This task was to ensure that participants paid close attention to the visual display. To avoid contamination of the ERP with eye movement artifacts, participants were to continuously fixate on a green fixation dot superimposed on the index finger of the viewed hand, approximately equidistant from the end positions of the cotton bud in the *touch* and *no touch* condition, respectively. Vocal responses were recorded with a free-standing microphone.

Task-irrelevant tactile stimuli were presented for 200 ms to participants' left index finger tip with the same stimulator described in Exp. 2.1., attached to participants' left index finger tip with adhesive tape.

Procedure. The experimental procedure was very similar to the one in Exp. 2.1. Participants sat in a dimly lit sound-attenuated experimental chamber resting both arms on a table in front of them, such that their hands were in a similar position to the observed hand, i.e. with the palms facing up. A wooden panel ensured that participants could not see their hands. The visual stimuli were presented on a computer screen located approximately 75 cm in front of the participants using E-Prime, Version 1.1. To mask any sounds made by the tactile stimulator, continuous white noise (65 dB SPL) was played through loudspeakers positioned to the right and left of the computer monitor.

Participants were instructed to fixate on the green fixation dot and to respond vocally by saying “pa!” as quickly as possible whenever the tip of the cotton bud briefly changed its colour to purple. They were instructed to entirely focus on this task and to ignore the presented hand as well as the tactile stimuli to their finger tip.

The trajectory of the cotton bud was manipulated on a trial-by-trial basis within each block. Each experimental block consisted of 58 trials presented in random order. On 25 trials each, the cotton bud touched the index finger or the empty space next to it, respectively. In 8 trials of each block, the movement of the cotton bud towards the hand was accompanied by a colour change of the tip of the cotton bud and a vocal response was required (catch trials; approx. 14 % of trials). Participants performed three blocks for each viewing perspective, with the order of viewing perspective being counterbalanced across participants (egocentric – allocentric vs. allocentric – egocentric). The experiment thus comprised 2 x 3 blocks, i.e. 6 experimental blocks in total.

Each trial started with a presentation of a hand image with the cotton bud in a neutral position for 500 ms which was followed by a brief 20 ms presentation of an image showing the cotton bud halfway between its initial and its final position on or next to the finger, which was subsequently shown for a total of 200 ms. The onset of this latter, critical stimulus image was aligned with the presentation of a tactile stimulus for 200 ms. To create the impression of a smooth backwards movement, the cotton bud was then once more shown in its slightly retracted position for 20 ms and finally for a variable duration between 800 and 1300 ms back in its neutral starting position to complete the trial. In order to avoid any contamination of ERPs with response-related artifacts, the duration of the image of the cotton bud back in its neutral position at the end of each trial was prolonged by 500 ms for all trials in which a correct or incorrect (false alarm) vocal response occurred.

Participants were encouraged to take breaks to relax and move between the blocks to counteract tiredness and the associated increase in ERP contaminating alpha waves.

To demonstrate the tactile feedback associated with being touched in the observed way, the experimenter showed the participants a short presentation of the involved visual stimuli from both viewing perspectives and then gently touched the participants’ own index finger tip twice with a cotton bud prior to the experiment. Subsequently, participants performed a short practice block (equivalent to an experimental block except for a reduced number of trials (25 trials including 5 catch trials)) to familiarise them with the colour change detection task at hand.

At the end of the experiment, participants were asked to complete the 60-item *Empathy Quotient* (EQ) questionnaire (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) as well as the 28-item *Interpersonal Reactivity Index* (IRI) by Davis (1983).

Recording and data. The procedures for recording the continuous EEG and pre-processing the obtained EEG data was the same as for Exp. 2.1, with the exception that only the vertical electrooculogram (VEOG) was recorded using an electrode below and above the right eye to detect vertical eye movements. The EEG data were again analyzed using Brain Vision Analyzer software (version 1.05; Brain Products GmBH, Gilching, Germany). EEG and VEOG were segmented off-line into 500 ms epochs starting 100 ms before the onset of the tactile stimulus until 400 ms thereafter, epoched separately for all four combinations of observed movement trajectory (touch vs. no touch) and viewing perspective (egocentric vs. allocentric). The artifact rejection criteria for the removal of trials with vertical eye movements, eye blinks or other artifacts were the same as in Exp. 2.1. Trials in which a (correct or incorrect) vocal response occurred were again excluded. For the remaining trials, ERPs for tactile stimuli were averaged relative to a 100 ms pre-stimulus baseline for all four combinations of observed movement trajectory and viewing perspective.

Data analysis. Statistical analyses were based on the same electrode clusters as in Exp. 2.1. ERP mean amplitudes were computed for successive latency windows centred on the peak amplitudes of early somatosensory ERP components typically observed in response to tactile stimulation: P50 (40-65 ms post- stimulus onset), N80 (65-85 ms post-stimulus onset), P100 (85-105 ms post-stimulus onset) and N140 (120-160 ms post-stimulus onset). The choice of the time epochs was based on visual inspection of the grand average ERP components elicited by tactile stimuli averaged across all four experimental conditions over contralateral somatosensory cortex at C4, Cp2 and Cp6 where SEPs in response to tactile stimuli to the hand are usually clearest.

To investigate whether the observation of a passive touch sensation on somebody else's hand modulates somatosensory processing of a concurrently delivered tactile stimulus and whether any such modulation might be influenced by the viewing perspective, 5-way repeated measures ANOVAs with the within-subject factors *hemisphere* (ipsilateral vs. contralateral), *anterior-posterior* (anterior vs. posterior), *viewing perspective* (egocentric vs. allocentric), *observed tactile feedback* (touch vs. no touch) and *electrode site* were conducted on the mean ERP amplitudes for a given latency window. Follow-up analyses of significant interactions involving the factors of interest were conducted in the same way as described in Exp. 2.1. Greenhouse-Geisser adjustments to obtained p-values were applied where appropriate. An alpha level of .05 was used for all ANOVAs.

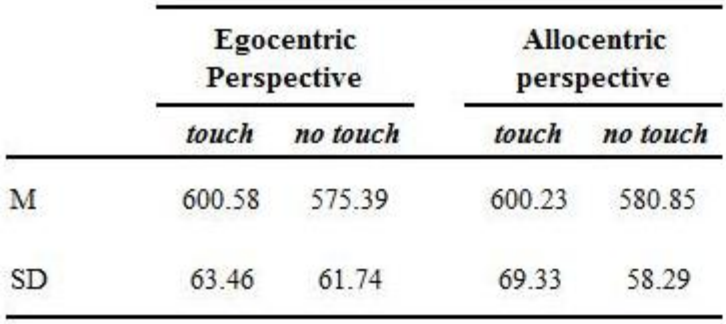
Again, an index of the strength of the revealed SEP modulations was computed as the difference between the mean ERP amplitudes for the two touch-related observation conditions for any time window and electrode cluster for which a significant touch observation-induced SEP modulations was found and correlated with the *Empathy Quotient* (EQ) and its three subscales (*cognitive empathy*, *emotional reactivity*, *social skills*; Baron-Cohen & Wheelwright, 2004; Lawrence et al. 2004) as well with the *perspective-taking*, *empathic concern*, *personal distress* and *fantasy* scales of the *Interpersonal Reactivity Index* (IRI; Davis, 1983) using Spearman’s correlation coefficients.

2.2.3 Results

Behavioural performance

Participants correctly detected 98.5 % of the infrequent colour changes of the fixation dot with only very few false alarms (< 1%), indicating that close attention was paid to the visual display. Table 2.2.a summarises the response times for this task for the four different observational conditions. Similar to Experiment 2.1, participants were somewhat slower in detecting a colour change when the cotton bud was simultaneously seen to touch the hand rather than merely the empty space next to it (F(1,15) = 26.838, p < .001, η^2_p = .641), irrespective of the viewing perspective (F(1,15) = .135, p = .719, η^2_p = .009). Response times did not vary as a function of the viewing perspective per se (F(1,15) = .135, p = .719, η^2_p = .018).

Table 2.2.a. Means and standard deviations of response times in colour change detection task (in ms) as a function of *observed tactile feedback* and *viewing perspective.*



	Egocentric Perspective		Allocentric perspective	
	touch	*no touch*	*touch*	*no touch*
M	600.58	575.39	600.23	580.85
SD	63.46	61.74	69.33	58.29

Electrophysiological data

The effects of the sight of touch on somatosensory processing

Whether observing somebody else’s hand being touched modulates somatosensory processing and if so, whether the perspective from which the model’s hand is viewed plays a role, was determined by comparing ERPs obtained when task-irrelevant tactile stimuli were accompanied by seeing a cotton bud either touch the index finger tip of a left hand or merely the empty space next to it while the hand as such was presented either from an egocentric, first-person perspective or an allocentric, third-person perspective. Figures 2.2.b and 2.2.c contrast the obtained SEP waveforms for the two types of observed tactile feedback for all analysed anterior (b) and posterior (c) electrode sites, separately for the two different viewing perspectives. A visual inspection of posterior electrode sites contralateral to the stimulated hand (see Fig. 2.2.b) where somatosensory components are usually clearest showed a pronounced somatosensory P50 and N140 component while the somatosensory N80 and P100 were identifiable but had rather small amplitudes (see, for instance, C4 in Fig. 2.2.c).

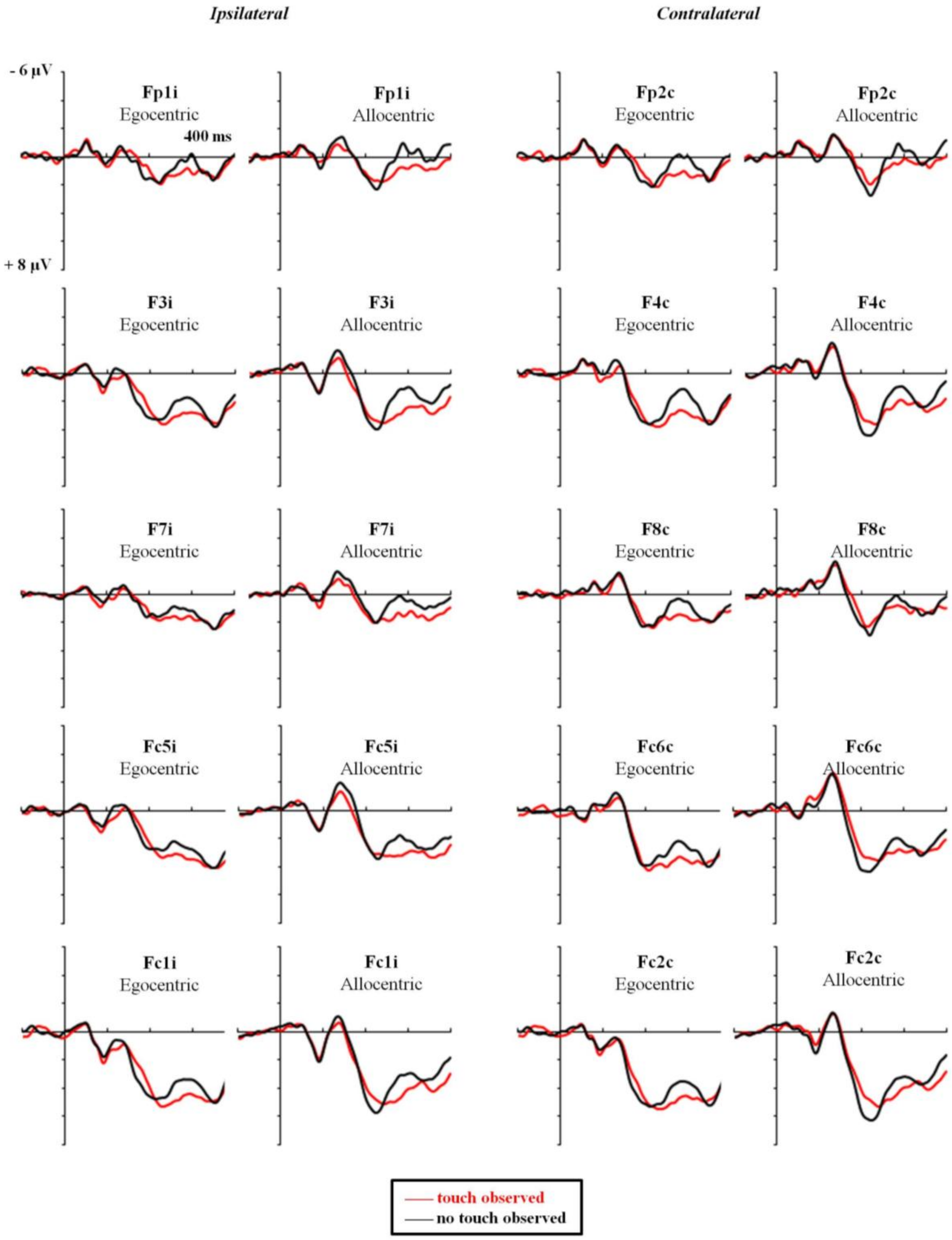


Fig. 2.2.b. Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the left index finger tip during the observation of touch (red) or no touch on somebody else’s hand from either an egocentric or an allocentric viewing perspective. Shown are all anterior electrode sites included in the statistical analysis.

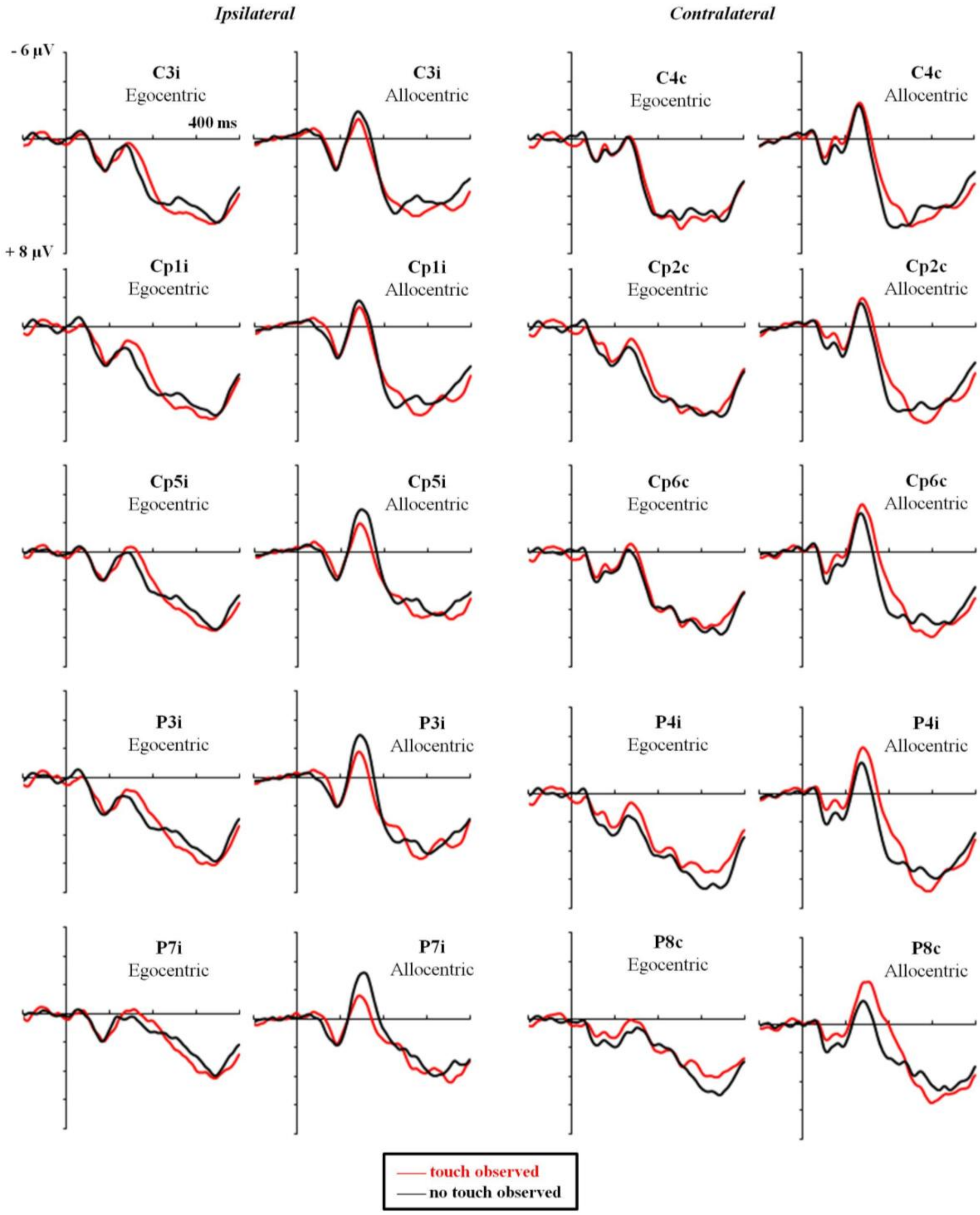


Fig. 2.2.c. Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the left index finger tip during the observation of touch (red) or no touch on somebody else's hand from either an egocentric or an allocentric viewing perspective. Shown are all posterior electrode sites included in the statistical analysis.

No modulations of mean SEP amplitude as a function of whether the cotton bud was observed to touch the hand or merely the empty space next to it where found for the P50 and P100 components, neither in the form of a main effect nor in the form of any interaction effects with the factors *hemisphere, anterior-posterior* and/or *viewing perspective* (post hoc analyses following up the significant *hemisphere* by *observed tactile feedback*-interaction for the P100 were not significant; all other $F(1,15) < 3.707$, $p > .073$, $\eta^2_p < .198$).

For both the N80 and N140 component, however, the sight of touch on somebody else's hand did alter the mean amplitude of the corresponding component. For the N80 component, a significant *anterior-posterior* by *observed tactile feedback*-interaction ($F(1,15) = 6.293$, $p = .024$) was found, with post hoc analyses based on two separate *hemisphere* (2) by *viewing perspective* (2) by *observed tactile feedback* (2) by *electrode site* (5)-*ANOVAs* for the anterior and posterior electrode cluster suggesting that the N80 mean amplitude was significantly more negative-going when observing the hand being touched rather than merely approached at posterior electrodes ($F(1,15) = 6.369$, $p = .023$, $\eta^2_p = .298$) but not at anterior ones ($F(1,15) = .050$, $p = .827$, $\eta^2_p =.003$). Whether the hand was seen from an egocentric or an allocentric perspective did not modulate the effect of observing touch (all $F(1,15) \leq .718$, $p \geq .410$, $\eta^2_p \leq .046$).

For the N140 component, following-up a significant *hemisphere* by *anterior-posterior* by *observed tactile feedback*-interaction ($F(1,15) = 15.006$, $p = .001$, $\eta^2_p = .500$) with separate 3-way ANOVAs (*viewing perspective* (2) by *observed tactile feedback* (2) by *electrode site* (5)) for the four different electrode clusters indicated that the mean amplitude of this component was more negative-going when observing the cotton actually touch the hand rather than merely approach it, but only at the cluster of posterior electrodes over the hemisphere contralateral to the tactually stimulated hand ($F(1,15) = 7.914$, $p = .013$, $\eta^2_p = .345$; for the three remaining clusters, all $F(1,15) \leq .964$, $p \geq .342$, $\eta^2_p \leq .060$). Fig. 2.2.d shows the revealed viewing perspective-independent N80 and N140 modulations as a function of the observed tactile feedback at a representative contralateral-posterior electrode (Cp6), along with the scalp topography of the associated difference in SEP amplitude in the N80 and N140, respectively, time epoch.

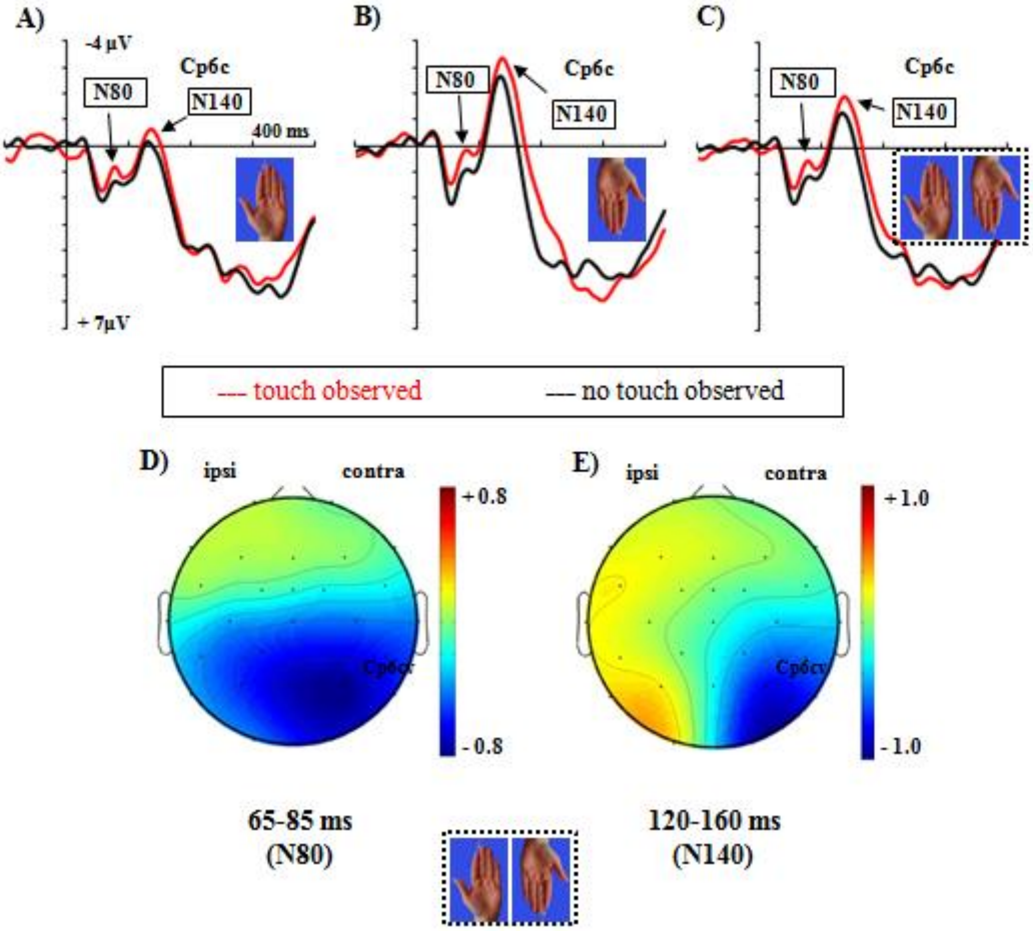


Fig. 2.2.d. ***A-C)*** Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the hand during the observation of touch (red) or no touch (black) on somebody else's hand from either an egocentric **(A)** or an allocentric viewing perspective **(B)** and collapsed across both viewing perspectives **(C)**, at a representative electrode (Cp6c). ***D-E)*** Topographic distribution of the difference in mean SEP amplitude between the two types of observed tactile feedback (mean amplitude$_{touch}$ – mean amplitude$_{notouch}$), collapsed across the two viewing perspectives, in the N80 **(D)** and N140 **(E)** latency range. Note that a negative difference indicates for both the N80 and the N140 an increased amplitude during the sight of touch.

Importantly, there was, however, also a significant 4-way interaction between *hemisphere*, *anterior-posterior*, *viewing perspective* and *observed touch* in the N140 time epoch which, when followed-up with separate 2-way ANOVAs (*observed tactile feedback* (2) by *electrode site* (5)) for the four different electrode clusters and the two viewing perspectives, revealed an interesting pattern of results for the effect of the sight of touch as a function of the two different perspectives: First of all, when considering the touch observation-induced enhancement of the N140 component at the contralateral-posterior electrode cluster described above separately for the egocentric perspective only, it was no longer consistent enough to be significant ($F(1,15) = 1.433$, $p = .250$, $\eta^2_p = .087$). For the allocentric perspective, on the other hand, the increase in the negativity of the N140 mean amplitude was still marginally significant (F(1,15) = 4.491, p = .051, $\eta^2_p = .230$).

At the same time, however, the sight of touch from an allocentric perspective also induced a N140 modulation over the posterior electrode cluster over the ipsilateral hemisphere. Crucially, this effect was reversed in that the mean N140 amplitude was less rather than more negative-going when observing the hand being touched rather being merely approached (F(1,15) = 5.030, p = .040, $\eta^2_p = .251$). Fig. 2.2.e contrasts the ERP waveforms for the observation of touch rather than non-touch on the hand as seen from an allocentric viewing perspective at two representative posterior-ipsilateral (panel A) and posterior-contralateral electrodes (panel B).

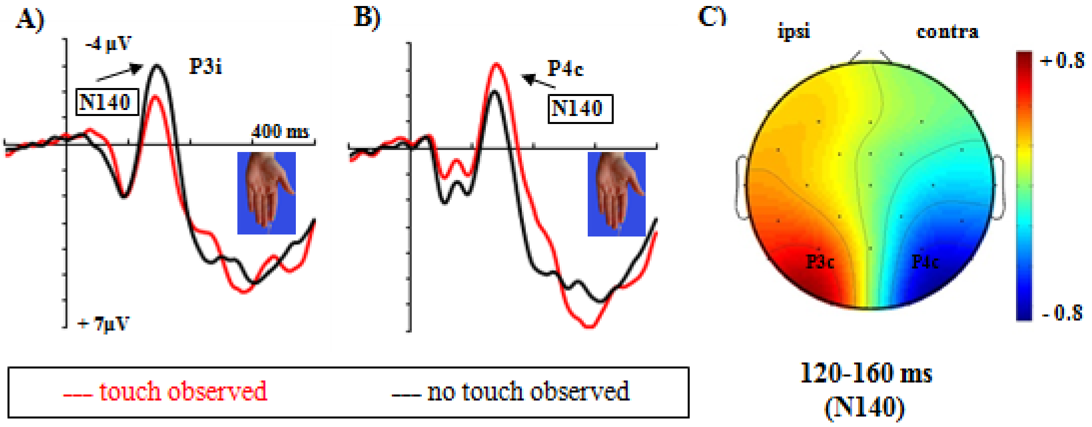


Fig. 2.2.e. ***A-B)*** Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the hand during the observation of touch (red) or no touch (black) on somebody else's hand from an allocentric viewing perspective, at an representative electrode **(A)** ipsilateral (P3i) and **(B)** contralateral (P4c) to the stimulated hand. **(C)** Topographic distribution of the difference in mean SEP amplitude between the two types of observed tactile feedback for an allocentric viewing perspective at the N140 latency range. Note that a positive difference indicates an increased N140 amplitude while a negative difference reflects a decreased N140 amplitude for the sight of touch.

All in all, the sight of passive touch on somebody else's hand seemed to affect the N140 component similarly for both viewing perspectives in that observing touch on the hand rather than no touch resulted in a more negative-going N140 amplitude over contralateral-posterior electrode sites. However, when analysed separately in the context of following up a complex 4-way interaction involving *hemisphere*, *anterior-posterior*, *viewing perspective* and the *observed tactile feedback*, only the sight of touch from an allocentric perspective rendered this modulation marginally significant. In addition, the sight of touch from an allocentric perspective also systematically altered the N140 amplitude at posterior electrodes over the ipsilateral hemisphere, however, in a reversed manner as when compared to the corresponding electrode cluster over the contralateral hemisphere, i.e. the N140 amplitude was less negative-going for the observation of touch on the hand.

The effects of viewing perspective on somatosensory processing

In addition to the touch observation-related SEP modulations for the N80 and N140 components, the viewing perspective in itself seemed to affect somatosensory processing rather profoundly across all four analysed SEP components, irrespective of the type of observed tactile feedback. Fig. 2.2.f compares the SEP waveforms elicited by the task-irrelevant tactile stimuli to the left index finger tip for the sight of somebody else’s hand from an egocentric and from an allocentric perspective.

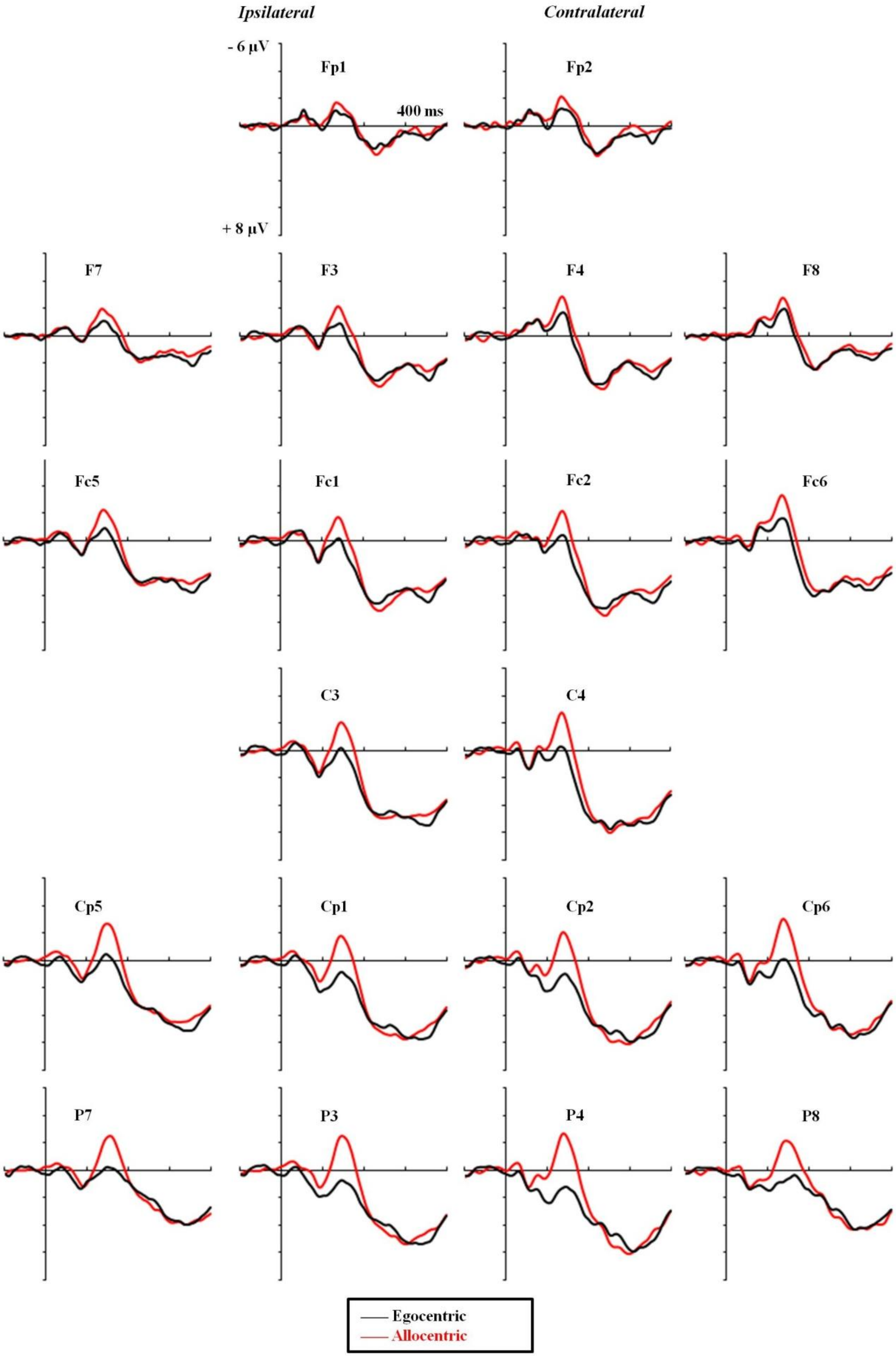


Fig. 2.2.f. Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the left index finger tip as a function of the viewing perspective (egocentric vs. allocentric) at all analysed electrode sites.

For the somatosensory P50, N80 and P100 components, the viewing perspective-dependent SEP modulations were mostly confined to the posterior-occipital electrode sites over the ipsilateral and/or contralateral hemisphere while the N140 effect was more wide-spread: During the early time window of 40-65 ms after tactile stimulus onset (P50 component), following-up a significant *hemisphere* by *anterior-posterior* by *viewing perspective* – interaction ($F(1,15) = 17.757$, $p = .001$, $\eta^2_p = .542$) with separate 3-way ANOVAs (based on the factors *viewing perspective*, *observed tactile feedback* and *electrode site*) for the four different electrode clusters indicated that the mean amplitude in this time epoch was significantly less positive-going when seeing the hand from an allocentric perspective as compared to seeing it from an egocentric perspective, however only at the posterior electrode cluster over the ipsilateral hemisphere ($F(1,15) = 10.209$, $p = .006$, $\eta^2_p = .405$; for the three remaining clusters all $F(1,15) \leq .741$, $p \geq .403$, $\eta^2_p \leq .047$). For the subsequent somatosensory N80 component, follow-up analyses for a significant *anterior-posterior* by *viewing perspective*-interaction ($F(1,15) = 23.687$, $p < .001$, $\eta^2_p = 0.612$) based on two separate 4-way ANOVAs (*hemisphere* (2) by *viewing perspective* (2) by *observed tactile feedback* (2) by *electrode site* (5)) for the anterior and posterior electrodes separately suggested that an allocentric viewing perspective resulted in an enhanced N80 mean amplitude as compared to an egocentric viewing perspective for posterior electrode sites ($F(1,15) = 7.502$, $p = .015$, $\eta^2_p = .333$) but not for anterior ones ($F(1,15) = .501$, $p = .490$, $\eta^2_p = .032$). A significant *hemisphere* by *viewing perspective* -interaction ($F(1,15) = 6.385$, $p = .023$, $\eta^2_p = 0.299$), on the other hand, was found for the somatosensory P100 component: A significant effect of the viewing perspective could only be found over the hemisphere contralateral ($F(1,15) = 8.051$, $p = .012$, $\eta^2_p = .349$) but not ipsilateral $F(1,15) = .693$, $p = .418$, $\eta^2_p = .044$) to the stimulated hand when following up the revealed interaction with separate *anterior-posterior* (2) by *viewing perspective* (2) by *observed tactile feedback* (2) by *electrode site* (5)-ANOVAs for the two hemispheres.. While there was no significant *hemisphere* by *anterior-posterior* by *viewing perspective*-interaction ($F(1,15) = 2.420$, $p = .141$, $\eta^2_p = .139$), the just significant *anterior-posterior* by *viewing perspective*-interaction ($F(1,15) = 4.594$, $p = .049$, $\eta^2_p = 0.234$) indicated that the P100 modulations were more reliable over posterior ($F(1,15) = 5.481$, $p = .033$, $\eta^2_p = .268$) rather than anterior electrode sites ($F(1,15) = 1.389$, $p = .257$, $\eta^2_p = .085$). For the somatosensory N140 component, the viewing perspective had the most wide-spread effect on the SEP mean amplitude as indicated by a highly significant main effect ($F(1,15) = 54.679$, $p < .001$, $\eta^2_p = .785$). Following-up an also significant *anterior-posterior* by *viewing perspective*-interaction ($F(1,15) = 24.413$, $p < .001$, $\eta^2_p = .619$) with separate 4-way ANOVAs (see N80 analysis above) confirmed that N140 mean amplitude was significantly increased during the sight of a hand in an allocentric rather than an egocentric perspective for both posterior ($F(1,15) = 59.154$, $p < .001$) and anterior ($F(1,15) = 25.801$, $p < .001$) with the effect being, however, more pronounced posteriorly ($\eta^2_p = .798$ and $\eta^2_p = .632$, respectively). Fig. 2.2.g depicts the perspective-related differences in the somatosensory ERP waveforms at two representative parietal electrodes (P3i/P4c), along with the topographic distribution of the corresponding difference in SEP mean amplitude in all four analysed time epochs.

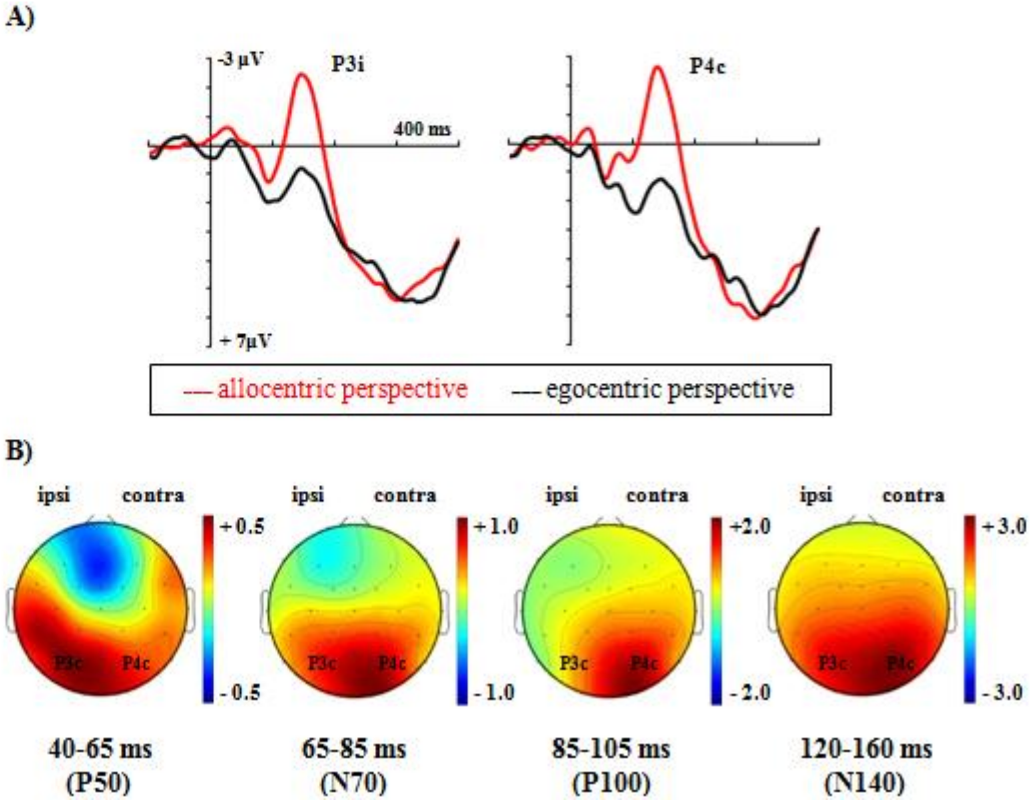
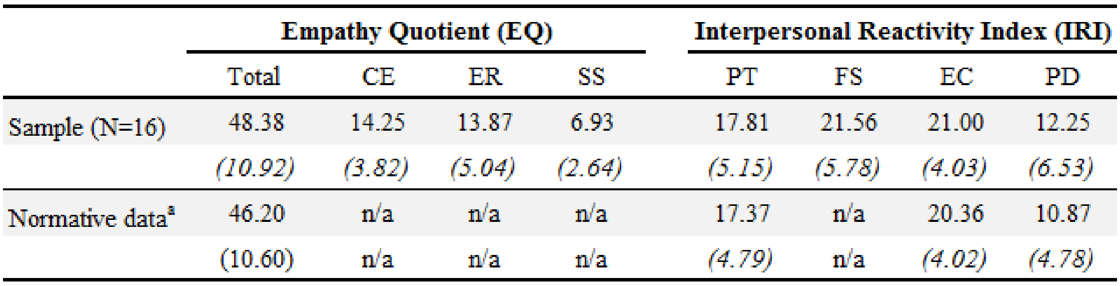


Fig. 2.2.g. A) Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the left index finger as a function of the viewing perspective (egocentric vs. allocentric), at two representative parietal electrodes (P3i/P4c). **B)** Topographic distribution of the difference in mean SEP amplitude between the two viewing perspectives (mean amplitude$_{\text{Egocentric}}$ – mean amplitude$_{\text{Allocentric}}$), collapsed across the two types of observed tactile feedback. Note that a positive difference indicates a decreased amplitude for the P50 and P100 components during an allocentric viewing perspective while a it reflects an increased amplitude for the N80 and N140 components.

Empathy correlations

Table 2.2.b summarises the obtained trait empathy-related measures for the present sample of participants which were quite similar to the available normative data. Note that correlation analyses to investigate possible links between individual empathic skills and the strength of touch observation-induced SEP modulations were again restricted to those components and electrode clusters for which significant SEP modulations were found and reported only if correlations were found at least three electrodes within a given electrode cluster.

Table 2.2.b. Mean scores and standard deviations for the self-report measures of dispositional empathy.



	Empathy Quotient (EQ)				Interpersonal Reactivity Index (IRI)			
	Total	CE	ER	SS	PT	FS	EC	PD
Sample (N=16)	48.38	14.25	13.87	6.93	17.81	21.56	21.00	12.25
	(10.92)	*(3.82)*	*(5.04)*	*(2.64)*	*(5.15)*	*(5.78)*	*(4.03)*	*(6.53)*
Normative data[a]	46.20	n/a	n/a	n/a	17.37	n/a	20.36	10.87
	(10.60)	n/a	n/a	n/a	*(4.79)*	n/a	*(4.02)*	*(4.78)*

[a)] Normative data are derived from: Lawrence et al., 2004 (EQ) and Bellini et al. (2002) (IRI).

EQ: CE = Cognitive Empathy ER = Emotional reactivity SS = Social skills

IRI: PT = Perspective taking FS = Fantasy scale EC = Empathic concern PD = Personal distress

Maximal scores: Total score of EQ = 80; Cognitive empathy (EQ) = 22, Emotional reactivity (EQ) = 22, Social skills (EQ) = 12; each subscale of the IRI = 28.

Only for the touch observation-induced N140 modulations for the allocentric viewing perspective, systematic correlations between the strength of these modulations and individual trait empathy measures could be found (all $p > .05$ for the N80 and N140 modulations found “across perspectives”). At all five electrode sites within the contralateral-posterior electrode cluster identified to show a (marginally) significant touch observation-induced increase of the N140 mean amplitude when touch was seen from an allocentric perspective, the strength of this modulation correlated significantly with the scores on the *empathic concern* scale of the IRI (C4: $r_s(16) = -.521$; Cp2: $r_s(16) = -.598$; Cp6: $r_s(16) = -.644$; P4: $r_s(16) = -.675$; P8: $r_s(16) = -.629$; all $p \leq .05$). Several of the most posterior electrode sites within this cluster also showed significant correlations with the *social skills* subscale of the EQ (Cp2: $r_s(16) = -.502$; Cp6: $r_s(16) = -.596$; P4: $r_s(16) = -.653$; P8: $r_s(16) = -.665$; all $p \leq .05$) as well as with the total score of the EQ (Cp6: $r_s(16) = -.550$; P4: $r_s(16) = -.562$; P8: $r_s(16) = -.571$; all $p \leq .05$). For all three measures of self-reported dispositional empathy, higher scores were associated with a more pronounced N140 modulation for observed touch seen from an allocentric perspective (see Fig. 2.2.h). Both the EQ’s *social skills* subscale and the total score of the EQ correlated positively with the IRI’s *empathic concern* scale ($r_s(16) = .842$ and $r_s(16) = .701$, respectively; $p \leq .002$).

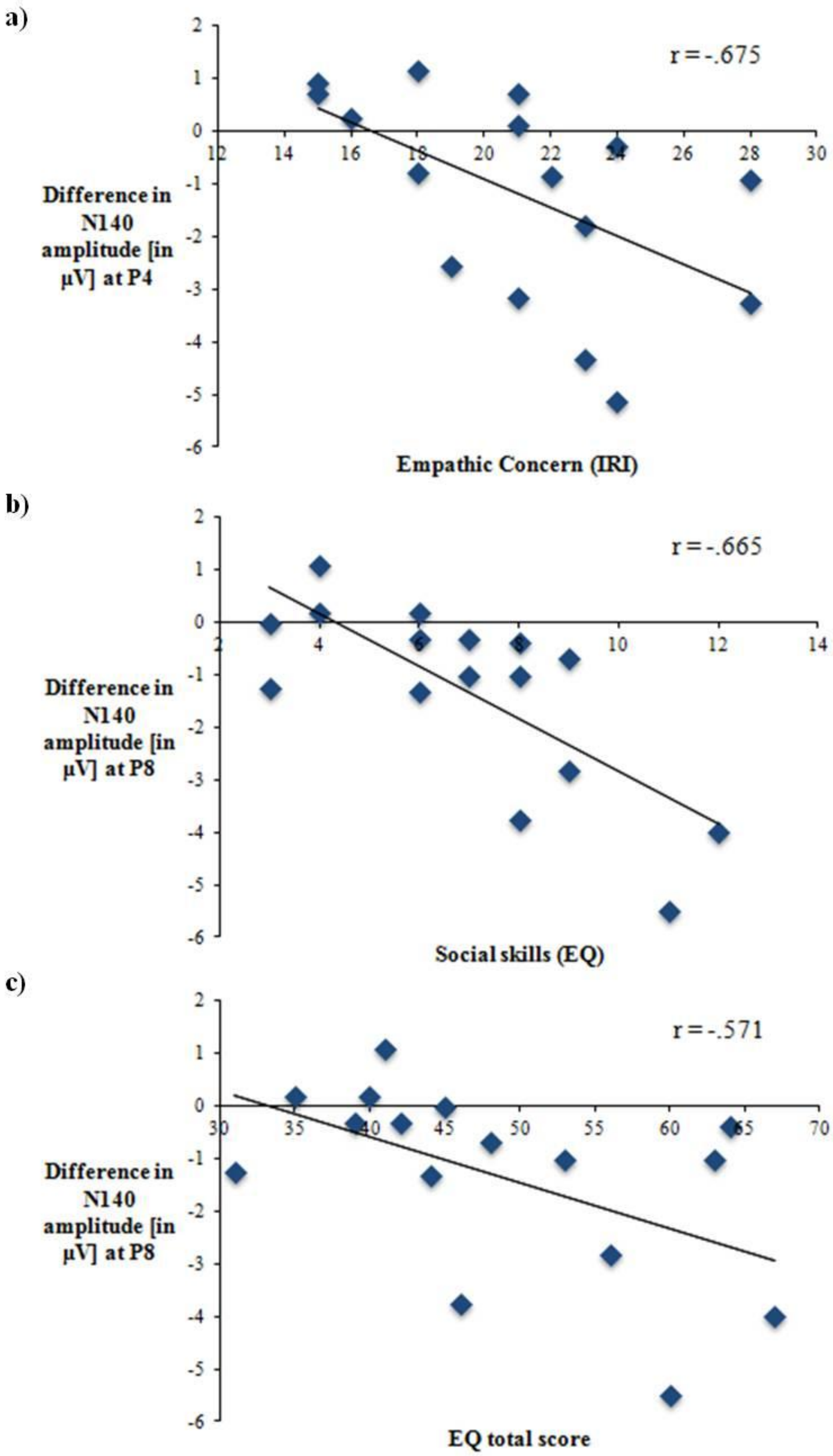


Fig. 2.2.h. Difference in N140 mean amplitude between the two types of observed tactile feedback during an allocentric viewing perspective, as a function of different measures of individuals' trait empathy **(a-c).**

2.2.4 Discussion

The present study aimed to investigate whether the sight of somebody else's body being touched rather than merely approached modulates concurrent somatosensory processing in the observer differently as a function of the viewing perspective from which somebody else's hand is observed. Participants were presented with tactile stimuli to their index finger tip while they observed a cotton bud either touch a hand or merely the empty space next to it. Importantly, the viewed hand was seen from either an egocentric or an allocentric perspective.

Unexpectedly, seeing somebody else's hand from an allocentric rather than an egocentric perspective, regardless of whether the sight of touch was involved or not, was found to have in itself a quite substantial effect on somatosensory processing of the tactile stimuli presented to the observer's own hand. These unforeseen and strong viewing perspective-related ERP modulations will be elaborated first, followed by the discussion of the touch observation-related modulations which were, in turn, contingent on the viewing perspective, at least during later-stage somatosensory processing.

The effects of viewing perspective on somatosensory processing

The ERP mean amplitudes in all four analysed latency windows were found to be significantly modulated by the viewing perspective as such. For the early- and mid-latency components (P50/N80 and P100, respectively), the revealed ERP modulations were restricted primarily to the posterior electrode clusters, starting as a small effect over the ipsilateral-posterior electrode cluster for the P50, followed by posterior modulations over both hemispheres for the N80 and a contralaterally located P100 modulation (again with a tendency for more reliable modulation at contralateral-posterior electrode sites). The late-latency N140 component, finally, showed the most wide-spread effect of the viewing perspective: A strong amplitude difference over the posterior electrode clusters that also reached anterior recording sites where it appeared, however, much smaller. With the exception of the early-latency P50, the revealed ERP difference in fact tended to be maximal over the (right) *occipital* scalp region and thus over and close to the (right) visual cortex. Given that the visual stimuli in this study involved a human hand, it is very likely that the visual stimuli in all experimental conditions triggered activity in the extrastriate body area (EBA), a subregion of the visual cortex selectively involved in the visual processing of images of human bodies and body parts (Downing, Jiang, Shuman, & Kanwisher, 2001). Crucially, the *right* EBA has been found to respond more strongly to the sight of body parts from an allocentric perspective (Chan, Peelen, & Downing, 2004; Saxe et al., 2006) rather than an egocentric perspective and the viewing perspective-dependent differential response in the right EBA might have modulated somatosensory processing. Not only the sight of one's own body (Haggard, Christakou, & Serino, 2007; Kennett et al., 2001; Longo et al., 2011; Taylor-Clarke et al., 2002; Tipper et al., 1998) but also of somebody else's body (Haggard, 2006) has been shown to modulate somatosensory processing and the described body-selectivity of the EBA points to this cortical area as an area that might provide the necessary body-related visual input to the somatosensory cortices, possibly via connections to multimodal areas in the posterior parietal cortex (David et al., 2007). Interestingly, Saxe et al. (2006) found that while the sight of body parts from an allocentric rather than an egocentric perspective was associated with an increase in activity in the right EBA, concurrent activity in the left SI was suppressed. While co-activation does not necessarily imply causality and with the exact functional connectivity being unclear, it is nevertheless conceivable that the strong activation in the EBA in response to the sight of an allocentrically presented body part resulted in an inhibited somatosensory response to a body part for which the viewing perspective suggests that it cannot be part of the onlooker's own body (note that neural subpopulations in the right EBA respond differentially to images of one's own body and of other people's bodies, irrespective of the view point (Myers & Sowden, 2008)).

Alternatively, it could be argued that the revealed ERP modulations as a function of whether the presented hand was shown from an egocentric or an allocentric perspective were associated with participants' tendency to spontaneously mentally rotate the inverted hand images into an upright position to maybe align it with the orientation of their own hand. Given that there was no instruction whatsoever to mentally rotate the task-irrelevant hand images and given that the viewing perspective was manipulated block-wise and not on a trial-by-trial basis, this does, however, not seem very plausible. There was also no task performance-related incentive for mentally rotating the hand images. It also appears unlikely that the slightly different spatial locations of the fixation dot participants were instructed to fixate on throughout the experiment, had a systematic enough effect on somatosensory processing: Due to the fact that the hand images used in the allocentric conditions were merely inverted and flipped versions of the hand images used in the egocentric condition, the fixation dot was located in the upper half of the hand image in the egocentric condition and in the lower half the hand image in the allocentric condition (see also Schaefer et al. (2009)'s stimulus material), with the latter resulting in an attentional focus slightly closer to the participants' tactually stimulated hand positioned below the monitor. Given that the monitor used to present the visual stimuli was positioned outside of the immediate peripersonal space of the participants, it seems, however, unlikely that this shift in spatial attention might have had an effect on somatosensory processing. Overall, the distinct occipital maximum of the viewing perspective-related ERP modulations for most of the analysed ERP components along with its right lateralisation points to the perspective-dependent differential response in the right EBA as the most likely explanation for the observed modulations in the somatosensory-related brain response for the upright and inverted hand images, assuming the EBA might play a role in relaying body-related visual input to the somatosensory areas (see David et al., 2007). It should, however, been borne in mind that spatial resolution of the EEG technique is rather poor so that a recorded difference in brain activity does not necessarily arise from the neural structures underlying the recording sites where this difference is found to be largest. The discussed possible role of the (right) EBA is thus rather speculative.

All in all, the sight of somebody else’s hand from an allocentric perspective modulated ongoing somatosensory activity differently as compared to the sight of the same hand from an egocentric perspective. Note that the viewing perspective of the presented hand was manipulated by simply inverting (and flipping) the respective egocentric hand images. At least for faces and (whole) bodies, inversion has previously not only been found to interfere with their recognition (face/body inversion effect; e.g. Reed, Stone, Bozova, & Tanaka, 2003) but also to affect ERPs: Visual-evoked potentials (VEPs) showed an enhanced and delayed N170 component in response to inverted as compared to upright images of faces and (whole) bodies (Rossion et al., 2000; Stekelenburg & Gelder, 2004). While it is unclear to what extent also isolated body parts such as hands might be affected by such an inversion effect, it is important to note that the recorded ERPs in the present study reflect primarily the electrical brain response to the presented tactile stimuli. The ERPs were time-logged to the sudden onset of the presented tactile stimuli (in contrast to the visual stimulation which was continuous) and were thus SEPs rather than VEPs. Since the inversion-/viewing perspective-related ERP modulations are thus assumed to index changes in somatosensory processing (brought about cross-modally by body-related visual input) rather than visual processing per se, the present study thus suggests that the sight of inverted rather than upright body part images might not only modulate visual but also somatosensory processing

The effects of the sight of touch on somatosensory processing

The sight of touch was found to significantly modulate somatosensory activity in response to the presented tactile stimuli at two separate latency ranges, namely for the early-latency somatosensory N80 component 65-85 ms post-stimulus onset and for the late-latency somatosensory N140 component 120-160 ms post-stimulus onset.

For the somatosensory N80 component which is thought be generated in contralateral SI (Allison et al., 1992), observing the cotton bud touch the hand rather than merely the empty space next to it resulted in a (posteriorly) significantly larger N80 amplitude, in line with previous findings that the observation of others' passive touch experiences recruits not only SII (Keysers et al., 2004) but also SI (Blakemore et al., 2005; Bufalari et al., 2007; Ebisch et al., 2008; Pihko et al., 2010; Schaefer et al., 2012; 2009; Wood et al., 2010). Crucially, this increase in N80 amplitude was, however, not further modulated by the viewing perspective from which the model's hand was observed to be touched, in contrast to a recent fMRI study by Schaefer et al. (2009) who found that (different subareas in) SI responded differently to the sight of touch from an egocentric as compared to an allocentric viewing perspective. On the one hand, it cannot be ruled out that the relatively small number of experimental trials in the present study might not have allowed to detect a systematic modulation of a mirror touch response in the N80 latency range as a function of the viewing perspective, especially given the unexpectedly strong effect of the viewing perspective per se (regardless of whether touch on the hand occurred or not) on somatosensory processing which might have somewhat obscured possibly smaller deviations in somatosensory processing as a function of an interaction between the observed tactile feedback and the viewing perspective. In addition, unlike in Schaefer et al. (2009)'s study where participants had to count the brush strokes on the observed hand, participants in the present study also merely passively observed the touch-related visual input which might in itself have resulted in less pronounced mirror touch activity in SI (see chapter 1.2.1), making it more difficult to detect further modulations as a function of the viewing perspective. Importantly, it is, however, also possible that the lack of a perspective-dependent modulation of touch observation-related changes in N80 mean amplitude indicates that the *initial* vicarious SI response occurs indeed in a similar fashion for both viewing perspectives and that the differential SI activation patterns found by Schaefer et al. (2009), measured with fMRI and thus a much lower temporal resolution, might actually emerge only somewhat later during the vicarious SI response as a result of reentrant feedback to SI from SII or other higher-order cortical areas.

As for the late-latency N140 component, a possible index of activity in SII (Tarkka et al., 1996; Valeriani et al., 2001a; see, however, Allison et al., 1992) for which it has previously been shown that vicarious touch observation-related activity is insensitive to the perspective from which touch on somebody else's body is viewed (Keysers et al., 2004; Schaefer et al., 2009), somatosensory processing was revealed to be modulated in a complex fashion: Apart from the profound and wide-spread effect the viewing perspective as such had on this ERP component (see above), it was also found that the viewing perspective systematically altered the effect of the observed tactile feedback. Similar to Exp. 2.1 in this thesis, the sight of touch was overall associated with a significantly enhanced N140 amplitude, albeit in a much less wide-spread fashion than in Exp. 2.1 since this change in amplitude in this study was restricted to posterior electrodes sites over the hemisphere contralateral to the tactually stimulated hand.

When the different viewing perspective were, however, taken into account, the statistical analyses indicated that the observation of touch on the model's hand from an egocentric perspective did actually not result in a sufficiently consistent N140 modulation to render it statistically significant when considered on its own. The observation of touch from an allocentric perspective, on the other hand, was associated with a systematic increase in contralateral-posterior N140 amplitude (albeit only marginally significant). At ipsilateral-posterior electrode sites, the touch observation-related N140 modulation during the allocentric viewing perspective, was, however, reversed, resulting in a significant decrease in N140 amplitude for the sight of touch.

Observing touch from an allocentric perspective thus seemed to modulate somatosensory processing in the N140 latency range more reliably than the sight of touch from an egocentric perspective. Were it not for Exp.s 2.1. in this thesis where the sight of touch on somebody else's hand as seen from an *egocentric* perspective was found to be associated with a significant increase in N140 amplitude, this pattern of a viewing perspective-dependent N140 modulation could be interpreted as an indication that at least parts of the putative tactile mirror system (SII) might respond preferentially to the sight of a body being touched if an allocentric viewing perspective substantiates that the seen body is not one's own. As it is, it is somewhat unclear why the present study failed to reveal a similarly pronounced N140 modulation as the one found in Exp. 2.1 during touch observation from, too, an egocentric viewing perspective. The slightly smaller sample size along with a reduced number of experimental trials in the present study might account for this. There were also some other seemingly subtle differences between the hand images used in the present experiment as compared to Exp. 2.1 (orientation of the hand, movement trajectory of the cotton bud, experimental task) which might nevertheless have influenced the experimental outcome with respect to electrophysiological correlates of possibly somewhat fragile mirror touch responses during passive touch observation. As for the finding that the touch observation-related N140 enhancement in the present study were more reliable during an allocentric viewing perspective than during an egocentric viewing perspective, it should be noted that the observed touch occurred in two slightly different spatial locations in the two viewing perspectives: As already mentioned above, the fixation dot and also the location where the touch was seen to occur were located in the lower rather than upper half of the hand images in the allocentric viewing perspective (see also Schaefer et al. (2009)'s stimulus material), possibly resulting in an attentional focus slightly closer to the participants' own hidden hand which was positioned in front of and below the monitor. This might have increased the salience of the observed touch in the allocentric viewing perspective since participants perceived it as somewhat closer to their own body. Future studies should thus ensure that the observed touch occurs in the same spatial location in the visual stimulus display and relative to participants' concurrently stimulated body part.

As for the touch observation-related N140 modulations during an allocentric viewing perspective, it was also found that they were expressed differently for the two hemispheres. Contralaterally, the N140 modulation resembled the (non-significant) amplitude enhancement for the sight of touch from an egocentric perspective (see also Exp. 2.1). Ipsilaterally, the sight of touch was, however, associated with a decrease in N140 amplitude. This reversal might indicate that the sight of touch from an allocentric perspective might be processed differently in the two hemispheres. Interestingly, it was only the contralateral N140 effect for which correlations between the strength of touch observation-related N140 increase and empathy-related self-report measures was found. While highly speculative, this might indicate that the contralateral N140 effect might indeed have been associated with an embodied empathic response to the observed touch on somebody else's body whereas the ipsilateral N140 effect might be reflective of some other process. In the view of parietal-occipital maximum of the touch observation-related SEP amplitude difference for both viewing perspectives and relating back to the speculations discussed above with respect to the extrastriate body area (EBA; Downing et al., 2001) and its potential role in relaying the required body- and viewing perspective-related visual input to the somatosensory cortices (David et al., 2007), it seems interesting that only the right EBA responds more strongly to the sight of body parts from an allocentric rather than an egocentric perspective while the left EBA is indifferent with respect to the viewing perspective (Saxe et al., 2006). A subregion of the left but not the right SI, on the other hand, was found to respond differently contingent on the perspective a visually presented body part was seen from (Saxe et al., 2006). While is entirely unclear if and how the aforementioned findings might provided an explanation as to why the N140 modulations during an allocentric viewing perspective were reversed for the two hemispheres, they nevertheless make it more conceivable that changes in viewing perspective might result in asymmetric and/or reversed somatosensory responses in both hemispheres. Future research will have to shed more light on the role of the somatosensory cortices in the perception of others' bodies from different viewing perspectives, on how the body-related visual information finds its way from visual structures (such as the EBA) to the somatosensory system and on how body-, touch- and perspective-related visual information is eventually integrated in the context of vicarious activations in the somatosensory system.

Variations in touch observation-related modulations in somatosensory processing as a function of interindividual differences in trait empathy

The strength of the (marginally significant) touch observation-related increase in N140 mean amplitude revealed at the contralateral-posterior electrode cluster during an allocentric viewing perspective was found to co-vary significantly with participants' self-reported tendency to respond with *empathy concern* (IRI) to others' negative experiences. The more participants reported to respond emotionally to witnessing others in distress, the more pronounced was the touch observation-related increase in N140 amplitude (at least when they observed the touch from an allocentric perspective). Similar to Exp. 2.1, this finding yet again implicated an emotional empathy-related personality disposition with the tendency to recruit one's own somatosensory system (SII in particular) when merely observing others' touch experiences. Several recording sites within the contralateral-posterior electrode cluster showed, in addition, a similarly positive relationship between the participants' scores on the *social skills* subscale of the EQ as well as with the total score of the EQ, extending the link between interindividual differences in trait empathy and the strength of mirror touch responses also to less affective dimensions of empathy (even though all three measures were highly intercorrelated). These empathy-related correlations will be discussed in more detail in the light of recent research findings in chapter 2.5.

Summary and conclusion

The sight of touch on a model's hand was found to be associated with in a significant increase in N80 mean amplitude, regardless of whether the touch was observed from an egocentric or an allocentric perspective, suggesting that early vicarious touch observation-related activity in SI is insensitive to the viewing perspective and that perspective-dependent SI activations previously revealed with fMRI (Schaefer et al., 2009) might have been the result of only somewhat later arriving reentrant feedback to SI from SII or higher-order cortical areas. The N140 component, on the other hand, showed a similarly unspecific increase in contralateral-posterior mean amplitude when the model's hand was seen to be touched, but further statistical analyses indicated that this amplitude increase was actually more reliable during an allocentric as compared to an egocentric viewing perspective. In addition, the touch observation-related N140 effect during an allocentric viewing perspective was for some reason found to ipsilaterally reversed, possibly pointing to two different mechanisms having been at work, especially since only the contralateral but not the ipsilateral N140 modulation was associated with differences in individuals' trait empathy. Further research will be needed to clarify in what way the viewing perspective influences touch observation-related ERP modulations in the N140 latency range, not only during an allocentric perspective but also during an egocentric perspective since it is unclear why the present study failed to find, in contrast to Exp. 2.1, a significant N140 effect when touch was viewed from an egocentric perspective.

An unexpected but highly interesting finding in the present study was that the viewing perspective as such, regardless of whether touch was observed or not, profoundly affected somatosensory processing. The sight of somebody else's body part from allocentric rather than an egocentric perspective was associated with increased ERP amplitudes in all analysed time windows, suggesting that the sight of a body affects somatosensory processing (Haggard, 2006) even if the observed body part is presented in a self-inconsistent orientation and outside the observer's immediate peripersonal space.

Experiment 2.3

Modulations in somatosensory processing as a function of the anatomical congruence between the observed-to-touched finger location and the concurrently stimulated finger location on the observer's hand

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2.3.1 Introduction

Exp. 2.1 and 2.2 demonstrated electrophysiologically that observing others' passive touch sensations modulates somatosensory processing of tactile stimuli concurrently delivered to the observer's hand (see also Bufalari et al., 2007), indicating that both personally experienced touch and merely observed touch recruit indeed similar neural networks as suggested by recent neuroimaging evidence (Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Schaefer et al., 2012; 2009). What has so far not been investigated very extensively is to what extent touch observation-related vicarious activity in the somatosensory cortices might actually represent the precise body location the observed touch was directed at. Overlapping somatosensory activations during the experience of touch on a given body part such as one's hand (Schaefer et al., 2012, 2009), one's arm (Ebisch et al., 2008; 2011) or one's leg (Keysers et al., 2004) and the mere sight of touch on somebody else's corresponding body part seem to suggest that mirror touch responses might follow to some extent the somatotopic organisation of somatosensory activity triggered by actual touch on one's own body. This notion is further corroborated by the finding that the sight of touch on a human face was associated with (lateralised) activity in the head area in SI while the sight of touch on a human neck was not, also suggesting that at least the vicarious somatosensory activity in SI is sensitive to which body part is seen to be touched. SII, on the other hand, has been found to respond not only to the sight of touch on body parts, but also to the sight of touch on objects (Ebisch et al., 2008; Keysers et al., 2004; Exp. 2.1 in the present thesis) which can be considered as an indication that vicarious activity in SII might generally be more unspecific and less somatotopically organised since the location of the observed touch on an object can usually not very clearly be matched with a certain location on a human body.

It is, however, unclear how fine-grained such a somatosensory organisation during touch observation might be when it comes to different locations within a given body part. In most studies in which shared neural networks for felt and observed touch are demonstrated by showing that the sight of touch modulates ongoing somatosensory processing, the specific location on a body part that is observed to be passively touched and the location of the observer's own body that is simultaneously tactually stimulated coincide, e.g. seeing a face being touched on the facial cheeks resulted in modulated processing of tactile stimuli on the observer’s own facial cheeks (Serino et al., 2008b) and seeing an index finger tip being touched is associated with modulated somatosensory processing of tactile stimuli to the homologous index finger tip (Exp. 2.1 and 2.2 in the present thesis). It is, however, unclear whether such touch observation-related effects might be modulated when the degree of anatomical congruency between the observed-to-touched and the tactually stimulated skin area (within e.g. a hand) is varied.

The aim of the present study was thus to investigate to what extent visuo-tactile modulation effects might be contingent (within a body part) upon a congruency between the observed-to-touched skin area and the concurrently tactually stimulated skin area of the observer. Similar to Exp. 2.1 and 2.2., somatosensory evoked potentials (SEPs) in response to the tactile stimuli were recorded as a measure of somatosensory processing while participants observed a cotton bud touch either a presented hand on the index finger tip or merely the empty space next to it. Crucially, the location of the simultaneously presented tactile stimuli to the observer’s own hand was manipulated such that they were either delivered to the anatomically congruent index finger tip, an alternative location on the same finger (the base segment) or the tip of the adjacent middle finger. In addition, tactile stimuli were also presented to the homologous index finger tip of the other, unobserved hand. Due to the high temporal resolution of the EEG technique, this approach would not only allow to determine to what extent the sight of touch affects somatosensory processing in a finger location-specific or in a more general fashion but also whether the onset of any such modulations might vary in time as a function of the degree of anatomical congruency between the observed-to-be-touched finger location and the concurrently tactually stimulated finger location.

Similar to Exp. 2.1 and 2.2, participants were, in addition, asked to complete two standard empathy questionnaires at the end of the experiment to allow to investigate possible links between extent of touch observation-related modulations in somatosensory processing and empathic dispositions.

2.3.2 Methods

Participants. Seventeen neurologically healthy volunteers took part in the experiment. One had to be excluded due to a lack of reasonably distinguishable SEP components. Thus, sixteen participants (8 males and 8 females), aged between 20 and 33 years (mean age: 25.6 years; SD = 4.2) remained in the sample. Participants were naive as to the purpose of the experiment and gave informed consent to participate after a detailed explanation of the involved procedures. Two participants were left-handed and all had normal or corrected-to-normal vision by self-report. Participants were paid £ 7/h for their participation in the study. The procedures were approved by the local ethics committee.

Stimuli. The task-irrelevant visual stimuli depicting a cotton bud approach and the either touch a left hand on the index finger tip or merely the empty space next to were the same as the ones in the "hand"-condition in Exp. 2.1, except that the hand was superimposed on a grey rather than a blue background (see Fig. 2.3.a) and that the fixation cross was orange rather than green. In addition, the position of the fixation cross was adjusted such that its location on the observed hand was not only equidistant from the end positions of the cotton bud in the *touch* and *no touch* condition but also approximately equidistant from the finger locations that were to be tactually stimulated on the participants' own left hand.

The task-irrelevant tactile stimuli were again presented for 200 ms to participants' fingers using a 12-volt solenoid which was tapped to the currently stimulated finger. Importantly, where the stimuli were presented was manipulated within a blocked design and involved four different locations across both hands of the participants (see Fig. 2.3.a): i) left index finger tip (i.e. same segment, same finger, same hand as observed to be touched) ii) base segment of the left index finger (i.e. different segment, same finger, same hand) iii) left middle finger tip (i.e. same segment (tip), adjacent finger, same hand) iv) right index finger tip (i.e. same segment, same finger, different hand). Thus, the extent to which the tactually stimulated body location of the observer matched the body location that was observed being touched with the cotton bud (always left index finger tip) was varied. To mask any sounds made by the tactile stimulator, continuous white noise (65 dB SPL) was played through headphones.

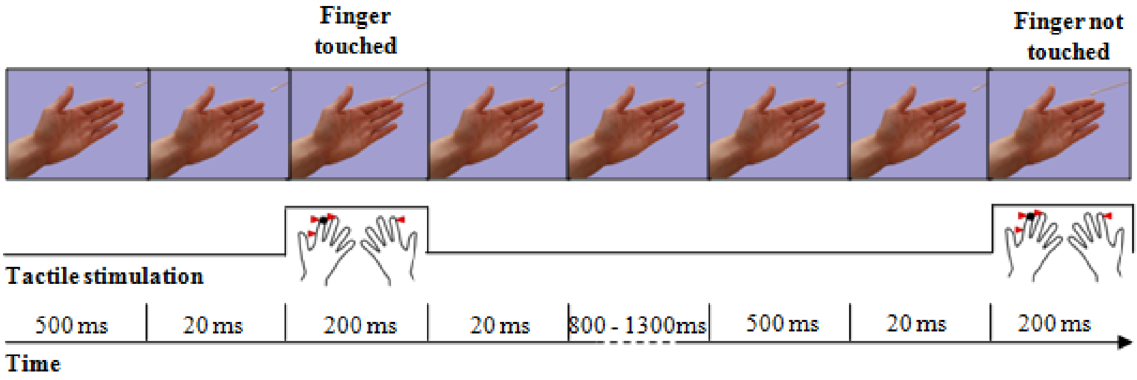

Fig. 2.3.a. Schematic representation of the typical sequence of visual and tactile events in *touch* and *no touch* trials, respectively. The hand icons depicted the four different tactually simulated finger locations. The finger tip anatomically congruent with the observed-to-be-touched finger tip is highlighted in black. Which finger location was stimulated was manipulated blockwise. On infrequent catch trials, a brief colour change of the fixation cross (not shown here) required a vocal response.

Procedure. The experimental procedure (hand position of the participants, timing of visual and tactile events in a given trial, colour change detection task etc.) was almost identical to the one in the “hand”-condition in Exp. 2.1, with the following modifications: Participants were tactually stimulated on four different finger locations rather than just the anatomically congruent index finger tip. The location of the concurrently presented tactile stimulus was manipulated in a blocked design, with each of the four finger location being stimulated for three consecutive blocks. The order in which the four different locations were stimulated for three consecutive blocks each was randomised across participants using a random number generator. Overall, the experiment thus comprised 4 x 3 blocks, i.e. 12 experimental blocks in total. The number of catch trials on which vocal response to a brief colour change of the fixation cross was required was slightly decreased to 9 catch trials per block (approx. 15 %).

Prior to the experiment, participants were presented with a short demo of the visual stimuli. They were then gently touched twice with a cotton bud on all four later stimulated finger locations to demonstrate the different tactile consequences associated with the observed events on the screen, even though no such explanation was given to them. This was followed by a short practice block consisting of 25 trials (5 catch trials) to familiarise participants with the colour change detection task at hand.

At the end of the experiment, participants were again asked to complete the 60-item EQ questionnaire (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) as well as the 28-item IRI by Davis (1983).

Recording and data. The procedures for recording the continuous EEG and HEOG with a Brain Vision 32 channel system and the pre-processing of the obtained electrophysiological data was the same as in Exp. 2.1. The off-line segmenting into 500 ms time epochs, separately for all eight combinations of observed tactile feedback (touch vs. no touch) and stimulus location (left index finger tip, left index finger base segment, left middle finger tip, right index finger tip) as well as the subsequent artifact removal and the grand-averaging of the obtained somatosensory EPRs for all eight combinations of observed tactile feedback and stimulus location, was also carried out in accordance with the criteria described in Exp. 2.1.

Data analysis. Statistical analyses involved the same electrode clusters as in Exp. 2.1. ERP mean amplitudes were computed for successive latency windows centred on the peak amplitudes of the somatosensory ERP components identified within the first 200 ms after tactile stimulus onset as follows: P50 (40-60 ms post- stimulus onset), N80 (65-90 ms post-stimulus onset), P100 (95-115 ms post-stimulus onset) and N140 (120-160 ms post-stimulus onset). The choice of the time epochs was based on visual inspection of the grand average ERP components elicited by tactile stimuli averaged across all eight experimental conditions over contralateral somatosensory cortex at C4, Cp2 and Cp6.

To investigate whether the observation of somebody else's touch sensation modulates somatosensory processing of a concurrently delivered tactile stimulus and whether any such modulation might be contingent upon a close anatomical congruency between observed and stimulated finger location, 5-way repeated measures ANOVAs with the within-subject factors *hemisphere* (ipsilateral vs. contralateral), *anterior-posterior* (anterior vs. posterior), *stimulus location* (left index finger tip, base segment left index finger, left middle finger tip, right index finger tip), *observed tactile feedback* (touch vs. no touch) and *electrode site* were conducted on the mean ERP amplitudes for a given latency window. Greenhouse-Geisser adjustments to obtained p-values were applied where appropriate. Any revealed *anterior-posterior* by *observed tactile feedback*-interactions (see below) were followed up by conducting two separate *hemisphere* (2) by *stimulus location* (4) by *observed tactile feedback* (2) by *electrode site* (5)-ANOVAs for the anterior and the posterior electrode cluster. An alpha level of .05 was used for all ANOVAs.

Non-parametric correlation analyses to test whether the strength of ERP modulations found to be contingent upon the observation of others' touch experiences is linked to trait empathy were carried out based on the same criteria as in Exp. 2.1.

2.3.3 Results

Behavioural performance

The mean accuracy rate in the colour change detection task was 99.7 % with only very few false alarms (< 1%), indicating that participants paid close attention to the visual display. The response times for correctly detecting a colour change of the fixation dot did not differ as a function of the observed tactile feedback, ($F(1,15) = 1.478$, $p = .243$, $\eta^2_p = .090$), the concurrently stimulated finger location, ($F(3,45) = .857$, $p = .471$, $\eta^2_p = .054$), or an interaction of both factors, ($F(3,45) = 1.546$, $p = .216$, $\eta^2_p = .093$) suggesting that attention to the visual display was similar in all conditions (see Table 2.3.a).

Table 2.3.a. Means and standard deviations of response times in colour change detection task (in ms) as a function of *observed tactile feedback* and *concurrently tactually stimulated finger location.*

	IndexTip$_{\text{left}}$		**IndexBase$_{\text{left}}$**		**MiddleTip$_{\text{left}}$**		**IndexTip$_{\text{right}}$**	
	touch	***no touch***	***touch***	***no touch***	***touch***	***no touch***	***touch***	***no touch***
M	544.61	540.69	549.79	548.95	536.85	552.00	536.01	543.41
SD	63.97	65.85	67.70	70.33	77.71	72.37	69.85	66.76

Electrophysiological data

Visually-induced effects of observing somebody else's touch sensations on somatosensory processing were determined by comparing ERPs obtained when tactile stimulation was accompanied by observing a cotton bud either touch the index finger tip of a left hand or the empty space next to it. Figures 2.3.b-e show the obtained grand-averaged ERP waveforms elicited for the two observational conditions at all analysed electrode sites, separately for the four different tactually stimulated finger locations. Fig. 2.3.f contrasts the touch observation-related ERP modulations during the tactile stimulation of all four finger locations at a representative parietal electrode (P4) contralateral to the stimulated finger location.

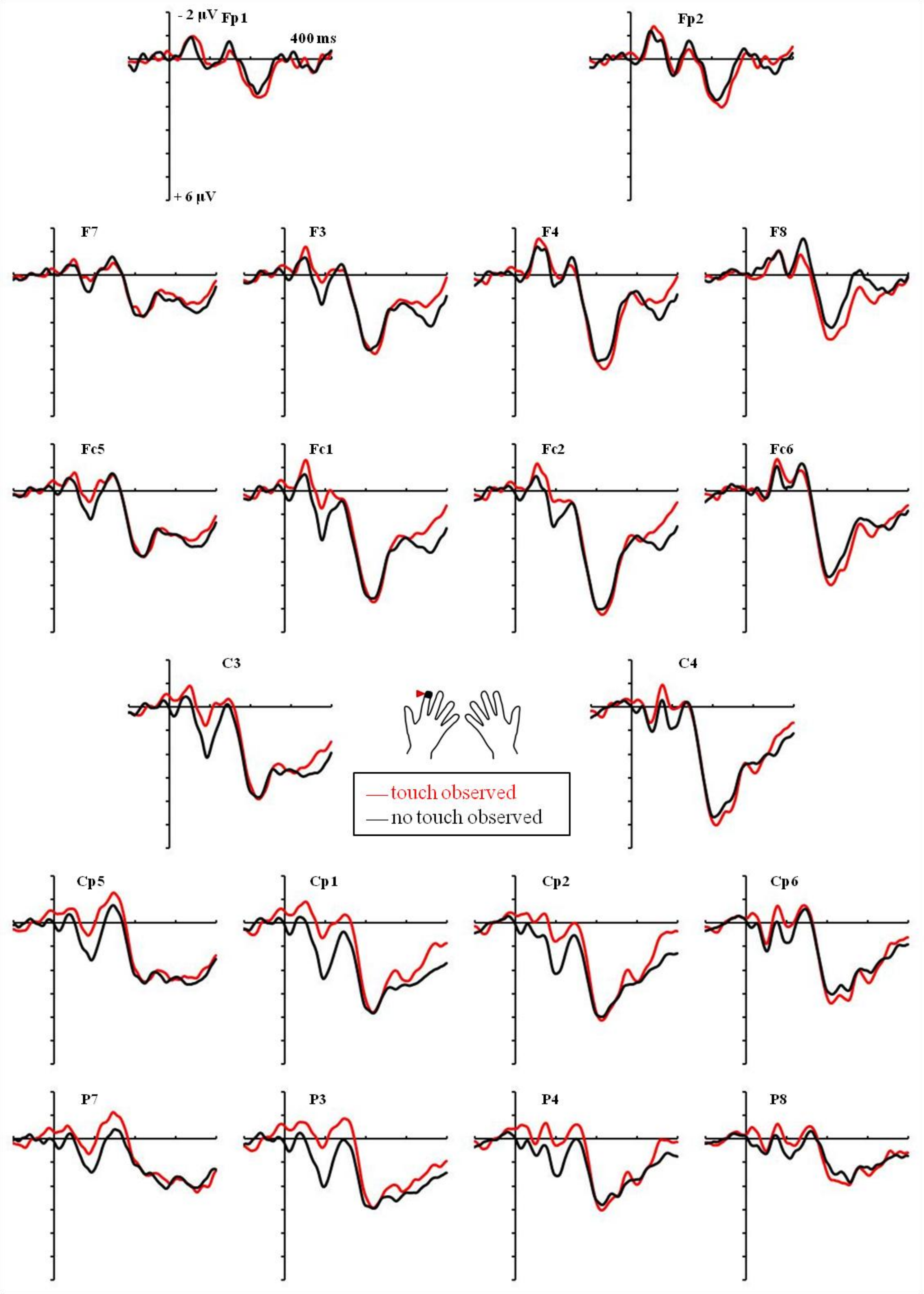

Fig. 2.3.b. Grand-averaged ERP waveforms in response to tactile stimuli to the left index finger tip (IndexTip$_{left}$) during the observation of touch (red line) resp. no touch (black line) on the model's index finger tip. Shown are all electrode sites included in the statistical analysis.

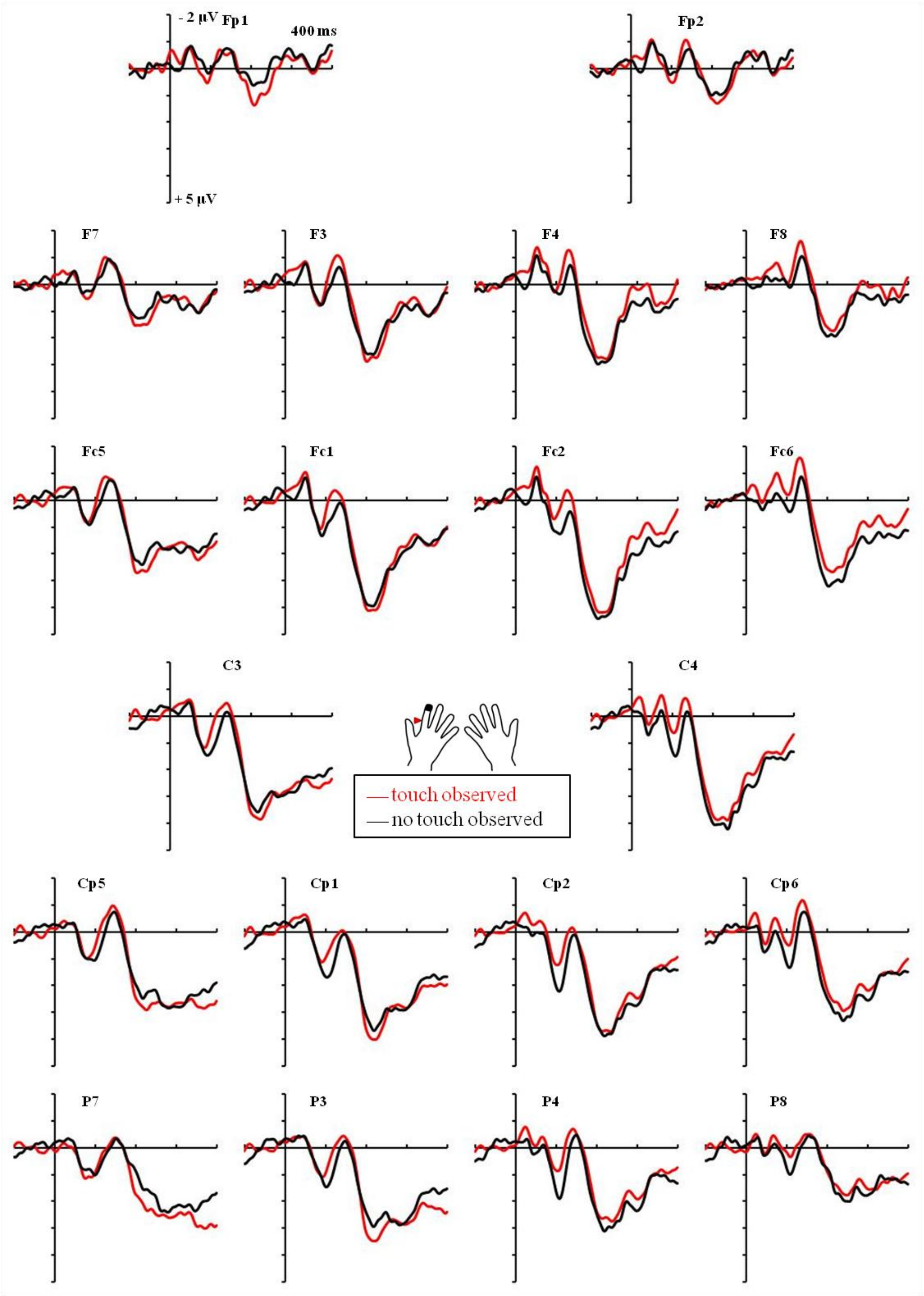

Fig. 2.3.c. Grand-averaged ERP waveforms in response to tactile stimuli to the base segment of the left index finger (IndexBase$_{left}$) during the observation of touch (red line) resp. no touch (black line) on the model's index finger tip. Shown are all electrode sites included in the statistical analysis.

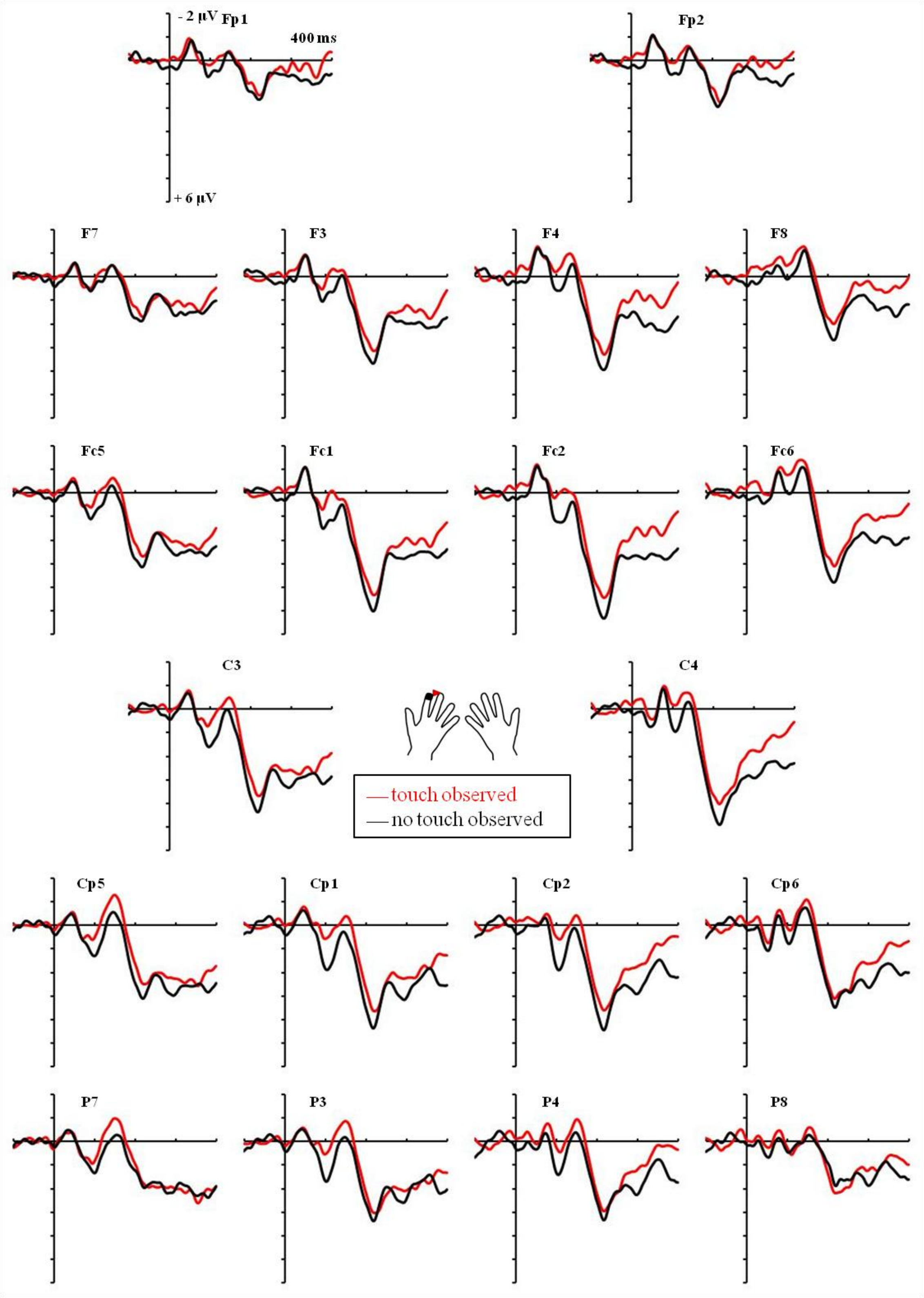

Fig. 2.3.d. Grand-averaged ERP waveforms in response to tactile stimuli to the left middle finger tip (MiddleTip$_{left}$) during the observation of touch (red line) resp. no touch (black line) on the model's index finger tip. Shown are all electrode sites included in the statistical analysis.

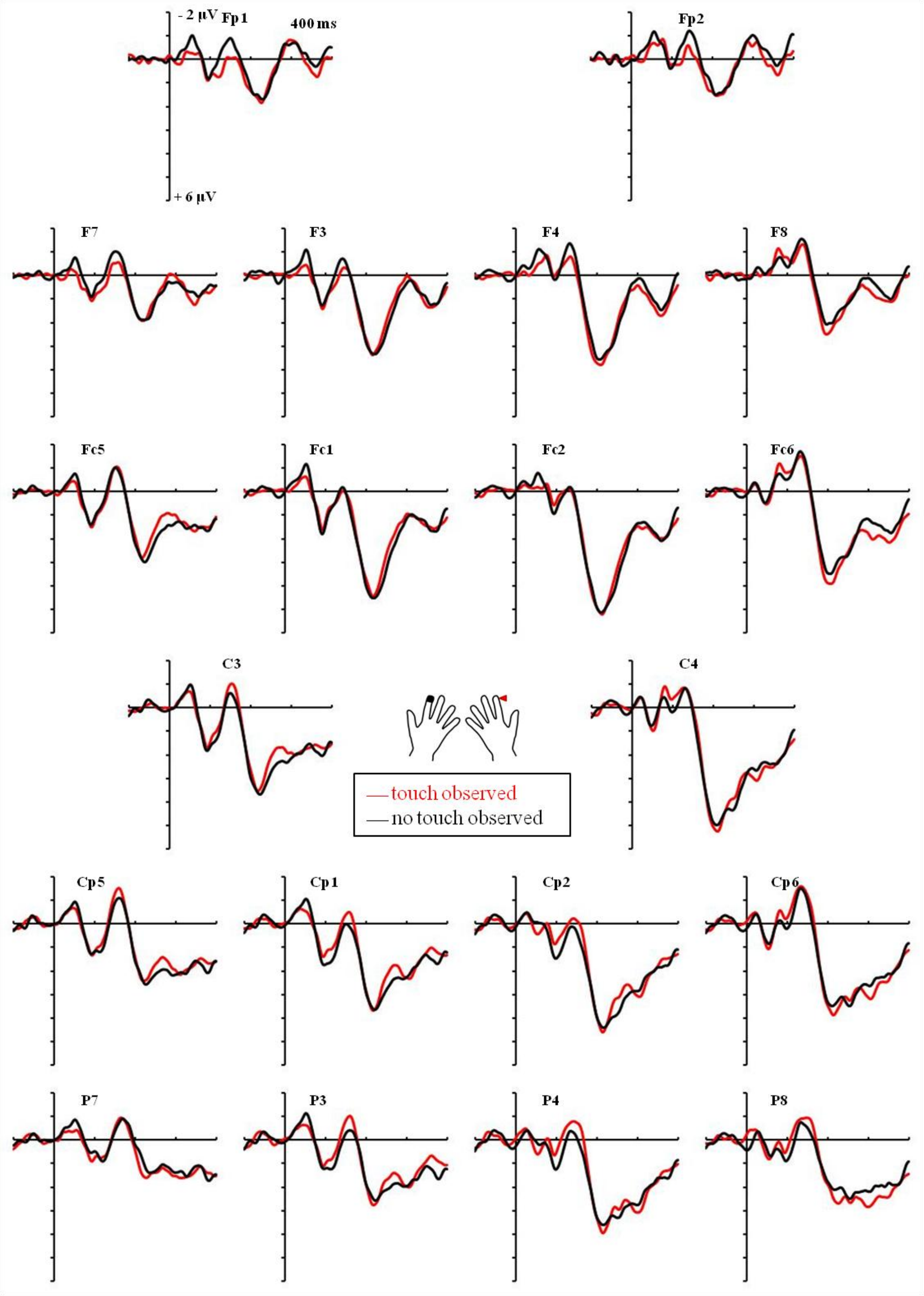

Fig. 2.3.e. Grand-averaged ERP waveforms in response to tactile stimuli to the right index finger tip (IndexTip$_{right}$) during the observation of touch (red line) resp. no touch (black line) on the model's index finger tip. Shown are all electrode sites included in the statistical analysis.

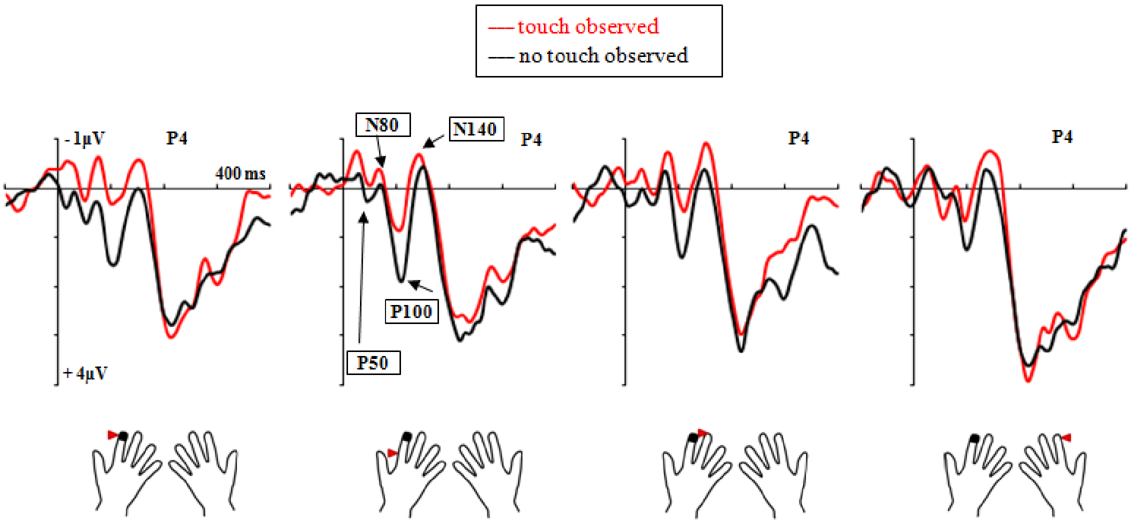

Fig. 2.3.f. Grand-averaged ERP waveforms in response to tactile stimuli to the four different finger locations during the observation of touch (red line) resp. no touch (black line) on the model's index finger tip, at a representative parietal electrode (P4) contralateral to tactile stimulation. Red triangles indicate the stimulated finger location for each plot.

Touch observation-related modulations of somatosensory processing

For the early time epoch 40-60 ms post-stimulus onset (P50), no significant modulations in somatosensory processing as a function of the observed tactile feedback were found, neither in the form of a main effect of the *observed tactile feedback* (F(1,15) = .334, p = .572, η^2_p = .022) nor in the form of any significant interaction effects with *hemisphere*, *stimulus location* and/or the *anterior-posterior* factor (all F(1,15) ≤ 1.605, p ≥ .225, $\eta^2_p \leq .097$).

The subsequent N80-P100-N140 component complex, however, did show systematic modulations in mean ERP amplitude as a function of the sight of touch (see e.g. Fig. 2.3.g): For the somatosensory N80 component, a significant *anterior-posterior* by *observed tactile feedback*-interaction was found (F(1,15) = 10.604, p = .005, η^2_p = .414) with post hoc comparisons (see page 98) revealing that the N80 amplitude was increased during the observation of touch as compared to the observation of no-touch, significantly so, however, only at posterior electrodes (F(1,15) = 5.859, p = .029, η^2_p = .281), but not at anterior electrodes (F(1,15) = 1.151, p = .300, η^2_p = .071). This interaction was not modulated by the site of the delivered tactile stimulation (F(3,45) = .394, p = .758, η^2_p = .026).

The mean amplitude of the somatosensory P100 component, on the other hand, was significantly reduced in a wide-spread fashion when the cotton bud was observed to touch the index finger rather than the empty space next to it (F(1,15) = 10.932, p = .005, η^2_p = .422).

Following-up a significant *anterior-posterior* by *observed tactile feedback*-interaction (F(1,15) = 28.697, p < .001, η^2_p = .657) suggested that this amplitude modulation was again more reliable at posterior electrode sites (F(1,15) = 21.490, p < .001, η^2_p = .199) than at anterior electrode sites (F(1,15) = 3.717, p = .073, η^2_p = .589). Once more, which finger location had been stimulated did not interact with the effects of the observed tactile feedback on somatosensory processing (p ≥ .164).

Similar to the findings for the two earlier components, the N140 component, too, showed a significant *anterior-posterior* by *observed tactile feedback*-interaction (F(1,15) = 12.068, p = .003, η^2_p = .446) with the N140 mean amplitude being significantly increased during the observation of touch only at posterior electrode sites (F(1,15) = 5.550, p = .033, η^2_p = .270) but not at anterior ones (F(1,15) = .151, p = .703, η^2_p = .010). Again, there was no significant interaction with the concurrently stimulated finger location (all F(1,15) ≤ 2.467, p ≥ .074, η^2_p ≤ .141).

All in all, the absence of any statistically significant interaction involving both the observed tactile feedback and the stimulated finger location suggested that the sight of touch on somebody else's index finger tip modulated somatosensory processing in the N80, P100 and N140 latency range in a similar fashion for all four tactually stimulated finger locations.[11,12] Fig.

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[11] In order to allow for a more direct comparison between studies in which visually-induced modulations in somatosensory excitability were contrasted for an observed-to-be-touched finger and the corresponding finger of the other, unobserved hand (Schaefer, Heinze, & Rotte, 2005b; Wood et al., 2010), the present data were exploratively reanalysed including only the two critical finger locations, i.e. the anatomically congruent, observed-to-be-touched left index finger tip and the unobserved right index finger tip. The respective analysis no longer revealed significant modulations for the somatosensory N80 or N140 components for neither location (all p > .05). For the somatosensory P100 component, however, a significant *hemisphere* by *finger location* by *observed tactile feedback*-interaction was found (F(1,15) = 6.069, p = .026, η^2_p = .288) with follow-up comparisons based on separate *anterior-posterior* (2) by *observed tactile feedback* (2) by *electrode site* (5)-ANOVAs for the two hemispheres and the two stimulus locations suggesting that a significant effect of the observed tactile feedback on somatosensory processing could be found in the ipsilateral hemisphere only and for the anatomically congruent finger location only (left index finger/ipsilateral: F(1,15) = 5.479, p = .033, η^2_p = .268; left index finger/contralateral: F(1,15) = 2.362, p = .145, η^2_p = .136; right index finger/ipsilateral: F(1,15) = .016, p = .902, η^2_p = .001; right index finger/contralateral: F(1,15) = .1404, p = .254, η^2_p = .086). When restricting the analysis in this way, touch observation induced effects on concurrent somatosensory processing did depend on side congruency, in line with previous findings (Schaefer et al., 2005b; Wood et al., 2010).

[12] With respect to possible ERP differences as a function of which finger location was concurrently tactually stimulated (regardless of the observed tactile feedback), the main analysis pointed to small modulations in the N80 and P100 latency ranges: In the former latency range, following up a significant *hemisphere* by *anterior-posterior* by *site of stimulation*-interaction (F(1,15) = 3.877, p = .050, η^2_p = .205) indicated that the N80 mean amplitude at contralateral-anterior recording sites was significantly smaller during tactile stimulation of the base segment of the left index finger as compared to tactile stimulation of the tip of the same finger (F(1,15) = 6.617, p = .021, η^2_p = .306) while it did not significantly differ at any of the electrode clusters from N80 amplitude evoked during tactile stimulation of any of the other stimulated finger locations (all p > .05; the conducted pairwise comparisons for all stimulated finger locations for all four different electrode clusters were based on separate *site of stimulation* (2) by *observed tactile feedback* (2) by *electrode site* (5)-ANOVAs). In the P100 latency range, following up a

2.3.g thus shows the grand-averaged ERPs waveforms during the observation of touch as compared to no touch at a representative parietal electrode (P4), when collapsing across the four stimulated finger locations. In addition, it depicts the topographic distribution of the corresponding mean difference in SEP amplitude for the concurrent sight of touch versus no touch for the N80, P100 and N140 time epochs.

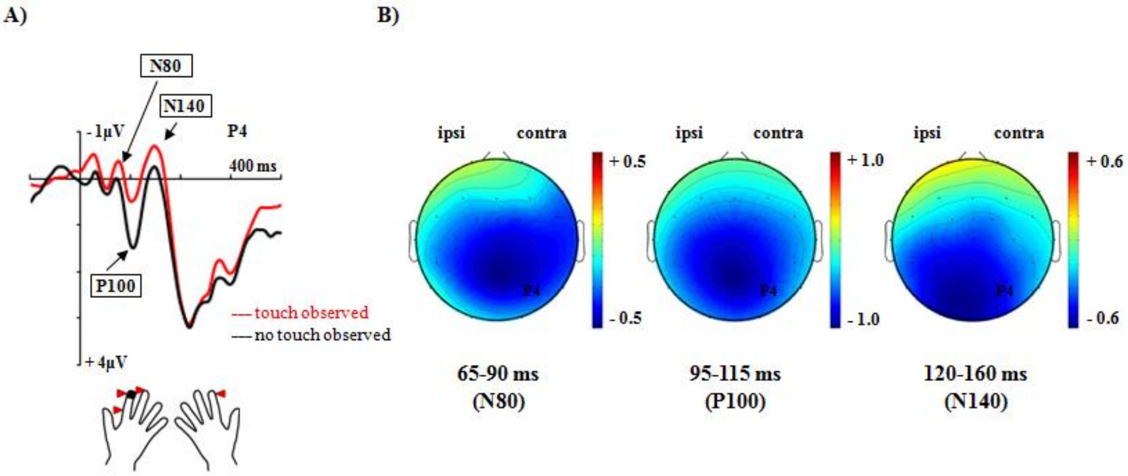

Fig. 2.3.g. ***A)*** Grand-averaged ERP waveforms in response to tactile stimuli during the observation of touch (red line) resp. no touch (black line) on the model's index finger tip, when collapsed across the four tactually stimulated finger locations, at a representative parietal electrode (P4) contralateral to tactile stimulation. ***B)*** Topographic distribution of the difference in mean ERP amplitude between the two types of observed tactile feedback (averaged across the four tactually stimulated finger locations) in the N80, P100 and N140 latency range where significant touch-observation related ERP modulations were found. Note that a negative difference indicates an increased negativity for the N80 and N140 component and a decreased positivity for the P100 component during the sight of touch.

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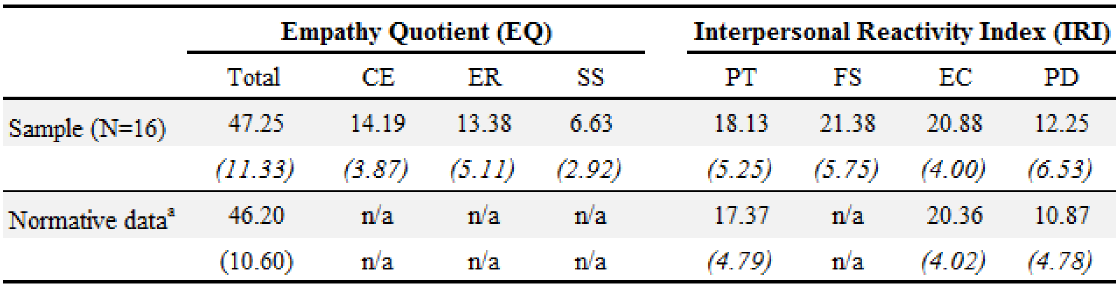
significant *hemisphere* by *site of stimulation*-interaction (F(1,15) = 7.100, p = .008, η^2_p = .321) pointed significant difference in contralateral P100 amplitude during tactile stimulation of the base segment of the left index finger and the tip of the right index finger (F(1,15) = 4.723, p = .046, η^2_p = .239) but neither of the two finger locations differed from any of the remaining ones (all p > .05; here, the conducted pairwise comparisons for all stimulated finger locations were based on separate *anterior-posterior* (2) by *site of stimulation* (2) by *observed tactile feedback* (2) by *electrode site* (5)-ANOVAs for the two hemispheres). In the light of SEP amplitude differences during tactile stimulation of the (left) index as compared to the (left) middle finger tip repeatedly observed in Exp.s 3.2-3.5 in this thesis (see chapter 3), possible differences in somatosensory processing depending on which finger was concurrently tactually stimulated were re-run exploratively comparing only the left index finger tip and the left middle finger tip. Even when restricting the statistical analysis in this way, no significant main or interaction effects involving the factor *site of stimulation* were found for any of the analysed time epochs (with the exception of a *hemisphere* by *site of stimulation*-interaction (F(1,15) = 5.394, p = .035, η^2_p = .265) in the P100 latency range for which post hoc comparisons, however, yielded no significant results (for both hemispheres, p > .05; based on separate *anterior-posterior* (2) by *site of stimulation* (2) by *observed tactile feedback* (2) by *electrode site* (5)-ANOVAs for the two hemispheres), suggesting that somatosensory processing of tactile stimuli to both index and middle finger tip was generally comparable.

Empathy correlations

Table 2.3.b shows the means and standard deviations for the obtained self-report measures of trait empathy which were very similar to the normative data presented by Lawrence et al. (2004) and Bellini et al. (2002).

Table 2.3.b. Mean scores and standard deviations for the self-report measures of dispositional empathy.



	Empathy Quotient (EQ)				Interpersonal Reactivity Index (IRI)			
	Total	CE	ER	SS	PT	FS	EC	PD
Sample (N=16)	47.25	14.19	13.38	6.63	18.13	21.38	20.88	12.25
	(11.33)	*(3.87)*	*(5.11)*	*(2.92)*	*(5.25)*	*(5.75)*	*(4.00)*	*(6.53)*
Normative data[a]	46.20	n/a	n/a	n/a	17.37	n/a	20.36	10.87
	(10.60)	n/a	n/a	n/a	*(4.79)*	n/a	*(4.02)*	*(4.78)*

[a)] Normative data are derived from: Lawrence et al., 2004 (EQ) and Bellini et al. (2002) (IRI).

EQ: CE = Cognitive Empathy ER = Emotional reactivity SS = Social skills

IRI: PT = Perspective taking FS = Fantasy scale EC = Empathic concern PD = Personal distress

Maximal scores: Total score of EQ = 80; Cognitive empathy (EQ) = 22, Emotional reactivity (EQ) = 22, Social skills (EQ) = 12; each subscale of the IRI = 28.

For the N80 latency window (65-90 ms), the sight of touch (as compared to no touch) on the model's hand resulted in a significantly increased ERP amplitude at posterior electrode sites. For several of these central and (centro)-parietal electrodes, significant positive correlations with the *emotional reactivity*-subscale of the EQ were found bilaterally (C3: $r_s(16) = .521$; C4: $r_s(16) = .545$; Cp1: $r_s(16) = .619$; Cp2: $r_s(16) = .530$; Cp5: $r_s(16) = .552$; P3: $r_s(16) = .501$; $p \leq .05$; Cp6 showed a marginally significant correlation: Cp6: $r_s(16) = .487$, $p = .055$). Fig. 2.3.h illustrates that this correlation reflected that participants who scored low on this empathy-related subscale showed the strongest effects in terms of an posteriorly increased mean N80 amplitude during the observation of touch.[13]

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[13] Three posterior electrodes over the contralateral hemisphere also showed (marginally) significant correlations with the IRI's *fantasy scale* in this latency range but those were clearly driven by two participants with unusually low scores on this scale and were thus not reliable.

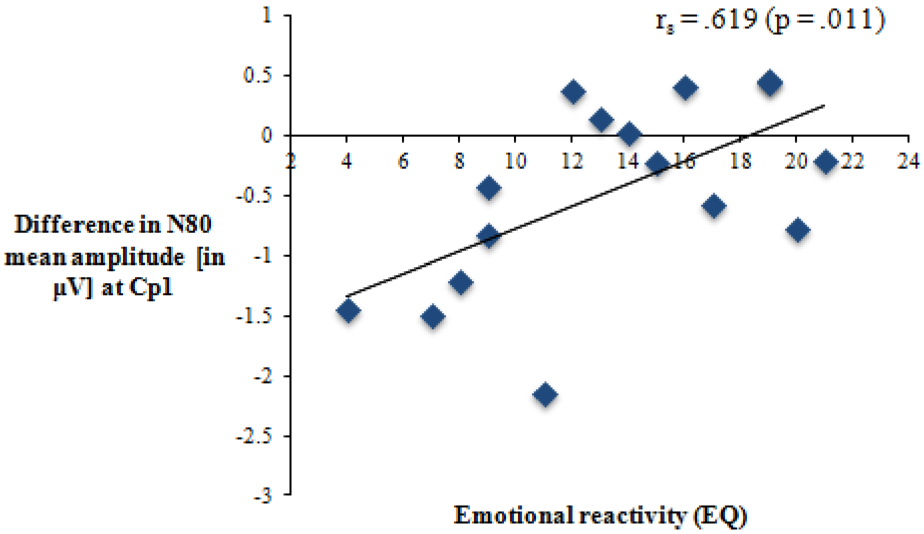


Fig. 2.3.h. Difference in SEP mean amplitude (touch – no touch) in the N80 latency window (65-90 ms post-stimulus onset) as a function of self-reported *emotional reactivity* (EQ), shown for a representative electrode with the strongest correlation (Cp1).

For the N140 component, three centro-parietal and parietal electrodes over the contralateral hemisphere showed (marginally) significant negative correlations with the IRI's *personal distress* scale (Cp6: $r_s(16) = -.562$; P4: $r_s(16) = -.520$; both $p < .05$; P8: $r_s(16) = -.480$; $p = .060$). Here, the increase in N140 amplitude during the sight of touch was more pronounced, the more participants reported a tendency to experience personal distress when witnessing others' misfortunes (see Fig. 2.3.i).

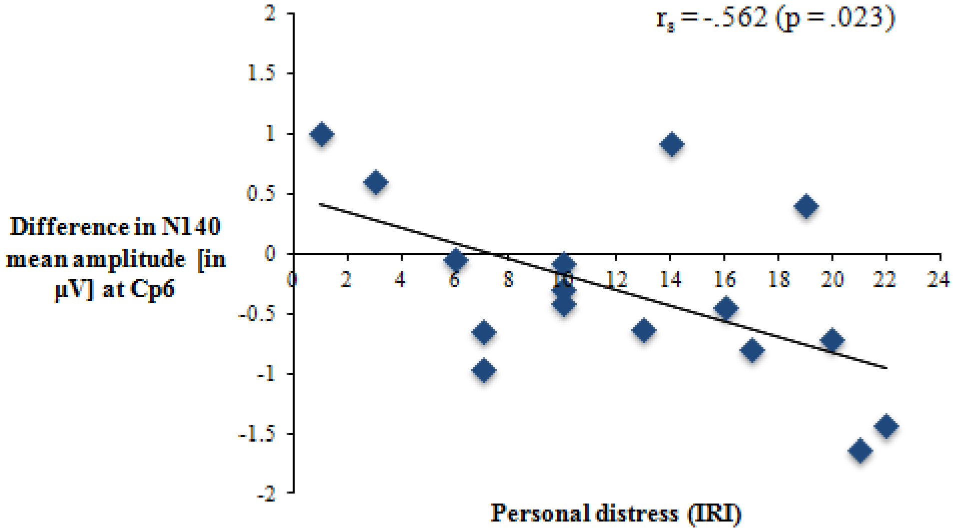


Fig. 2.3.i. Difference in SEP mean amplitude (touch – no touch) in the N140 latency window (120-160 ms post-stimulus onset) as a function of self-reported *personal distress* (IRI), shown for a representative electrode with the strongest correlation (Cp6).

The two empathy-related scales for which an association with the strength of the mirror touch response was found in the early (N80) and late (N140) latency range did not correlate among themselves ($r_s(16) = .027$, $p = .922$).

For the somatosensory P100 component for which the observed tactile feedback actually resulted in the strongest and most wide-spread SEP modulations, empathy-related correlations were found only at isolated electrodes (when analysed non-parametrically and thus more conservatively) and will thus not be reported.

2.3.4 Discussion

Participants in the present study observed a cotton bud either touch a left hand on the index finger tip or the empty space next to it while tactile stimuli were delivered to either their own left index finger tip or three other, anatomically less congruent locations across their hands, namely the base segment of same index finger, the adjacent middle finger tip or the index finger of the unobserved right hand.

The effects of the sight of touch on somatosensory processing

Mean amplitudes of the early (N80), mid- (P100) as well as late (N140)-latency ERP component were found to be significantly altered by the touch-related visual input. The somatosensory N80 component is thought to reflect late SI-processing (Allison et al., 1992) whereas both the somatosensory P100 and the N140 are assumed to be generated in bilateral SII (Tarkka et al., 1996; Valeriani et al., 2001a; see, however, Allison et al., 1992). The observation of touch on somebody else's hand thus engaged both SII and SI (see also Exp. 2.1 and 2.2), in line with previous findings that suggest that mirroring other's tactile sensations activates not only SII (Keysers et al., 2004) but also SI (Blakemore et al., 2005; Ebisch et al., 2008; Pihko et al., 2010; Wood et al., 2010).

Importantly, the statistical analyses did not indicate for any of the three modulated components that effect of the observed tactile feedback might interact in a significant fashion with the stimulus location on the observer's hands. Instead, the revealed ERP modulations were found in the form of a general effect across the four stimulated finger locations, i.e. viewing an index finger being touched on its tip modulated somatosensory processing of concurrently delivered tactile stimuli in SI and SII in a similar fashion irrespective of the degree of anatomical congruency between the observed to-be-touched location and the simultaneously stimulated finger location.

The cortical representations of the different fingers of both hands, however, overlap strongly in SII (Hoechstetter et al., 2001; Ruben et al., 2001), and also SI shows such overlapping representation at least for the different fingers of one hand (Simoes et al., 2001). Vicarious somatosensory activations in response to observing an index finger being touched might therefore easily have "spilt over" to cortical regions representing adjacent fingers, modulating somatosensory processing also of tactile stimuli concurrently presented to fingers other than the corresponding index finger. Interestingly, Hoechstetter et al. (2001) found that somatosensory processing of tactile stimuli to an index finger in SI was significantly modulated by concurrent stimuli to other finger sites of the same hand. Processing in SII was even altered by simultaneous tactile input from digits of both hands. If experienced and observed touch share common cortical substrates, it might well be possible that the somatosensory processing of actual tactile stimuli to a finger tip can be influenced by merely "mirrored" touch on a different finger - similar to interactions between simultaneous "real" tactile input to different fingers.

Alternatively, the observation of touch on an index finger might not even have activated specifically the cortical representation of the corresponding finger (which then overlaps with the representation of adjacent skin areas) in the first place but might simply have triggered the somatosensory representation of the whole hand in a rather unspecific fashion. Testing touch observation-related modulation in somatosensory processing also for tactile stimuli delivered to finger not immediately adjacent to the index finger (e.g. the little finger) or e.g. the middle of the palm would allow to shed more light on the question to what extent vicarious somatosensory activation represent different areas within a observed-to-be touched body part. The tactile stimulus locations (within one hand) in the present study might simply have been too densely spaced, given the strong overlap of finger representations in SII (Hoechstetter et al., 2001; Ruben et al., 2001) but also SI (Biermann et al., 1998; Krause et al., 2001; Simoes et al., 2001).

In the statistical main analysis conducted in this study, all four tactually stimulated finger locations were entered in the overall analysis, including the index finger tip of the right, unobserved hand. Both at a behavioural (Schaefer et al., 2005b) and at a neural level (Wood et al., 2010), it has, however, previously been found that observing touch results in effects for the corresponding hand but not at the other, unobserved hand. It was therefore somewhat unexpected that the statistical analysis did not indicate the presence of a significant interaction between the observed tactile feedback and the stimulated finger site for which follow-up analyses might have singled out the index finger of the unobserved hand as a finger location for which somatosensory processing was much less or not at all affected by the observation of touch on the other hand. While an EEG-approach might have allowed to detect small but yet nevertheless consistent touch observation-related modulations during tactile stimulation of the non-homologous index finger, it should also be noted that an explorative analysis (see footnote

11) which included only the anatomically congruent left index finger and the unobserved right index finger (i.e. only the two finger locations compared also by Schaefer et al. (2005b) and Wood et al. (2010) did result in a significant *hemisphere* by *location* by *observed tactile feedback*-interaction for the somatosensory P100 component, with follow-up analyses showing that a significant touch observation induced P100 effect could only be found ipsilaterally for the observed-to-be-touched index finger, but not for the unobserved one. This might tentatively suggest that the SEP modulations for tactile stimuli presented to the homologous finger of the unobserved hand might indeed be much smaller than for stimuli presented to the observed finger. They nevertheless seemed to occur in the same direction, contributing to the finding of finger-unspecific modulation effects if analysed in conjunction with the three other stimulated finger locations of the observed left hand.

Variations in touch observation-related modulations in somatosensory processing as a function of interindividual differences in trait empathy

Standard correlation analyses of the difference in mean SEP amplitude for observed touch vs. no touch for the somatosensory N80 and N140 components and participants' scores on two standard empathy questionnaires revealed that the strength of the SEP modulations was related to the observer's empathic traits in a very complex fashion.

For the long-latency somatosensory N140 component, the extent of the SEP modulation covaried systematically with participants' individual scores on the *personal distress* scale at several electrode sites over and close to contralateral somatosensory cortex: The higher participants scored on this scale, the more pronounced was the increase in N140 mean amplitude during the observation of touch. This subscale of the IRI (Davis, 1983) taps into an aspect of affective empathy and measures feelings of anxiety, apprehension and discomfort in response to observing somebody else's negative experience (e.g. 'When I see someone who badly needs help in an emergency, I go to pieces.'). Unlike in Exp.s 2.1. and 2.2 where the strength of the touch observation-related N140 modulations tended to be contingent on individuals' propensity to show an other-oriented emotional response to others' distress (IRI's *empathic concern*), the correlational relationship revealed here concerned individuals' tendency to exhibit a self-oriented emotional response. Individual differences in the dispositional tendency to respond with distress to others' negative experiences have recently been implicated in the context of internally simulating pain observed on others' faces, with participants high on *personal distress* showing stronger activations in certain (albeit non-somatosensory) brain areas involved in mirroring others' pain (left AI, left IFG; Saarela et al., 2007). The present findings, however, suggest a relationship between this affective empathy component and the tendency to internally simulate others' bodily sensations even in the less affectively laden context of neutral, pain-unrelated touch stimuli and with respect to vicarious activity in somatosensory structures.

The extent of the touch observation induced SEP modulations for the N80 was found to significantly correlate with the EQ's *emotional reactivity* subscale (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004), an empathy scale that is assumed to measure other- rather than self-related emotional responses to others' states, in contrast to the aforementioned *personal distress* subscale of the IRI with which it consequently does not correlate (Lawrence et al., 2004); see also Exp. 2.1 and the present study). Surprisingly enough but similar to the correlational relationship revealed for the very same empathy scale for the SI-associated P50 (Allison et al., 1992; Hämäläinen et al., 1990) in Exp. 2.1, the pattern of empathy-related correlations for the also SI-generated N80 suggested that it was actually the participants with *low* scores on these subscales who showed the strongest SEP modulations during the observation of touch versus no touch on somebody else's hand. This might indicate the possibility that the high temporal resolution of EEG might have allowed to detect an initially counterintuitive relationship between the strength of vicarious somatosensory activity in SI and individuals' emotion-related empathic dispositions which might no longer be detectable when lumping together neural activity across a larger time window (fMRI). Possible mechanisms that might bring about such a counterintuitive effect will be discussed in chapter 2.5.

Overall, the present study suggests that observing somebody else's index finger tip being passively touched alters concurrent somatosensory processing in SI and SII not only for tactile stimuli presented to the onlooker's homologous index finger tip but also for other locations on that very hand (modulations for the other unobserved hand are somewhat unclear and require further testing). The strength of these touch observation-related ERP modulations at different stages of somatosensory processing was found to correlate in a complex fashion with self-reported empathic tendencies to show other- but also self-oriented emotional responses to others' negative experiences.

Experiment 2.4

Body part specificity of touch observation-related vicarious somatosensory activity

2.4.1 Introduction

In Exp. 2.3, participants were tactually stimulated at different finger locations while they observed somebody else's index finger tip being touched with a cotton bud in order to investigate to what extent touch observation-related mirror touch responses in SI and SII might represent the exact skin area within the observed-to-be-touched body part. While it was ultimately unclear whether the sight of touch on an index finger might simply have triggered the somatosensory representation of the whole hand or whether the revealed location-unspecific ERP modulations were due to the strong overlap of the cortical representations of immediately adjacent fingers especially in SII (Hoechstetter et al., 2001; Ruben et al., 2001), but also SI (Biermann et al., 1998; Krause et al., 2001; Simoes et al., 2001), the findings of Exp. 2.3 nevertheless suggest that the degree of somatotopic organisation of vicarious somatosensory activations is not fine-grained enough to distinguish whether the observed touch occurred on the homologous finger tip or e.g. an adjacent skin area on that finger or an entirely different but adjacent finger. At the level of different body parts (rather than different areas *within* a given body part, as tested in Exp. 2.3), this might, however, be quite different. Findings by Blakemore et al. (2005) suggest that somatosensory mirror touch activations might be specific to the observed-to-be-touched body part. What has, however, not be tested yet is whether the sight of touch on a given body part might consequently modulate somatosensory processing only for tactile stimuli presented to that very body part or whether the touch observation-related modulatory effect might also affect somatosensory processing of tactile stimuli to body parts other than the observed one, especially when the cortical representations of the involved body parts are close to each other in the somatosensory cortices. That body-related visual information is capable of modulating tactile processing not only for the viewed body part but also for a body part cortically represented close-by was recently demonstrated in the context of non-informative vision of one's own body by Serino, Padiglioni, Haggard, and Làdavas (2008a): Viewing one's hand (rather than a neutral object positioned in the same spatial location) has been found to improve tactile sensitivity in the viewed hand (Harris, Arabzadeh, Moore, & Clifford, 2007; Kennett et al., 2001; Press, Taylor-Clarke, Kennett, & Haggard, 2004), a cross-modal enhancement effect most likely associated with modulations in SI (Fiorio & Haggard, 2005; Longo et al., 2011; Taylor-Clarke et al., 2002). Importantly, Serino et al. (2008a) showed that viewing the hand did not only improve tactile perception in the viewed hand, but also in the face. Tactile sensitivity in the foot, on the other hand, was unaffected by concurrent sight of the hand. Crucially, the cortical representation of the face is close the one of the hand in the lateral post-central gyrus (Nguyen, Tran, Hoshiyama, Inui, & Kakigi, 2004; Yang, Gallen, Schwartz, & Bloom, 1993), while the foot is represented more medially and much further away from the hand (Nakamura et al., 1998).

While the SI-modulating effect of non-informative vision of one's own body as well as of the actual sight of touch on somebody else's body as such most likely depend on different (yet related) visuotactile mechanisms, it is nevertheless an interesting question whether the sight of touch on somebody's hand might in a similar way not only modulate somatosensory processing of tactile stimuli to the homologous hand but also of tactile stimuli to the face (at least during early-stage somatosensory processing in SI), due to the closeness of the cortical representations of those body parts in SI. To study this issue, participants in the present study observed, similar to Exp.s 2.3, a cotton bud touch either touch a presented hand or merely the empty space next to it. Somatosensory evoked potentials (SEPs) as a measure of somatosensory processing were recorded in response to tactile stimuli presented to three different body parts, namely, in analogy to Serino et al. (2008a), the homologous hand, the face and the foot. Since different somatosensory-related ERP components index either SI or SII activity, it was possible to explore the body part specificity of touch observation-related modulations and thus the issue of how somatotopically organised mirror touch responses for both SI and SII by analysing early as well as late time epochs.

In order to be able to explore possible links between the extent of touch observation-related modulations in somatosensory processing and individuals' empathic dispositions, participants were again asked to complete two standard empathy questionnaires at the end of the experiment.

2.4.2 Methods

Sample. 24 participants were recruited to take part in this study. Three participants (all of whom participated in an EEG study for the very first time) had to be excluded from the analysis after the artifact rejection rendered them with less than 30 trials in one or more of the six conditions. Thus, 21 participants remained in the sample (11 females, 10 males), ranging in age from 18 to 36 years (M = 27.0 years, SD = 4.7). All but one were right-handed and all had normal or corrected-to-normal vision by self-report. All participants were naive as to the purpose of the study and gave written consent to participate after being informed in detail about the involved procedures, in particular with respect to the EEG recording and the (non-painful) tactile stimulation of their hand, face and foot. The study was approved by the local ethics committee.

Stimuli. The task-irrelevant visual stimuli were the same as those used in Exp. 2.3, depicting a cotton bud approach and then either touch a left hand on the finger tip or merely the empty space next to it.

The task-irrelevant tactile stimuli were presented by means of the same tactile stimulator described in Exp.s 2.1-2.3. Three different body locations were tactually stimulated: The left index finger tip as the body part anatomically congruent to the one actually observed to be touched, the left facial cheek and the bottom side of the left big toe. Adhesive tape was used to attach the tactile stimulator to the respective body part during stimulation. White noise was continuously played through two loudspeakers positioned to the right and the left of the computer screen to make sure participants could not hear the tactile stimuli being delivered. Since the stimulator was quite close to the ears during tactile face stimulation, participants were, in addition, asked to wear foam earplugs.

The presentation of both the visual and the tactile events was controlled using E-Prime (Psychology Software Tools, Inc, version 1.1).

Procedure. Experimental set-up, task and procedure were the same as in Exp. 2.3 with the following exceptions: Rather than stimulating different finger locations across both hands, varying the extent to which the tactually stimulated finger location matched the observed-to-be-touched finger location, different body parts were stimulated: For four consecutive blocks each, participants were presented with tactile stimuli to their left index finger tip (as the finger location matching the one being seen to be touched), their left facial cheek (as body part whose somatosensory representation in the somatosensory cortex is adjacent to the one of the hand; Nguyen et al., 2004; Yang et al., 1993) and their left big toe (as body part whose somatosensory representation in the somatosensory cortex is more distant from the one of the hand). The order in which the respective body parts were stimulated (6 possible orders) was counterbalanced across participants. During foot stimulation, participants were asked to remove their left shoe and sock and to rest their left foot on a foam cushion. This was to make sure that the attached stimulator did not touch the floor.

The sequence and timing of the visual and tactile stimuli (to a given body part) in each trial were exactly the same as in Exp. 2.3 (see also Fig. 2.4.a). In each block, participants observed the cotton bud either touch the hand or the empty space next to it, respectively, on again 25 trial each, presented in random order. The number of randomly interspersed catch trials was, however, increased by three (as compared to Exp. 2.3), resulting in a total number of 62 trials per experimental block (approx. 19 % catch trials). Participants performed four consecutive blocks for each of the three stimulated body parts, resulting in a total of 12 experimental blocks.

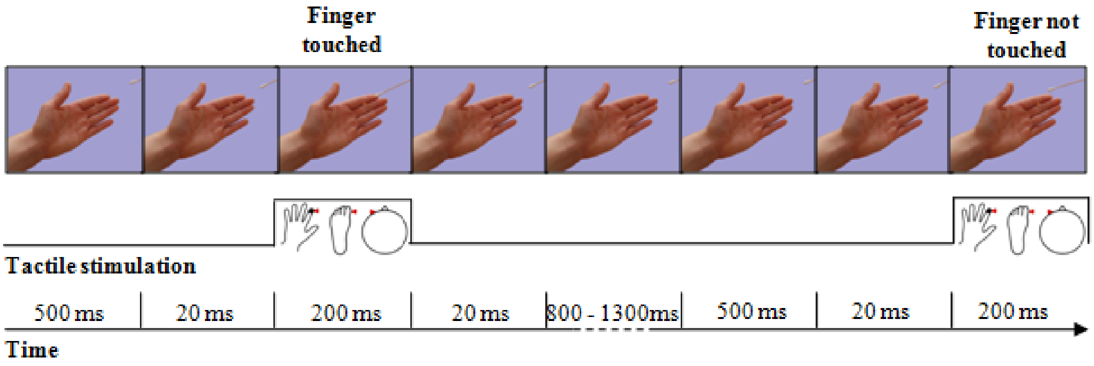


Fig. 2.4.a. Schematic representation of the typical sequence of visual and tactile events in *touch* and *no touch* trials, respectively. The body part icons depict the three different tactually simulated body locations. The finger tip anatomically congruent with the observed-to-be-touched finger tip is highlighted in black. Which body part was stimulated was manipulated blockwise.

Prior to attaching the tactile stimulator to a given body part to tactually stimulate it for a set of four blocks, the experimenter gently touched the respective body location twice with a cotton bud. While participants were told that this was done to show them exactly where the tactile stimuli would be presented next, it was in fact a casual reminder to them of what being touched with a cotton bud feels like, without drawing their attention to this too much. A very short demo of the visual stimuli was shown only once at the very beginning of the testing session (two trials for each observational condition, presented in random order), followed by a practice block (equivalent to an experimental block except for a reduced number of trials: 22 trials in total in random order, 6 catch trials) to familiarise participants with the colour change detection task at hand prior to the actual experiment.

At the end of the testing session, participants completed both the 60-item EQ questionnaire (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) and the 28-item IRI questionnaire (Davis, 1983). The order in which the two standard empathy questionnaires were completed was counterbalanced across participants.

Data and recording. As an exception from all other ERP studies in this thesis, continuous EEG in this experiment was recorded from 59 Ag-AgCl scalp electrodes using an Easycap 64-channel system with active electrodes. The electrodes were positioned equidistantly on the scalp surface with an inter-electrode distance of 37 ± 3 mm (given a head circumference of 58 cm). Fig. 2.4.b shows the arrangement of the electrodes on the head. While an average reference of all electrodes would have been more appropriate given the number of electrodes in this study, all scalp electrodes were nevertheless again referenced to an electrode on the right earlobe and re-referenced off-line to an average of both ear lobes for the subsequent analysis to keep the recording settings as similar as possible with respect to the other ERP studies in this thesis. A frontal midline electrode served as ground electrode. The horizontal electrooculogram (HEOG) was recorded bipolarly from two scalp electrodes close to the outer canthi of both eyes to detect horizontal eye movements (channels 51 and 61). The vertical electrooculogram (VEOG) was recorded bipolarly from two electrodes positioned above and below the right eye (channels 64 and 36).

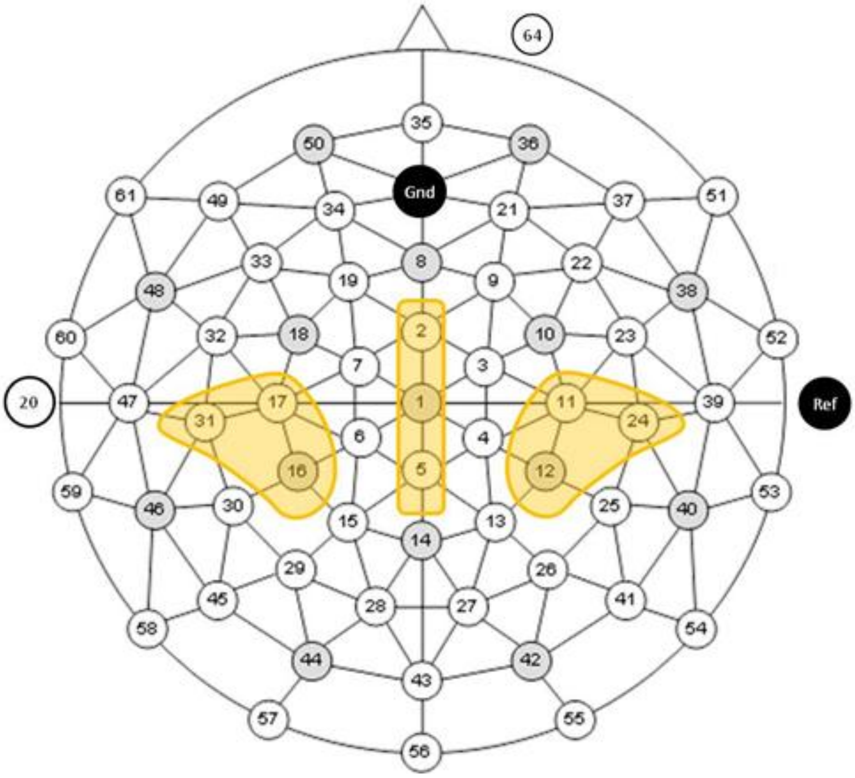


Fig. 2.4.b. Equidistant 61-channel-arrangement for Exp. 2.4 (as adapted from the manufacturer’s M10 montage: http://www.easycap.de/easycap/e/electrodes/13_M10.htm). The electrode clusters included in the statistical analyses are highlighted in orange.

EEG and EOG were sampled at a digitisation rate of 500 Hz with a bandpass filter of 0.016 to 100 Hz and subsequently filtered off-line with a low pass filter of 30 Hz.

EEG data were analyzed using Brain Vision Analyzer software (version 1.05; Brain Products GmBH, Gilching, Germany). EEG and EOG were segmented off-line into 500 ms epochs starting 100 ms before the onset of the tactile stimulus until 400 ms thereafter, epoched separately for all six combinations of observed tactile feedback (touch vs. no touch) and stimulated body part (hand, face, foot). Artifact rejection criteria for (horizontal and vertical) eye movements, eye blinks and other artifacts on a given trial were the same as in Exp. 2.3. Trials in which a (correct or incorrect) vocal response occurred were also removed. For the remaining trials, ERPs for tactile stimuli were averaged relative to a 100 ms pre-stimulus baseline for all six combinations of observed tactile feedback and stimulated body part.

Statistical analyses. Importantly, the statistical analyses for this experiment were based on only a small subset of central and centro-parietal electrodes over both hemisphere as well as the midline. Unlike the hand and the face which are represented in lateral parts of the somatosensory cortex (Nguyen et al., 2004; Yang et al., 1993), resulting in ERP waveforms in response to tactile stimuli to either of the two body parts that are clearest over lateral electrode sites, the foot is represented more medially (Nakamura et al., 1998) and respective SEP amplitudes tend to be largest over the midline electrodes (e.g. Xu et al., 1995). For this reason, midline electrodes were incorporated in the analysis. The included electrode sites were channels 17, 31 and 16 over the hemisphere ipsilateral to the tactually stimulated body part (roughly corresponding to C3, C5 and Cp3 in the international 10-20 system), homologous channels 11, 24 and 12 over the hemisphere contralateral to the tactually stimulated body part (roughly corresponding to C4, C6 and Cp4) and channels 2, 1 and 5 over the midline (corresponding to Fcz, Cz and Cpz). Fig. 2.4.b shows the respective electrode clusters highlighted in orange.

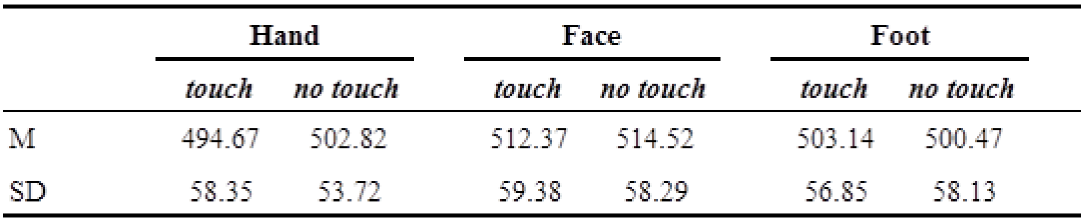
Since tactile stimuli were found to evoke slightly different ERP waveforms with different peaks and peak latencies for the three different body locations, the effect of observing a model's hand being touched on concurrent somatosensory processing was analysed separately for the three stimulus locations. In this way, different time epochs – based on the identified ERP peaks – could be chosen for analysis (see below). The ERP mean amplitudes for a given latency window and body part were then subjected to a 3 x 2 x 3 repeated measures ANOVA with the within-subject factors *electrode cluster* (ipsilateral vs. contralateral vs. midline), *observed tactile feedback* (touch vs. no touch) and *electrode site*. Importantly, also interactions involving the factor *electrode site* were considered here. Any significant interactions between the *observed tactile feedback* and *electrode cluster* were followed up with separate ANOVAs for the three electrode clusters. Significant interactions involving the *observed tactile feedback*, *electrode cluster* and *electrode site* were followed up with t-tests comparing the effects of the sight of touch at separate electrodes. Greenhouse-Geisser adjustments to obtained p-values in the conducted ANOVAs were applied where appropriate. If a significant effect of the observed tactile feedback was indicated for a given body part and latency, a standard correlational analysis was conducted using Spearman's rank correlation coefficient to test whether the strength of the revealed SEP modulation (mean $\text{amplitude}_{\text{touch}}$ – mean $\text{amplituden}_{\text{otouch}}$) varied with participants' self-reported empathic skills as quantified by their EQ and IRI scores.

2.4.3 Results

Behavioural performance

Participants detected 99.8% of the infrequent colour changes of the fixation cross and produced only very few false alarms (< 1 %), indicating that they paid very close attention to the visual display. Response times (see Table 2.4.a) did not differ as a function of the observed tactile feedback (F(1,20) = 1.020, p = .325, η^2_p = .049) but they did vary as a function of the tactually stimulated body part (F(1,20) = 3.815, p = .030, η^2_p = .160): Follow-up comparisons indicated that response times were somewhat slower when tactile stimuli were presented to the face (M = 513.45 ms, SD = 12.62) rather than to the hand (M = 498.74 ms, SD = 12.01) or the foot (M = 501.81 ms, SD = 12.41) (t(20) = -2.630, p = .016 and t(20) = -.510, p = .038, respectively). With a Bonferroni-adjusted significance level of α = .0167, only the response time difference between hand and face stimulation remained significant. Participants might have found tactile stimulation in the face more distracting than tactile stimuli to the hand and, tendentially, also compared to the foot, which might have slowed them down slightly in the experimental task at hand. There was, however, no significant interaction between the stimulated body part and the observed tactile feedback (F(2,40) = 1.521, p = .231, η^2_p = .071).

Table 2.4.a. Reponses times for detecting infrequent colour changes of the fixation cross as a function of the concurrently tactually stimulated body part and the observed tactile feedback.



	Hand		**Face**		**Foot**	
	touch	*no touch*	*touch*	*no touch*	*touch*	*no touch*
M	494.67	502.82	512.37	514.52	503.14	500.47
SD	58.35	53.72	59.38	58.29	56.85	58.13

Electrophysiological data

Fig. 2.4.c shows the ERP waveforms elicited by task-irrelevant tactile stimuli to participants' left index finger tip, left facial cheek and left big toe at three representative electrode sites included in the statistical analysis (ipsilateral vs. contralateral hemispheres vs. midline). Tactile stimulation to the hand (see top panel in Fig. 2.4.c) elicited the typical sequence of ERP deflections also seen in previous data sets in this thesis: A contralaterally positive and ipsilaterally negative peak at around 48-54 ms post-stimulus onset (P50), followed by a contralateral negative peak at approximately 76-82 ms (N80), a bilaterally positive peak at

108-112 ms (94-96 ms ipsilaterally) (P100) and an also bilaterally observable negative peak between 142 – 162 ms (N140). The first clearly discernible peak elicited by tactile stimuli delivered to the face (see middle panel in Fig. 2.4.c), on the other hand, was a positive deflection at a latency of 94-98 ms over the contralateral hemisphere (possibly comparable to a P100 during hand stimulation, taking into account that ERPs in response to face stimuli tend to peak somewhat earlier due to the shorter conduction time (Larsson & Prevec, 1970) which peaked earlier (74-84 ms) and was less pronounced over the ipsilateral hemisphere. This was followed by a clear negative deflection visible over both hemispheres between 124 to 138 ms post-stimulus onset (N140). There were also some earlier ERP deflections in response to tactile stimulation to the face which could be characterised as a N40-P50-N65 sequence but the amplitudes of these deflections were very small, especially in comparison with the subsequent components P100 and N140 components.

As for tactile stimuli to the foot, a clearly discernible ERP deflection within the first 200 ms after presentation of the tactile stimulus could only be found over midline electrodes where there was a negative peak between 92-94 ms post-stimulus onset (N90). This was followed by a large positivity with a maximum across the analysed electrodes between 218 and 234 ms (see the midline electrode in the bottom panel in Fig. 2.4.c).

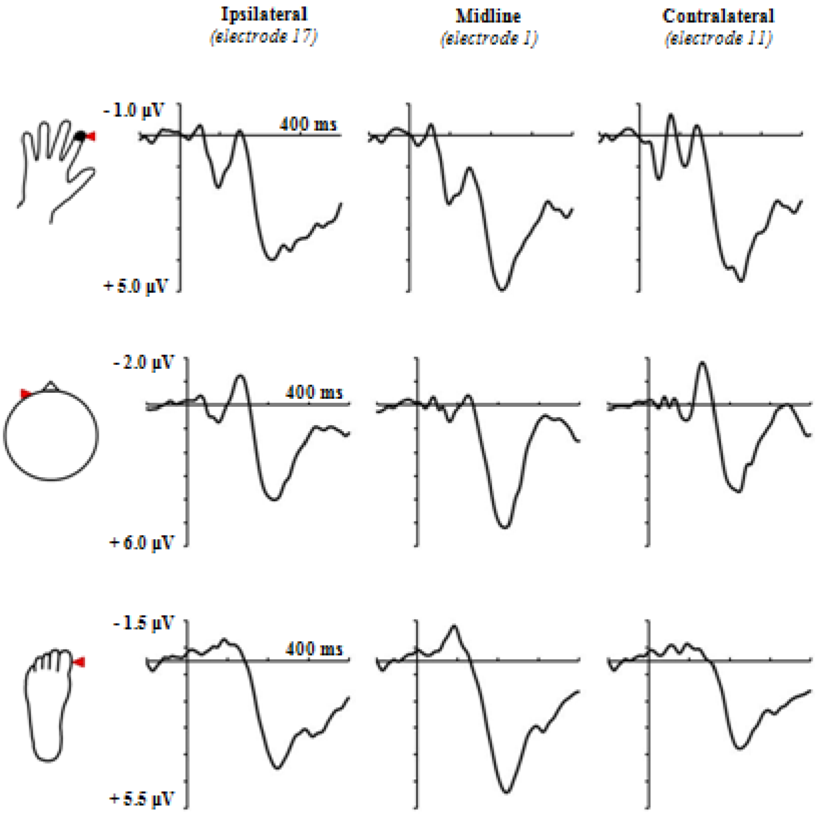


Fig. 2.4.c. ERP waveforms in response to tactile stimuli presented to the hand (top), the cheek (middle) and the big toe (bottom) at three representative electrodes over the ipsilateral (electrode 17) and contralateral (electrode 11) hemispheres as well as over the midline (electrode 1).

Since tactile stimuli thus clearly evoked ERP waveforms with different peaks and peak latencies for the three different body locations, the effect of observing a model's hand being touched on concurrent somatosensory processing was analysed separately for the three stimulus locations. Different time epochs – based on the ERP peaks identified for each stimulated body part by visual inspection of the ERP waveforms at the analysed electrode sites – were thus chosen for analysis: For hand ERPs, the analysed time epochs were 40-60 ms post-stimulus onset (P50), 70-95 ms post-stimulus onset (N80), 95-120 ms post-stimulus onset (P100) and 140-170 ms post-stimulus onset (N140), similar to the latency ranges selected in Exp. 2.1-2.3. For the face ERPs, the time epochs 75-105 ms and 135-170 ms after tactile stimulus onset were chosen for analysis. For the sake of completeness, it was also attempted to analyse the very small components evoked immediately after stimulus onset by means of very narrow 10 ms time windows (35-45 ms (N40), 45-55 (P50) ms, 60-70 ms (N65)). As for the foot ERPs, the only analysed time epoch was the 80-110 ms post-stimulus onset interval since this latency range was the only one that contained a discernible SEP component at midline electrodes. Importantly, if a significant touch observation-related ERP modulation was revealed for a given body part and a given latency window, the very same latency window was then also tested for touch observation-related ERP differences during tactile stimulation of the other two body parts to clarify to what extent the revealed modulation in a given time window was body part-specific.

Touch observation-related effects on concurrent somatosensory processing of tactile stimuli to the hand

Fig. 2.4.d contrasts the ERP waveforms evoked by tactile stimulation of the hand during the observation of the model's hand being either touched or merely approached at all analysed electrodes. Here, the sight of somebody else's hand being touched by a cotton bud modulated concurrent somatosensory processing only in the 70-95 ms post-stimulus latency range (N80) where a significant main effect of the *observed tactile feedback* was found ($F(1,20) = 4.934$, $p = .038$, $\eta^2_p = .198$). The mean SEP amplitude in this time epoch was significantly less-negative going when the cotton bud touched the hand rather than the empty space next to it (see, for instance, electrode 12 in Fig. 2.4.d). This small effect was restricted to somatosensory processing of tactile stimuli to the hand. Processing of tactile stimuli to the face or to the foot was not altered in this very latency range by the sight of touch to a hand (for all F for main effects of the factor *observed tactile feedback* as well as for interactions involving this factor: $F \leq .864$, $p \geq .429$, $\eta^2_p \leq .041$ and $F \leq 2.615$, $p \geq .086$, $\eta^2_p \leq .116$, respectively).

The somatosensory P50 and N140 components, on the other hand, did not show any modulations in their mean amplitude at all, neither in the form of a main effect of the *observed tactile feedback* (both $F(1,20) \leq .891$, $p \geq .357$, $\eta^2_p \leq .043$) nor in the form of any interactions involving this factor (all $F \leq 2.061$, $p \geq .141$, $\eta^2_p \leq .093$). For the 95-120 ms post-stimulus latency arrange associated with the somatosensory P100 component, a *hemisphere* by *electrode site* by *observed tactile feedback*-interaction did reach significance ($F(4,80) = 3.388$, $p = .041$, $\eta^2_p = .143$) but pairwise comparisons to identify the respective electrode sites did not yield any significant results (all $t(20) \leq .1.608$, $p \geq .123$).

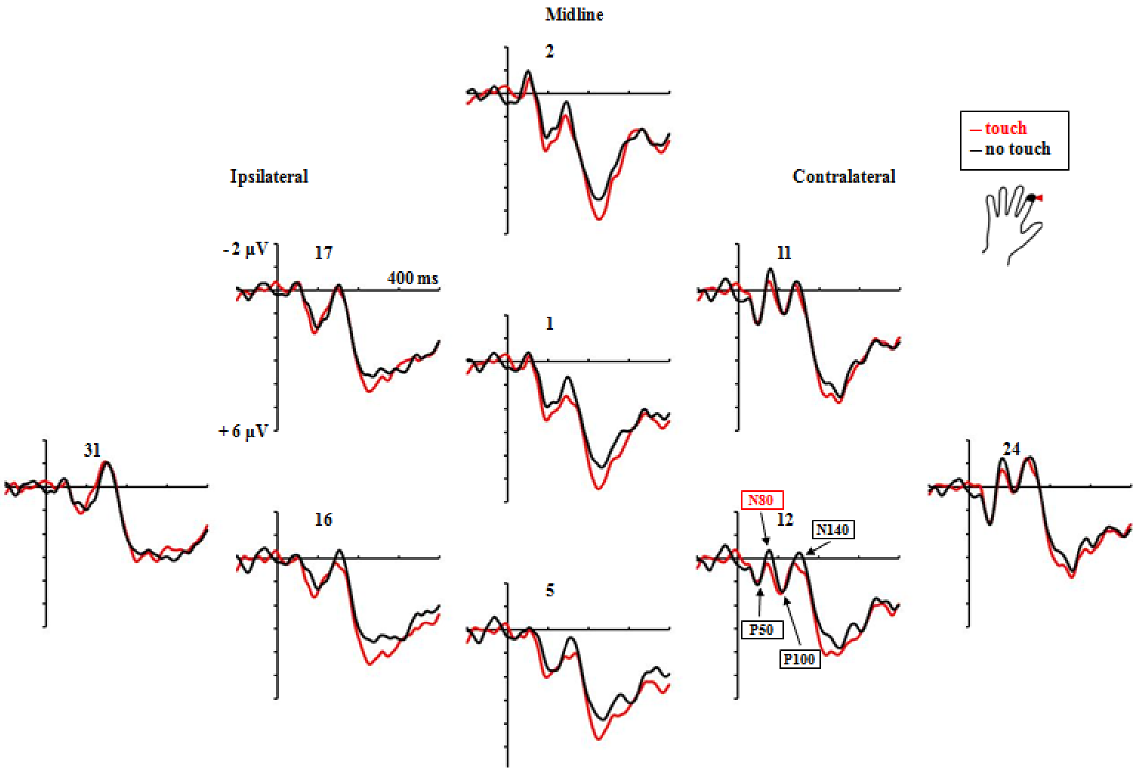


Fig. 2.4.d. ERP waveforms in response to tactile stimuli presented to the hand during the observation of a cotton bud either touch (red line) a model's hand or merely the empty space next to it (black line). The analysed components are indicated at electrode 12.

Touch observation-related effects on concurrent somatosensory processing of tactile stimuli to the face

As far as the very small and difficult to distinguish ERP deflections immediately after tactile stimulus onset were concerned (N40-P50-N65), no significant effects of the sight of touch on somatosensory processing were found (for all main and interaction effects involving the factor *observed tactile feedback*, all $F \leq 1.608$, $p \geq .180$, $\eta^2_p \leq .074$; following-up a just significant *electrode site* by *observed tactile feedback*-interaction in the 45-55 ms latency range (P50) did also not reveal any significant modulations for a subset of electrodes).

The two time epochs in which more clearly discernibly ERP deflections occurred during tactile stimulation to the face where the latency ranges 75-105 ms and 135-170 ms post-stimulus onset. In the former, no systematic effects of the *observed tactile feedback* on somatosensory processing were found either (all $F \leq .874$, $p \geq .425$, $\eta^2_p \leq .042$). In the subsequent latency range, however, the observation of touch on a hand did affect somatosensory processing in that the mean N140 amplitude was significantly more negative-going when the cotton bud made contact with the model's hand rather than merely move through empty space ($F(1,20) = 4.451$, $p = .048$,

$\eta^2_p = .182$). Yet again, this effect was small but specific to somatosensory processing of tactile stimuli to the face while a hand seen to be touched. No such modulation in the same latency range was found during hand or foot stimulation (for all F for main effects of the factor *observed tactile feedback* as well as for interactions involving this factor: $F \leq 2.010$, $p \geq .147$, $\eta^2_p \leq .091$ and $F \leq 1.693$, $p \geq .208$, $\eta^2_p \leq .078$, respectively). Fig. 2.4.e contrasts the ERP waveforms evoked by tactile stimulation of the face during the observation of a cotton bud touch a hand or merely the empty space next to it.

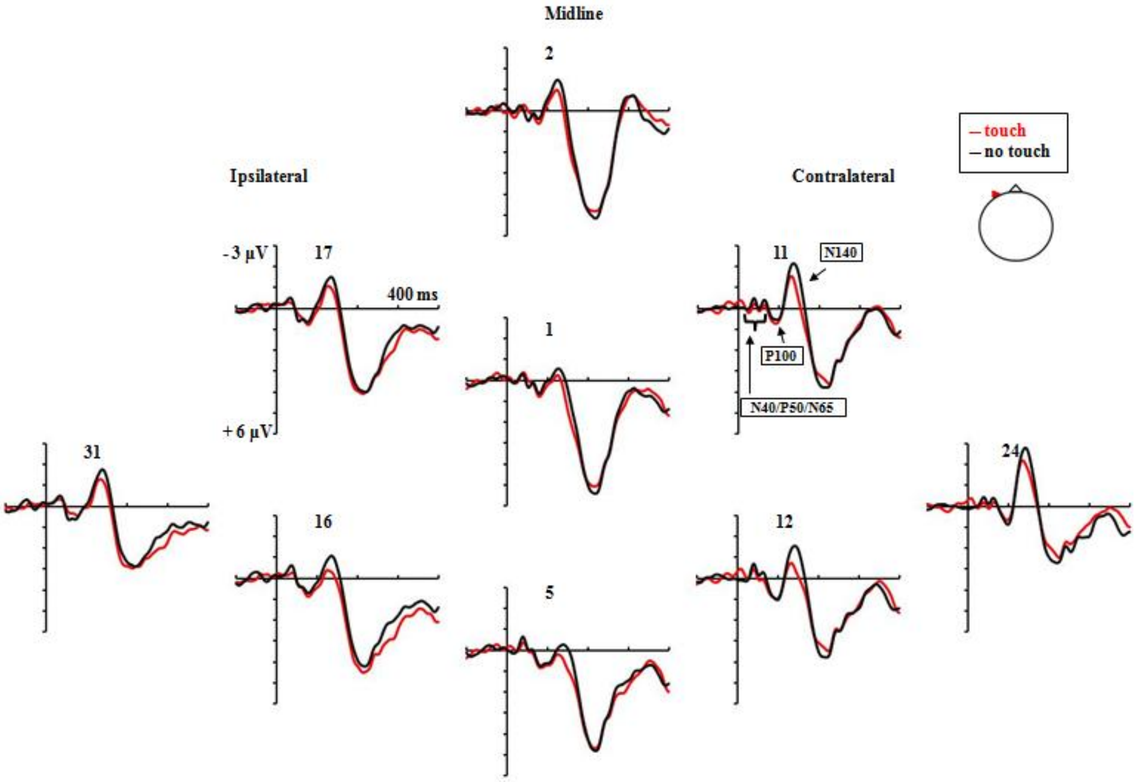


Fig. 2.4.e. ERP waveforms in response to tactile stimuli presented to the face during the observation of a cotton bud either touch (red line) a model's hand or merely the empty space next to it (black line). The analysed components are indicated at electrode 11.

Touch observation-related effects on concurrent somatosensory processing of tactile stimuli to the foot

Early somatosensory processing of tactile stimuli to the foot was not found to be significantly altered by the sight of touch on a hand in the 80-110 ms latency range where the only clearly discernibly ERP deflection within the first 200 ms post-stimulus onset was observed (for all F for main effects of the factor *observed tactile feedback* as well as for interaction involving this factor: $F \leq 1.777$, $p \geq .182$, $\eta^2_p \leq .082$). Fig. 2.4.f depicts the somatosensory ERP waveforms in response to tactile stimulation of the foot during the observation of a hand being touched or merely approached.

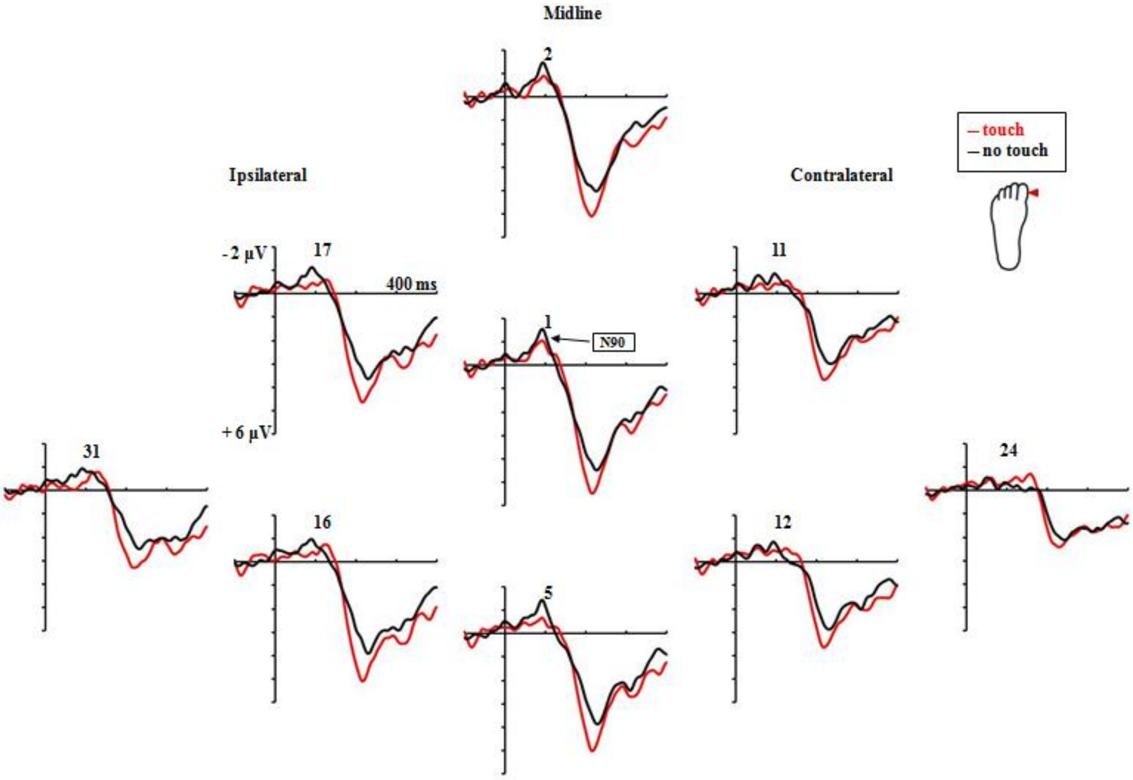


Fig. 2.4.f. ERP waveforms in response to tactile stimuli presented to the foot during the observation of a cotton bud either touch (red line) a model's hand or merely the empty space next to it (black line). The analysed component is indicated at midline electrode 1.

Empathy correlations

Table 2.4.b shows the trait empathy measures obtained with the two standard empathy questionnaires EQ (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) and the IRI (Davis, 1983) at the end of the experiment.

Table 2.4.b. Mean scores and standard deviations for the self-report measures of dispositional empathy.

	Empathy Quotient (EQ)				Interpersonal Reactivity Index (IRI)			
	Total	CE	ER	SS	PT	FS	EC	PD
Sample (N=21)	47.24	13.86	13.86	6.05	18.62	19.67	20.81	13.62
	9.87	4.51	4.59	2.18	5.11	5.99	4.84	6.23
Normative data[a]	46.20	n/a	n/a	n/a	17.37	n/a	20.36	10.87
	(10.60)	n/a	n/a	n/a	*(4.79)*	n/a	*(4.02)*	*(4.78)*

[a] Normative data are derived from: Lawrence et al., 2004 (EQ) and (Bellini, Baime, & Shea, 2002) (IRI).

EQ: CE = Cognitive Empathy ER = Emotional reactivity SS = Social skills

IRI: PT = Perspective taking FS = Fantasy scale EC = Empathic concern PD = Personal distress

Maximal scores: Total score of EQ = 80; Cognitive empathy (EQ) = 22, Emotional reactivity (EQ) = 22, Social skills (EQ) = 12; each subscale of the IRI = 28.

Systematic correlations between the strength of touch observation-related SEP modulations and individual levels of trait empathy were only found for the N80 effect during hand stimulation where almost all analysed electrode sites showed significant correlations with the *cognitive empathy* subscale of the EQ (1: $r_s(21) = -.575$; 11: $r_s(21) = -.477$; 12: $r_s(21) = -.460$; 17: $r_s(21) = -.524$; 2: $r_s(21) = -.466$; 5: $r_s(21) = -.477$; all $p < .05$; 31 showed a marginally significant interaction: $r_s(21) = -.430$, $p = .052$). Statistically, these correlations indicated that the higher participants scored on this subscale, the less likely they were to show a pronounced reduction in negative SEP mean amplitude in the 70-95 ms latency range during the sight of touch. For some participants, medium to higher scores were also associated with a reversed effect (see Fig. 2.4.g).

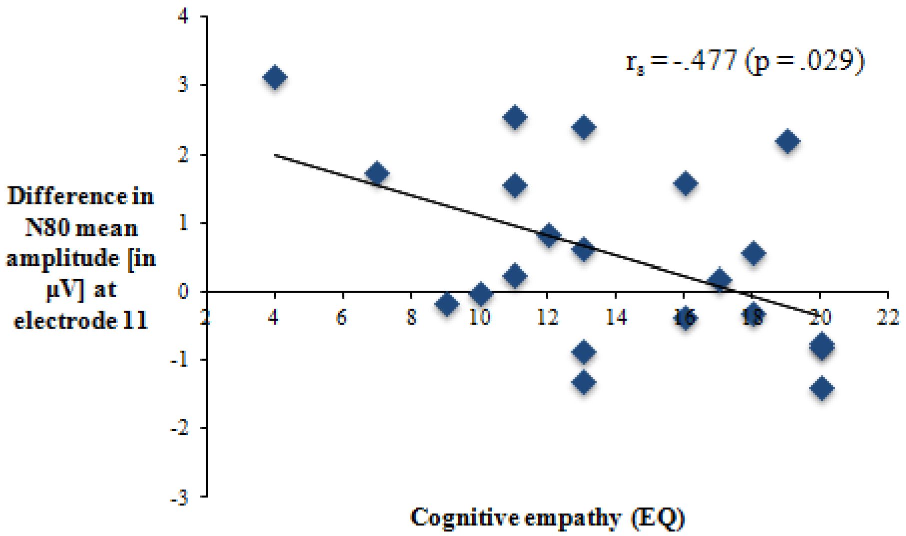


Fig. 2.4.g. Difference in N80 mean amplitude (touch - no touch) at a representative contralateral electrode (electrode 11) during tactile hand stimulation as a function of self-reported levels of *cognitive empathy* (EQ).

2.4.4 Discussion

The aim of the present study was to investigate whether the sight of touch on somebody else's body modulates somatosensory processing only for the observer's corresponding body part or whether a touch observation-related modulatory effect might also spread to other body parts, especially to those whose cortical representation (in SI) is close to the one of the observed-to-be-touched body part. To this end, participants observed a cotton bud either touch or merely approach somebody else's hand while somatosensory-related ERPs were evoked by tactile stimuli to either participants' own hand or, crucially, their face or their foot. While hand and face are represented in close spatial proximity in SI (Nguyen et al., 2004; Yang et al., 1993), the foot is presented more medially (Nakamura et al., 1998) and thus more distant from both hand and face.

Before discussing the actual results, it should be pointed out that the analysis of the SEPs elicited by tactile stimulation to different body parts entailed the problem as to how to deal with body part specific peculiarities in the evoked waveforms per se: Due to the different conduction distances from the stimulated body site to the brain, somatosensory ERPs in response to face stimulation tend to peak somewhat earlier than those in response to hand stimulation (Larsson & Prevec, 1970: approx. 16 ms earlier) while foot-related SEPs usually peak 20-30 ms later than hand-related SEPs (Kany & Treede, 1997; Treede, Kief, Hölzer, & Bromm, 1988). While these differences in neural transmission times could have been taken into account by simply shifting the to-be-analysed windows for face and foot ERPs accordingly (rather than using the same time epochs selected for analysis of the hand ERPs; see Heed & Röder, 2010), it was found that the ERP waveforms elicited by face and foot stimulation were altogether somewhat different from typical and easily discernible P50-N80-P100-N140 complex in response to somatosensory hand stimulation: Tactile stimuli to the face evoked a clear bilateral positive deflection followed by a similarly bilateral negative deflection that resembled the P100 and N140 components usually observed during hand stimulation (albeit with slightly earlier latencies); these, were, however, in contrast to the hand ERPs, preceded by a sequence of several unusually small positive and negative peaks. Tactile stimuli to the foot, on the other hand, elicited only one clearly discernible ERP deflection within the first 200 ms after tactile stimulus onset, namely a negative peak after approximately 90 ms, which could, however, only been seen at the midline electrodes (see also Xu et al., 1995), in line with the medial position of the foot representation in somatosensory cortex (Nakamura et al., 1998). Due to the fact that the evoked waveforms did apparently not simply differ with respect to the latencies of the elicited ERP deflections but also with respect to their general form, it was decided to analyse possible touch observation-related entirely separately for the three tactually stimulated body parts, selecting time epochs based on a visual inspection of the respective waveforms. However, *if* a touch observation-related ERP modulations was revealed for a given time epoch for a given body part, the very same time interval (i.e. without adjusting for the difference in transmission time) was tested for modulations also during stimulation of the other two body parts to check the degree of body part specificity at this very latency range.

Touch observation-related effects on concurrent somatosensory processing of tactile stimuli to the hand

In the present study, the only somatosensory-related ERP component that was found to be modulated in response to the observation of touch on a model's hand when participants were themselves tactually stimulated on the hand was the N80 component. Since this somatosensory component is thought to arise from contralateral SI (Allison et al., 1992), this touch observation-related modulation suggests once again that the observation of others' touch experiences is not a purely visual process but recruits parts of the observer's own somatosensory system, such as SI (Blakemore et al., 2005; Bufalari et al., 2007; Ebisch et al., 2008; Pihko et al., 2010; Schaefer et al., 2012; 2009; Wood et al., 2010). Importantly, a touch observation-related change in ERP amplitude in the N80 latency range of 70-95 ms after tactile stimulus onset was specific to tactile stimulation of the hand and could not be found in this time interval during tactile stimulation of neither the face nor the foot. This hand-specificity seems to indicate that the sight of touch on somebody else's hand triggers vicarious somatosensory activity in SI in a highly somatotopically organised fashion, activating the hand area seemingly in such a localised fashion that activity did not even spread to the adjacent face area (let alone the even more distant foot area) to modulate early processing of face stimuli. Blakemore et al. (2005) previously demonstrated that the sight of touch on a human face and a human neck activate separate, non-overlapping areas in SI. While face and neck are physically close, their cortical representations in SI are, however, quite distant and unlikely to overlap anyway. The present findings thus extends the body part specificity of touch observation-related mirror touch responses in SI even to body parts represented immediately adjacent of each other in SI (hand and face).

While the presence of an ERP modulation in the N80 latency range during the sight of touch on a hand was specific to concurrent tactile stimulation of participants' own hand, it is important to note that the qualitative nature of the revealed N80 modification was inconsistent with the N80 effect found in Exp.s 2.2 and 2.3 in this thesis: Here, the observing the cotton bud touch the hand rather than the empty space next to it was associated with a decrease of N80 mean amplitude whereas Exp.s 2.2 and 2.3 suggested a relative increase. An additional discrepancy was the absence of any significant touch observation-related ERP modulations at longer latencies: Exp. 2.1, 2.2 and 2.3 had implicated the SII-related somatosensory P100 and/or

N140 components (Allison et al., 1992; Hämäläinen et al., 1990; Tarkka et al., 1996; Valeriani, et al., 2001a) as possible neural correlates of mirror touch responses, in line with neuroimaging evidence suggests that also SII is involved in the embodiment of observed touch (Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Schaefer et al., 2012; 2009). It should, however, be noted that the N140 modulations in Exp. 2.1, 2.2 and 2.3 and the P100 effect in Exp. 2.3, respectively, were found in the form of general ERP amplitude changes when collapsing across different touch targets (Exp. 2.1), viewing perspectives (Exp. 2.2) or stimulated finger locations (Exp. 2.3), respectively, increasing the statistical power with which (potentially small) but nevertheless consistent effects can be detected as statistically significant (as long as the modulation occur in the same direction/are sufficiently similar in the different conditions). In the present study, touch observation-related ERP modulation during tactile index finger stimulation, were, on the hand, analysed in isolation, making it more difficult to detect mirror touch responses if these were to be only small. In addition, the statistical analysis of possible ERP modulations in the present study was conducted only on a small subset of central and centro-parietal electrodes over the both hemispheres as well as the midline, while the analyses in the previous experiments in this chapter were based on almost all recorded scalp electrodes, grouped into four electrode clusters, comprising posterior as well as anterior electrode sites. A visual inspection of the ERP waveforms obtained during hand stimulation in the present study suggested, however, that touch observation-related modulations tended to be present only in a very localised fashion at electrodes over and close to the somatosensory cortex. Initial analyses based on a similarly wide-spread selection of electrodes as in the previous three experiments did indeed fail to yield any significant ERP modulations during tactile hand stimulation (including the N80), even if they were merely extended to include more posterior-parietal electrodes (note that statistical analyses and/or the scalp maps in Exp.s 2.1, 2.2. and 2.3 had usually pointed to a maximum of the touch observation-related ERP amplitude difference over posterior-parietal electrode sites for e.g. the N140).

All in all, the touch observation-related ERP modulations during tactile hand stimulation in the present study deviated quite substantially from the pattern of modulations found in Exp.s 2.1, 2.2 and 2.3, with a decrease rather than an increase of the ERP amplitude in the N80 latency range in response to the sight of touch, the restrictedness of the N80 effect to only very few central/centro-parietal electrodes and an absence of any ERP modulations in the P100/N140 latency range[14]. Participants' EEG in the present study was recorded with a different EEG system than in the previous studies, namely with a 64-channel system with active electrodes

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[14] Note that the visual inspection of the ERP waveforms in response to hand stimulation suggested that the N140 amplitude was also reduced rather than enlarged during the sight of touch, in contrast to Exp. 2.1, 2.2 and 2.3.

rather than with the standard 32-channel system with passive electrodes. It is, however, rather unlikely that the described inconsistencies are simply due to the different EEG setup: The sampling rate in the present study was lower than in the previous studies, but the crucial location of the reference and ground electrodes during recording was the same, as was the offline re-referencing and filtering procedures. An initial speculation was that having previously been stimulated at one or even two non-homologous, i.e. non-observed body part(s) might have influenced the perception of touch on a hand when participants' own hand was eventually tactually stimulated: The order in which the hand, face and foot were stimulated was counterbalanced but this also meant that a considerable number of participants were presented with face and/or foot stimulation prior to hand stimulation. While the sample was not sufficiently large to analyse order effects in a statistically sound fashion, descriptive statistics suggested, however, that, for instance, the N80 amplitude was decreased also when hand stimulation condition was run as the very first experimental condition, indicating that the unexpected reversal of the N80 modulation was not associated with having been stimulated at non-observed body part first.

That a significant N80 modulation as such was found in the present study as well as in Exp.s 2.2 and 2.3 suggests, however, that this SI-associated SEP component might nevertheless be a somewhat reliable neural correlate of touch observation-related changes in somatosensory processing; future studies will, however, have to address what factors determine in what specific way this ERP component is eventually modulated in the context of observing touch on somebody else's body. The finding that the strength of the N80 modulations was yet again correlated with a self-report measure of trait empathy (see below) points to the possible role of systematic individual differences in the extent and the way in which the somatosensory system is recruited when touch-related visual input is processed. It might be this interindividual variability which results in somewhat inconsistent findings across studies with relatively small samples. Rather than discarding electrophysiological correlates of mirror touch responses as unreliable, these individual differences should be explored in more detail.

Touch observation-related effects on concurrent somatosensory processing of tactile stimuli to the face (but not the foot – or the hand)

The research question of interest in the present study was whether the sight of touch on somebody else's hand modulates somatosensory processing only for the (homologous) hand or whether the modulatory effect might also spread to other body parts. The initial assumption was that if the sight of touch were to be found to modulate somatosensory processing in SI also for body parts other than the hand, it would most likely be the face (and not the foot), since triggered vicarious somatosensory activity in the hand area could quite easily spread to the adjacent face area (Nguyen et al., 2004; Yang et al., 1993). As discussed above, an early-latency touch observation-related SEP modulation (N80) was, however, exclusively found during tactile hand stimulation whereas early-stage somatosensory processing during not only foot but, more crucially, also face stimulation was entirely unaffected by the concurrent sight of touch on a hand. Vicarious somatosensory activity in SI thus seem to be highly specific to the observed body part, spreading not even to cortically immediately adjacent represented body parts (face). Due to the generally less fine-grained somatotopic organisation in SII (Hari et al., 1993; Maeda et al., 1999) and previous findings of necessarily body part-unspecific mirror touch responses in SII during the sight of touch on objects (Ebisch et al., 2008; Keysers et al., 2004; Exp. 2.1), it had been unclear what degree of body part specificity to expect for SII. Interestingly enough, observing a hand being touched was indeed found to have a modulatory effect on (probably) SII-related somatosensory processing for a body part other than the hand: The sight of touch on hand resulted in a significant decrease in ERP amplitude at an N140-like latency range during tactile face stimulation. Curiously enough, this modulation was specific to face stimulation and could not be found during hand stimulation (and also not during foot stimulation for that matter). That no comparable N140 modulation was found for the hand and thus for the actually observed body part makes the interpretation of this face-specific effect somewhat difficult: If the face-related ERP modulation were to be brought about by either a rather unspecific vicarious SII activation in response to the sight of touch on a hand or a more localised activation in hand areas that then spreads to face areas, one would in either case expect to find a significant similar modulation in a comparable latency range also during hand stimulation (it should be mentioned that the hand-related N140 did appear to be reduced during the sight of touch in a similar fashion as the face-related one, but this effect clearly failed to reach significance for some reason). Hand- and face-related somatosensation is closely and reciprocally linked, as demonstrated by e.g. the modulatory effect of face stimulation on SEPs from the hand (Kakigi & Jones, 1985; Tanosaki, Iguchi, Hoshi, & Hashimoto, 2003) or the finding that stimulating the face evokes tactile sensations on amputated hands (Ramachandran & Hirstein, 1998) while stimulating the fingers can elicit tactile sensations in the deafferented face (Clarke, Ragli, Janzer, Assal, & de Tribolet, 1996). In this context, it is conceivable that also the mere sight of touch on a hand modulates somatosensory processing for the face. The fact that the touch observation-related ERP modulations were found in two different time windows and did not occur in parallel in either of them suggests, however, that the late face-related modulation is brought about by a different, possibly more complex mechanism than merely a spread of neural activity from vicariously activated hand areas. A possible first step to shed more light on this might be to test whether observing a face being touched while either the observer’s face or their hand is tactually stimulated is associated with a similarly early face-specific effect, followed by a delayed hand-specific hand that is, crucially, unparalleled by a similar effect for the face.

Another aspect that might be worthwhile pursuing in the context of the late face-specific EPR modulation is the fact that while the spatial location of the observed touch on the hand was clearly outside participants' immediate peripersonal space for all tactually stimulated body parts, it nevertheless coincided with the location of the tactile stimulation on participants' faces on a vertical axis (the tactually stimulated hand, on the other hand, was positioned below the monitor). If increasing the spatial discrepancy between where the other-related touch is observed and where it is felt (e.g. by position the monitor in way so it is no longer at the height of participants' head) or, alternatively, showing an object or an non-hand body part in the same spatial location, were to be found to abolish the late face-specific modulation effect, this would indicate that the touch observation-related modulation during face stimulation found here is not associated with the special reciprocal connectivity between hand and face (as opposed to e.g. hand and foot) but involves a different mechanism.

Somatosensory processing in response to foot stimulus was, in any case, entirely unaffected by the sight of touch on a hand (within the analysed first 200 ms after tactile stimulus onset). This in line with previous findings that demonstrate that e.g. somatosensory cortical excitability during tactile hand stimulation is modulated by the sight of hands but not feet in painful situations (Voisin et al., 2011a). It should, however, be noted that an analysis of somatosensory processing during foot stimulation was somewhat restricted by the fact that the foot SEPs where not very clear and showed only one clearly discernible deflection at a mid-latency range, rendering it somewhat unclear to what extent these stimuli were actually processed. This was most likely associated with participants being instructed to ignore the tactile stimulation and the possibility that tactile stimuli presented at the same intensity as during hand and face stimulation were perceived as less intense at the foot. In future studies, the tactile stimulus intensity should be adjusted more appropriately for the foot stimulation to evoke sufficiently clear SEPs (see Heed & Röder, 2010).

Variations in touch observation-related modulations in somatosensory processing as a function of interindividual differences in trait empathy

Possible correlations with self-report measures of dispositional empathy were investigated in the two time epochs (70-95 ms and 135-170 ms post-stimulus onset, respectively) for which significant touch observation-related ERP amplitude changes were found during hand or face stimulation, respectively. Significant empathy-related correlations were only found for the hand effect: The higher participants scored on the EQ's *cognitive empathy* scale, the less likely they were to show a decrease in N80 amplitude during the sight of touch on somebody else's hand. This finding is interesting with respect to two aspects: First of all, this counterintuitive relationship (i.e. the more empathic participants were, the less pronounced was their N80 effect) reproduced the pattern found in Exp. 2.1 and Exp 2.3. for EEG correlates of early touch observation-related vicarious activity in SI (P50/N80). Unlike in the two previous studies, the empathy dimension implicated here was, however, a cognitive (*cognitive empathy*) rather than an emotional one (*emotional reactivity/emotional concern*), which is particularly interesting given that Schaefer et al. (2012) recently demonstrated that the strength with which SI is activated during the observation of touch was contingent upon individuals' perspective-taking skills and thus also a cognitive component of empathy. The high temporal resolution of the EEG technique might, however, have allowed to detect an initially counterintuitive relationship between the strength of vicarious somatosensory activity in SI and individuals' cognitive empathic skills. This will be discussed in more detail in chapter 2.5.

Conclusion

All in all, the results of the present study suggest that observing somebody else's hand being touched rather than merely approached modulates somatosensory processing in the observer in a highly body part specific way: Early-stage somatosensory processing (N80) was found to be altered only for the observed-to-be-touched body part, i.e. the hand, but not for the face or the foot. The sight of touch on a hand also resulted in a later-stage SEP modulation at a N140-like latency range, but this effect was, unexpectedly, specific to tactile face stimulation, rather than being equally present during both hand and face stimulation as one would expect when assuming that "touch on hand" observation-related vicarious somatosensory activity is rather location-unspecific in higher-order somatosensory areas such as SII. More research is needed to shed light on how such a modulation of face-related somatosensory processing in the context of observing a hand being touched might be mediated.

Summary and discussion of chapter 2

Summary and discussion of Exp.s 2.1, 2.2, 2.3 and 2.4

Chapter 2 of this thesis presented a series of four ERP studies which aimed to investigate electrophysiological correlates of touch observation-related vicarious activity in the observer's somatosensory system. More specifically, these studies addressed five different research questions: 1.) To what extent does the somatosensory system resonate with touch on inanimate objects rather than human bodies? 2.) Is vicarious somatosensory activity modulated by the viewing perspective from which touch on somebody else's body is observed? 3.) How clearly does vicarious somatosensory activity present the precise location the observed touch is directed at within a given body part? 4.) To what degree is vicarious somatosensory activity body part specific? And finally 5.) Are interindividual difference in trait empathy linked to the extent to which the mere sight of touch triggers vicarious somatosensory activity? Importantly, questions 1 and 2 had previously been investigated by means of fMRI but a complimentary EEG approach appeared highly worthwhile due to its potential to pinpoint with a millisecond-range temporal resolution *when* the sight of touch affects the somatosensory system and how the precise time course of such modulations might be modified by factors such as the animacy of the touch target or the viewing perspective. In addition, the high temporal resolution of the EEG technique might also allow to detect short-lasting modulations in the somatosensory brain response that might not be registered in the context of a fMRI BOLD signal that that indexes neural activity over several seconds.

Touch observation-related modulations in somatosensory processing in Exp.s 2.1-2.4

Exp. 2.1 thus re-addressed the question whether the observer's somatosensory system resonates only with touch observed on somebody else's body or whether also the sight of touch on an inanimate object triggers a vicarious mirror touch response. In line with previous fMRI evidence that at least SII responds to the sight of *any* touch, irrespective of whether the touch target is biological or not (Ebisch et al., 2008; Keysers et al., 2004), it was found that higher-order somatosensory processing associated with SII activity (as index by the N140 component) was altered in a similar fashion when a cotton bud was seen to touch a hand or a wooden box. This suggests that vicarious SII activation triggered by the sight of touch represents indeed a rather abstract and actually not very body-related notion of touch (Keysers et al., 2004). This is somewhat reminiscent of findings in the motor domain where it was shown that vicarious motor activity can sometimes also be triggered by non-biological (i.e. robotic) action stimuli (e.g.

Engel, Burke, Fiehler, Bien, & Rösler, 2008; Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Liepelt, Prinz, & Brass, 2010; Oberman, McCleery, Ramachandran, & Pineda, 2007; Press, Bird, Flach, & Heyes, 2005; Press, Gillmeister, & Heyes, 2006; 2007; see, however, Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004), suggesting that the evoked motor activity represents more abstract action features (such as the goal) rather than the precise kinematic features of the movements.

What was somewhat unexpected was that Exp. 2.1 found a similarly touch target-unspecific mirror touch response also at a latency range that is associated with activity in SI (P50). While the statistical analyses did not corroborate this, there were, however, indications that the sight of touch on an object affected somatosensory processing in the P50 latency range only when participants had previously observed touch on a hand. In the light of SI's clear somatotopic organisation (Hari et al., 1993; Nakamura et al., 1998; Yang et al., 1993), it can be speculated that being able to match the observed-to-be-touched location on an object onto a location on one's own body might be a precondition for a mirror touch response in SI in the context of observing touch on an object. Further research is needed to shed more light on such carry-over effects.

Exp. 2.2 addressed the role of the viewing perspective from which touch on somebody else's hand is observed, revealing a perspective-independent touch observation-related SEP modulation in the latency range of the SI-generated N80 component, followed by a more perspective-dependent modulation during later-stage somatosensory processing (N140). Importantly, the temporally highly resolved finding of a perspective-insensitivity of early SI-related vicarious activity suggests that the perspective-related differences in SI activity previously demonstrated by Schaefer et al. (2009) by means of fMRI might actually have been contingent on reentrant feedback to SI from SII or other higher-order cortical areas and might not have been present during *initial* touch observation-related SI activations. The low temporal resolution of the fMRI technique might also explain why possibly initial but short-lived perspective-dependent vicarious SII responses were not detected in Schaefer et al. (2009)'s study. More research will, however be needed to shed more light on how the viewing perspective and thus the ease with which an observed body part can be attributed to one's own body affects vicarious somatosensory activity during the different processing stages, especially when it comes to the rather complex pattern of perspective-related modulations of mirror touch responses in SII found in Exp. 2.2 of the present thesis. With regards to the stimulus material used in future studies, it should, however, be noted that the viewing perspective in Exp. 2.2 was manipulated by simply inverting (and rotating) the egocentric hand images. While this is a quite common method for providing different viewing perspectives (see e.g. Saxe et al., 2006, and Schaefer et al., 2009), the resulting "upside down" images might still have appeared somewhat artificial. Stimulus images in which somebody else's hand is seen to point "towards" participants in the allocentric viewing condition (see e.g. Brass, Ruby, & Spengler, 2009) would most likely enhance the experimental reality of the body stimuli.

Finally, Exp. 2.3 and 2.4 investigated how clearly touch observation-related vicarious somatosensory activity in SI and SII codes the precise location somebody else's body is seen to be touched at. Exp. 2.3 found that observing a hand being touched at the index finger tip affected somatosensory processing of tactile stimuli presented to different finger locations in a quite similar fashion, indicating that the evoked vicarious somatosensory activity was not restricted to the specific cortical representation of the observed-to-be-touched skin area or of least the respective finger as a whole. This finding was in line with the tendency of cortical digit representations to overlap not only in SII (Hoechstetter et al., 2001; Ruben et al., 2001) but also SI (Biermann et al., 1998; Krause et al., 2001; Simoes et al., 2001) during the actual experience of touch.

The subsequently conducted Exp. 2.4., however, indicated that mirror touch responses at a primary level (SI) do represent the precise body part (rather than the precise touch location *within* a body part; Exp. 2.3) that was observed to be touched since the sight of touch on a hand did modulate only early somatosensory processing of tactile stimuli to hand, but not to the face (despite its cortical representation being immediately adjacent to the hand; Nguyen et al., 2004; Yang et al., 1993) or the foot. This extended fMRI-based evidence for a somatotopic organisation of mirror touch responses (Blakemore et al., 2005) by demonstrating that the triggered vicarious activity is so body part specifically localised in SI that it does not even spread to immediately adjacent body part representations. Interestingly, the sight of touch did nevertheless modulate face (but not foot) SEPs at a later secondary processing stage. Since there was, however, no significant effect on somatosensory processing for that actually observed body part, i.e. the hand, at a similar latency range, it was somewhat unclear what mechanism might have brought about the face-specific modulation effect during the observation of touch on a hand and possible approaches to pin down the its precise preconditions were discussed.

Interindividual differences in trait empathy and vicarious somatosensory activity in primary and higher-order somatosensory areas in the somatosensory system in Exp. 2.1-2.4

As described in chapter 1.3, mirror matching mechanisms such as the one in the tactile domain investigated in this thesis are thought to be the neural basis of empathy and our capacity to intuitively understand others (Gallese, 2003). The extent to which shared neural networks are activated during the observations of not only other's somatic sensations but also their actions and emotions has indeed repeatedly been found to be associated with interindividual differences in empathic traits (e.g. Avenanti et al., 2009; Cheng et al., 2008; Gazzola et al., 2006; Saarela et al., 2007; Schaefer et al., 2012; Singer et al., 2004). For this reason, participants in all four studies presented in chapter 2 of this thesis were asked to complete two standard empathy questionnaires at the end of the testing session to allow to test whether self-reported empathic dispositions might be linked to how strongly the sight of others' touch sensations affects ongoing somatosensory processing and thus how strongly the observer's somatosensory system resonates with the observed touch.

When taking the results of the correlational analyses in all four studies into account, the revealed variations in the strength of the identified SEP modulations as a function of individuals' empathic skills followed a highly interesting pattern: First of all, it was primarily empathy measures that tap the emotional dimension of empathy for which links with the strength of mirror touch responses were found, such as the EQ's *emotional reactivity* subscale or the IRI's *empathic concern/personal distress* scale (see Exp. 2.4 for an exception). This was somewhat unexpected since previous findings usually associate variations in the strength of vicarious activity in (non-affective) somatosensory brain regions with individual differences in the cognitive dimension of empathy (e.g. Avenanti et al., 2009; Cheng et al., 2008; Costantini et al., 2008; Gazzola et al., 2006), while differential vicarious activations in brain areas involved in the involuntary sharing of observed affective states such as pain or pleasure/disgust (ACC, AI) tend to be related to the individuals' emotional empathy (Jabbi et al., 2007; Lamm et al., 2007; Saarela et al., 2007; Singer et al., 2004). In fact, Schaefer et al. (2012) very recently demonstrated that various SI activity during the sight of touch in particular was contingent on participants' empathic perspective-taking skills but not on any emotional empathic dispositions. The findings in the presented series of studies, however, do implicate the emotional component of empathy with vicarious activity in SI as well as higher-order somatosensory areas, in the context of the observation of completely neutral, non-affective touch. More research is thus needed to address the question as to how and when the somatosensory system contributes differentially to cognitive but also emotional aspects of empathic experiences.

Apart from the fact that the revealed correlations in Exp. 2.1-2.4 implicated primarily the emotional rather than the cognitive side of empathy, there was an additional unexpected finding: While empathy-related correlations with the strength of vicarious activity in higher-order somatosensory areas (SII) indicated that highly empathic individuals recruited those areas more than less empathic individuals, this relationship was actually reversed with respect to earlier mirror touch responses: The more participants tended to report empathic dispositions, the less pronounced were their touch observation-related SEP modulations at latency ranges associated with vicarious activity in SI (P50/N80). This was a surprising finding since previous research commonly links high trait empathy with stronger observation-induced mirror responses in brain areas with overlapping representations for self and other (Gazzola et al., 2006; Kaplan & Iacoboni, 2006; Saarela et al., 2007; Schulte-Rüther et al., 2007; Singer et al., 2004; see, however, Costantini et al., 2008, and Perry et al., 2010). Even though a direct comparison of the revealed empathy correlations with those in other studies is difficult due to the differences in investigated domain, employed paradigms, temporal resolution of the neuroscientific method (fMRI vs. EEG) and used empathy measures, often focussing on different components of empathy, it is difficult to interpret the opposite finding that, at least for early-latency somatosensory processing (P50/N80), participants with high empathy scores tended to show smaller mirror touch effects. One possible explanation could be that participants who spontaneously tend to respond very empathically to others might have found it more difficult to follow the instruction to completely ignore the presented visual stimuli which clearly showed somebody else's body part. Highly empathic individuals indeed tend to be more susceptible to the rubber hand illusion, a body illusion in which an inanimate rubber hand is attributed to the observer's body when stroked synchronously with their own hidden hand, possibly indicating that strong bodily empathy for others might be associated with a reduced self-other differentiation (Asai, Mao, Sugimori, & Tanno, 2011). In the context of a task in which participants were explicitly instructed to disregard the visual input, the high empathy participants might have engaged in more active attempts to ignore the presented body part and to preserve a self-other-distinction, which might, in turn, have inhibited the automatic mirroring of the observed tactile feedback at least in SI. Interestingly enough, Costantini et al. (2008) found that more empathic participants showed less activity in (albeit higher-order) somatosensory areas in response to the sight of a needle penetrating somebody else's body than less empathic participants which was interpreted as an attempt of the very empathic individuals to control how much they vicariously shared the observed pain. This indicates that automatic stimulus-driven resonance activity can nevertheless be influenced by cognitive (top-down) mechanisms.

Conclusions

All in all, investigating neural correlates of the automatic embodiment of others' touch sensations by means of somatosensory ERPs proved highly worthwhile: While some of the findings of the EEG studies presented in chapter 2 reproduced previous fMRI-based evidence on vicarious somatosensory activity during the sight of touch (such as, for instance, the general involvement of both SII and SI in shared neural representations of touch or vicarious SII activity in response to the sight of touch on an object), others revealed some deviating result patterns (such as, for instance, with regards to the role of the viewing perspective), presumably due to the much higher temporal resolution of EEG recordings which allowed to detect more short-lived modulations. Also with respect to the revealed empathy correlations, the presented ERP studies provided valuable first glimpses into how much more complex than previously thought the relationship between low-level resonance mechanisms and the multidimensional construct of empathy might actually be and how much more research is needed to elucidate the intricate interplay between the two, given the counterintuitive links revealed here. That fMRI and EEG approaches sometimes lead to quite different outcomes highlights the importance of using complimentary neuroscientific methods when studying the neural correlates of sharing others' somatic sensations and the factors that modulate such somatosensory resonance responses in the observer.

Chapter 3

ERP investigations on the effect of observing others' action-related touch sensations on somatosensory processing in the observer

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The focus of the ERP studies presented so far was on how the sight of somebody else's body being passively touched affects concurrent somatosensory processing in the onlooker. Not all the touch sensations we experience (and observe) in daily life are, however, the result of objects approaching our body and making contact with our skin. Instead, a lot of the tactile input to our somatosensory system arises from our own active interactions with objects. We grasp them. We explore them. We manipulate them. And the somatosensory system then processes not only the proprioceptive-kinaesthetic feedback from receptors in the muscles, tendons and joints involved in the associated movements but also the cutaneous input from receptors in the skin in response to making contact with an object or a surface (see e.g. Lederman & Klatzky, 2009, for a review on haptic perception). The series of experiments reported in this chapter aimed to investigate whether the latter "tactile component" during the active interaction with objects or surfaces also results in dissociable somatosensory activity if we merely observe it in others, similarly to how we seem to recruit our own somatosensory system when we see somebody else being passively touched (Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012; 2009; Wood et al., 2010). While Exp. 3.1 was to explore whether seeing somebody else's index finger either tap on a table top as compared to lift into empty spaces modulates somatosensory processing of tactile stimuli concurrently presented to participants' homologous finger, subsequent Exp.s 3.2, 3.3 and 3.4 aimed to establish to what extent a mirror touch response triggered during "active touch" observation (rather than during "passive touch observation", see Exp. 2.1 in chapter 2) represented the exact finger location observed to perform the actual "touching". In an attempt to clarify unreliable modulations in somatosensory processing during tactile stimulation of the homologous finger along with unexpected findings with respect to alterations in somatosensory processing during tactile stimulation of the adjacent rather than the anatomically congruent finger, Exp. 3.5 and 3.6 investigated the role of the type of experimental task and the concurrently observed finger, respectively. Final Exp. 3.6 also allowed to follow-up on unexpected SEP modulations as a function of which finger location was concurrently tactually stimulated, regardless of the observed tactile action feedback, encountered in the earlier experiments of this series.

In order to explore variations in the strength of the triggered mirror touch responses during the observation of others' haptic touch sensations as a function of interindividual differences in trait empathy, participants were asked to complete standard empathy questionnaires at the end of each experiment (except for Exp. 3.2).

Experiment 3.1[15]

Modulations in somatosensory processing as a function of observing somebody else's touch-related finger movements

3.1.1 Introduction

Observing others' actions automatically activates a wide-spread fronto-parietal network of brain areas that are also involved in planning and executing our own actions, including the ventral premotor cortex (BA 6), the inferior frontal gyrus (BA 44) and the inferior parietal cortex (e.g. Buccino et al., 2001; Chong et al., 2008a; Kilner, et al., 2009; Rizzolatti et al., 1996b; Shmuelof & Zohary, 2006; 2007), along with the SMA (Holz et al., 2008; Mukamel et al., 2010) and possibly even M1 (Hari et al., 1998; Holz et al., 2008; Raos et al., 2004; 2007). In addition, it has recently been found that also SI and SII become active during the sight of others' actions (Avenanti et al., 2007; Avikainen et al., 2002; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004; Raos et al., 2004; 2007; Rossi et al., 2002), suggesting that the sight of others' action does not only trigger an internal simulation of the motor side of the observed actions but also of the somatosensory features of the observed movements, that is of what it would feel like to actually execute them. Of particular importance for the present thesis is the fact that such observed actions often involve a tactile component, for instance when a hand is seen to grasp and/or manipulate an object. To what extent the observer's somatosensory system resonates also with such haptic sensations of others has, however, been barely addressed yet: Mirroring others' touch sensations has so far almost exclusively been investigated in the context of observing somebody else being passively touched on their body (Blakemore et al., 2005; Bufalari et al., 2007; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012; 2009; Wood et al., 2010). The stimulus material in previous studies, in part, included human agents touching human bodies (Blakemore et al., 2005; Cardini et al., 2011; Pihko et al., 2010; Serino et al., 2008b), the focus, however, was on modulations in the passively touched body part rather than in the actively touching one. Studies that demonstrate the recruitment of SI and/or SII during action observation, on the other hand, do often involve observing somebody else grasp and/or haptically manipulate an object (Avikainen et al., 2002; Gazzola & Keysers, 2009; Raos et al., 2004; 2007; Voisin et al., 2011b)

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[15] The ERP data reported in this chapter 3.1 were obtained in the course of a more extensive ERP study on contextual modulations of the effects of observing others' action-embedded tactile sensations which is currently being prepared for publication (Gillmeister, H., Goss, S., Brass, M. & Forster, B. (in prep). *The mirroring of others' tactile sensations is constrained by context.*).

but the experimental setups do usually not allow to differentiate somatosensory activations in response to internally simulating the proprioceptive feedback from the finger/hand movements and those in response to internally simulating the tactile feedback from handling the object and touching its surface. An important exception is a recent study by Turella et al. (2012) where it was found that SI/BA2 is more strongly activated during the (partial) sight of a hand grasping an object rather than the same grasping movement without the object, indicating that SI/BA2 might be capable of representing others' haptic touch sensations detached from the kinematic features of their movements (see also an earlier finding by Pierno et al. (2009) that indicated that SI/BA2 responded more strongly to the sight of grasping rather than pointing at an object, even though the possible kinematic differences between grasping and pointing might have confounded this contrast).

All in all, little is known about the somatosensory resonance mechanisms with respect to the tactile rather than the proprioceptive component of others' (object-related) actions and to what extent it might actually be possible to isolate somatosensory activity related to the internal simulation of the observed tactile component of an observed action from the somatosensory activity associated with the internal simulation of the proprioceptive features of the observed movements.

The present study thus aimed to investigate possible modulations in somatosensory processing in the context of observing movements that did or did not contain a touch component. Somatosensory-related ERPs were recorded in response to tactile stimuli presented to the index finger while participants observed a model's index finger perform simple lowering and lifting movements. Crucially, lowering movements resulted in a brief contact with the table top the observed hand was resting on and thus in a haptic sensation for the model while the finger merely moved through empty space during the lifting movements. While Bufalari et al. (2007) found SEP modulations as early as the SI-associated somatosensory P50 component during the observation of others' passive touch sensations, Exp.s 2.1 and 2.3 in this thesis point to the somatosensory N80 component as the earliest processing stage at which touch-related visual information alters processing of concurrent tactile stimuli. Which latency ranges could possibly show modulations associated with a visually-induced mirror touch response in the context of the observation of somebody else's action-related haptic sensations is, however, unclear.

Since mirror-matching mechanisms are frequently discussed as the neural basis of empathy (Gallese, 2003), participants were, in addition, asked to complete, as in previous studies in this thesis, the EQ questionnaire (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) to assess their empathic dispositions and to test whether the strength of any revealed touch observation-related modulations in somatosensory processing might co-vary with individuals' trait empathy measures.

3.1.2 Methods

Sample. 16 neurologically healthy participants (9 females and 7 males) took part in this study, ranging in age from 20 to 35 years (M = 25.9 years, SD = 4.3). All but two were right-handed and all had normal or corrected-to-normal vision by self-report. All participants were naive as to the purpose of the experiment and gave written consent to participate after being informed in detail about the involved procedures. The study was approved by the local ethics committee.

Stimuli. The task-irrelevant visual stimuli consisted of a set of colour images depicting a right hand resting on a table top with the index finger in three different positions: In a neutral position, slightly elevated from the table top and "hovering" above it (neutral), in an even more elevated position (lift) and in a position in which the index finger was lowered down making contact with the surface of the table (tap). By rapidly replacing the neutral position (see Fig. 3.1.a for presentation times) with either the "lift" or the "tap" position and vice versa, the impression was created that the hand's index finger was briefly either lifted up in the air or lowered down to tap on the table. The amount of joint displacement during the taping vs. lifting movements and the length of the path of movement (if in different directions) was about the same.

The images subtended approximately 14.8° x 11.2° visual angle and where depicted on a black background. An orange fixation cross was superimposed centrally on all images. Visual stimuli were presented on a 12.2 inch x 9.1 inch computer screen at a distance of approximately 75 cm from the participants.

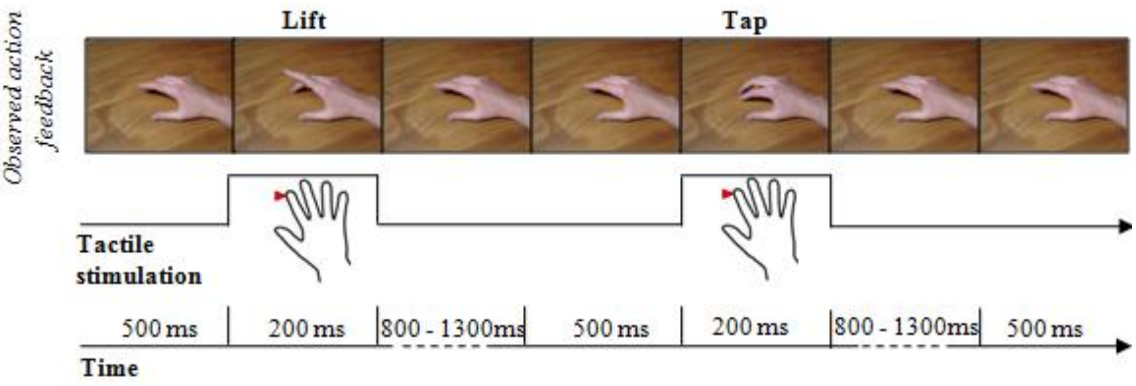


Fig. 3.1.a. Schematic representation of the typical sequence of visual and tactile events in *tap* and *lift* trials, respectively. Tactile stimuli were presented to participants' left index finger tip. On infrequent catch trials, a brief colour change of the fixation cross (not shown here) required a vocal response.

Task-irrelevant tactile stimuli were presented using a purpose-built 12-volt solenoid which drove a plastic rod with a blunt conical tip against the participants' skin for 200 ms whenever a current was passed through it. Adhesive tape was used to attach the stimulator to participants' right index finger tip. To mask any sounds made by the tactile stimulator, continuous white noise (65 dB SPL) was played through loudspeakers positioned to the right and left of the computer monitor. The presentation of both the visual and the tactile stimuli was controlled by E-Prime (Psychology Software Tools Inc., version 1.1).

Procedure. Participants sat in a dimly lit sound-attenuated experimental chamber resting both arms on a table in front of them, such that their hands were in a similar position to the observed hand, i.e. with the palms facing down. The tactually stimulated right index finger was to be held in a neutral position, not touching the table top. A wooden panel covered in black fabric ensured that participants could not see their hands during the experiment.

Participants were instructed to fixate on the orange fixation cross throughout and to respond by saying "pah" as quickly as possible whenever they detected an infrequent colour change of the fixation cross from orange to purple. The presented finger movements as well as the tactile stimuli were to be completely ignored. A camera positioned next to the computer screen allowed the experimenter to continuously monitor whether participants followed instructions and kept their gaze at the visual display. The vocal responses were recorded with a free-standing microphone. At the end of each block, participants were provided with feedback regarding their accuracy and average response time in the colour change detection task.

Each trial began with a presentation of the hand in a neutral position for 500 ms, followed by 200 ms presentation of the hand with the index finger in either a lifted (lift) or lowered position (tap). The onset of this critical stimulus image was accompanied by the presentation of a tactile stimulus for the same duration. Subsequently, the hand was again shown back in its neutral position for a variable duration of 800 to 1300 ms before the next trial began. On approx. 9 % of the trials, the onset of both the critical visual stimulus and the tactile stimulus was accompanied by a brief colour change of the fixation cross, requiring a speeded vocal response.

The type of observed movement (tap vs. lift) was manipulated on a trial-by-trial basis within each block: Participants observed the model's index finger perform a tapping or a lifting movement, respectively, on 25 trials each, presented in a random order. Another five randomly interspersed trials per block were catch trials. Each experimental block thus contained a total of 55 trials and each participant performed 4 blocks with short breaks in between to counteract fatigue and the associated increase in ERP contaminating alpha waves. At the end of the experiment, participants were asked to complete the 60-item EQ questionnaire by (Baron-Cohen & Wheelwright, 2004).

Prior to the experiment, participants were presented with a short demo of the visual stimuli they would later on be seeing (5 trials each for each type of movement, presented in random order) and then asked to try out the just observed finger movements for themselves a couple of times. This was to ensure that participants were aware of the difference in tactile sensation when executing the observed movements, though no such explanation was given to participants. Subsequently, participants performed a short practice block (equivalent to an experimental block except for a reduced number of trials (14 trials in random order, including 4 catch trials) to familiarise them with the colour change detection task at hand.

Recording and data. Using a Brain Vision 32 channel system, continuous EEG was recorded from 28 scalp sites in the same manner as in Exp. 2.1 - 2.4 in chapter 2, with the following exceptions: All scalp electrodes were referenced online to (linked) electrodes on both earlobes rather than a single lateralised electrode on the left ear. Both the horizontal and the vertical electrooculogram (HEOG/VEOG) were recorded at the same time using two electrodes each at the outer canthi of both eyes and above and below of the right eye, respectively, allowing detection of horizontal as well as vertical eye movements. Both EEG and EOGs were sampled at a digitisation rate of 5000 Hz with a bandpass filter 0.016 to 100 Hz, subsequently filtered off-line with a low pass filter of 30 Hz and then segmented into 500 ms epochs starting 100 ms before the onset of the tactile stimulus until 400 ms thereafter. The artifact rejection criteria were the same as those applied in Exp. 2.1 - 2.4 in chapter 2: Trials with eye movements (EOG exceeding ± 30 μV relative to the 100 ms pre-stimulus baseline), eye blinks or other artifacts (voltage exceeding ±60 μV at any electrode relative to baseline) measured in this epoch were excluded from analysis. Trials in which a (correct or incorrect) vocal response occurred were also excluded. For the remaining trials, ERPs for tactile stimuli were averaged relative to a 100 ms pre-stimulus baseline for the two types of observed movements (tap vs. lift).

Statistical analysis. ERP mean amplitudes were computed for four successive latency windows centred around the peaks of early somatosensory ERP components identified by visual inspection of the grand averaged ERP waveforms at posterior electrode sites over the hemisphere contralateral in response to tactile stimuli, irrespective of the type of observed finger movement: P50 (35-55 ms post-stimulus), N80 (65-85 ms post-stimulus onset), P100 (100-130 ms post-stimulus onset) and N140 (140-180 ms post-stimulus onset). To investigate whether somatosensory processing was systematically modulated in any of the selected time epochs by the observation of touch-related rather than touch-free finger movements, 4-way 2 x 2 x 2 x 5 repeated measures ANOVAs with the within-subject factors *hemisphere* (ipsilateral vs. contralateral), *anterior-posterior* (anterior vs. posterior), *observed movement* (tap vs. lift) and *electrode site* on the mean ERP amplitudes were conducted for each given latency window, based on the same four electrode clusters also analysed in Exp. 2.1 - 2.4 in chapter 2. Greenhouse-Geisser adjustments to obtained p-values were applied where appropriate. An alpha level of .05 was used for all statistical tests. Any significant interactions involving factor electrode site were not followed-up.

For any time window for which significant touch observation-induced SEP modulations was found, the difference between the mean ERP amplitudes for two observed finger movements was computed and correlated with the *Empathy Quotient* (EQ) and its three subscales (*cognitive empathy, emotional reactivity, social skills*; Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) using Spearman’s correlation coefficients. Like in chapter 2, significant empathy-related correlations are subsequently only reported if they were found at at least three electrodes in topographic proximity within electrode clusters for which the main analysis indicated a significant touch observation-related ERP modulation.

3.1.3 Results

Behavioural performance

A mean accuracy rate in the colour change detection task of 99.6 % and a very low rate of false alarms (< 1 %) indicated that participants followed the visual display closely throughout the experiment. Overall, participants were somewhat slower in detecting a colour change of the fixation cross when they concurrently observed the index finger tap the table top (M = 564.11 ms, SD = 60.53) rather than lift into empty space (M = 549.78 ms, SD = 60.20; t(15) = 2.584; p = .021).

Electrophysiological data

Fig. 3.1.b contrasts the obtained SEP waveforms in response to task-irrelevant tactile stimuli presented to the right index finger tip while somebody else’s right hand was observed to perform either tapping or lifting movements with its index finger. Crucially, the observed tapping movement involved a tactile sensation for the observed model’s finger tip when making contact with the table top while the lifting movements did not. Note that, unlike all other ERP studies in this thesis, tactile stimulation here was delivered to the right rather than the left hand. Oddly numbered electrode sites in Fig. 3.1.b are thus positioned over the hemisphere contralateral rather than ipsilateral to the tactually stimulated hand.

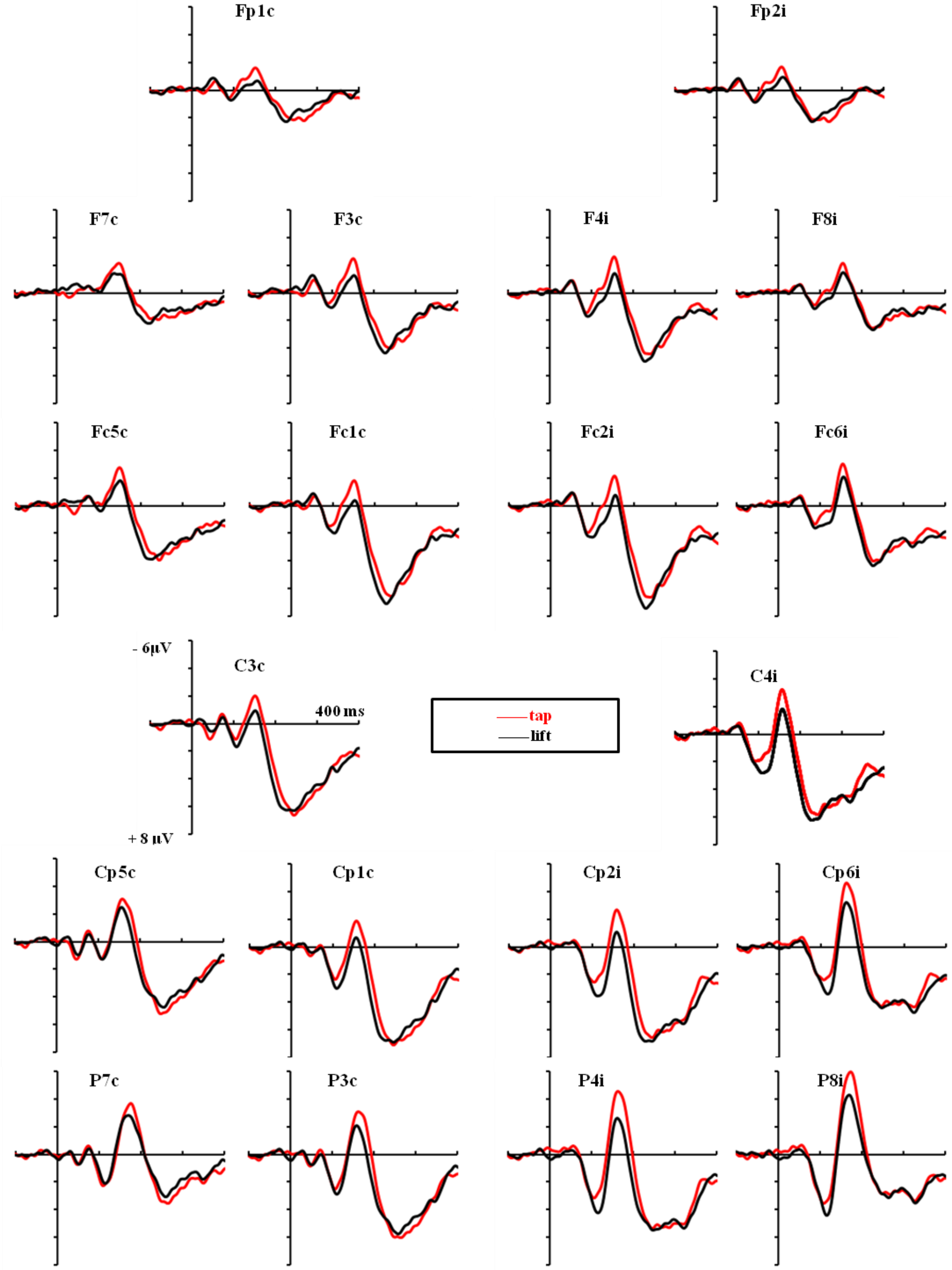


Fig. 3.1.b. Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the right index finger tip during the observation of touch-related tapping movements (red line) and touch-free lifting movements (black line), both ipsi- and contralateral to the tactile stimulation.

For the early-latency P50 and N80 components, no significant (main) effect of the *observed tactile feedback* on somatosensory processing could be found (all F < .799, all p > .386). For the P50, a significant *hemisphere* by *observed tactile feedback*-interactions (F(1,15) = 11.741, p =.004, η^2_p = .439) pointed to the possibility of slight touch-observation induced modulations over the hemisphere contralateral to the stimulated hand, but post hoc analyses with separate *anterior-posterior* (2) by *observed tactile feedback* (2) by *electrode site* (5)-ANOVAs for the two different hemispheres did not confirm this (for both hemispheres, F ≤ 3.738, p ≥ .072). Other interactions involving the *observed tactile feedback* and *hemisphere* and/or *anterior-posterior* did not reach significance (all F ≤ 1.793, p ≥ .200).

However, for both the somatosensory P100 and the subsequent somatosensory N140 component, the sight of a movement involving a tactile sensation for the observed agent did systematically alter how a concurrent tactile stimulus on the participants' finger was cortically processed when compared to a similar movement without such a tactile sensation: In the 100-130 ms time window, a significant main effect of the observed tactile feedback (F(1,15) = 6.846, p = .019, η^2_p = .313) indicated a significantly less positive-going P100 mean amplitude when viewing tapping rather than lifting movements. Following-up a significant *hemisphere* by *anterior-posterior* by *observed tactile feedback*-interaction with separate *observed tactile feedback* (2) by *electrode site* (5)-ANOVAs for the four different electrode clusters confirmed that the modulatory effect in this time window was reliably present at all analysed clusters (ipsilateral-anterior: F(1,15) = 7.817, p = .014, η^2_p = .343; ipsilateral-posterior: F(1,15) = 8.544, p = .010, η^2_p = .363; contralateral-anterior: F(1,15) = 5.676, p = .031, η^2_p = .275) but the contralateral-posterior one (F(1,15) =1.491, p = .241, η^2_p = .090).

The modulatory effect of the touch-related visual information was even more wide-spread for the somatosensory N140 component: The mean SEP amplitude in the time window 140-180 ms after tactile stimulus onset was found to be significantly more negative-going during the sight of tapping rather than lifting movements (main effect of *observed tactile feedback*: F(1,15) = 23.329, p < .001, η^2_p = .609). An also significant *hemisphere* by *anterior-posterior* by *observed tactile feedback*-interaction (F(1,15) = 16.833, p =.001, η^2_p = .529; post hoc analyses: see interaction effect for P100) suggested that the touch observation-induced modulations in somatosensory processing were indeed present at all four analysed electrode clusters (ipsilateral-anterior: F(1,15) = 9.604, p =.007, η^2_p = .390; ipsilateral-posterior: F(1,15) = 35.962, p < .001, η^2_p = .706; contralateral-anterior: F(1,15) = 16.529, p =.001, η^2_p = .524; contralateral-posterior: F(1,15) = 11.754, p =.004, η^2_p = .439) but were most pronounced at the posterior electrode cluster over the ipsilateral hemisphere (η^2_p = .706). Fig. 3.1.c depicts the topographic distribution of the mean difference in SEP amplitude for the two observational conditions for the P100 and the N140 latency range where somatosensory processing was thus found to be significantly modulated by the observed tactile action feedback.

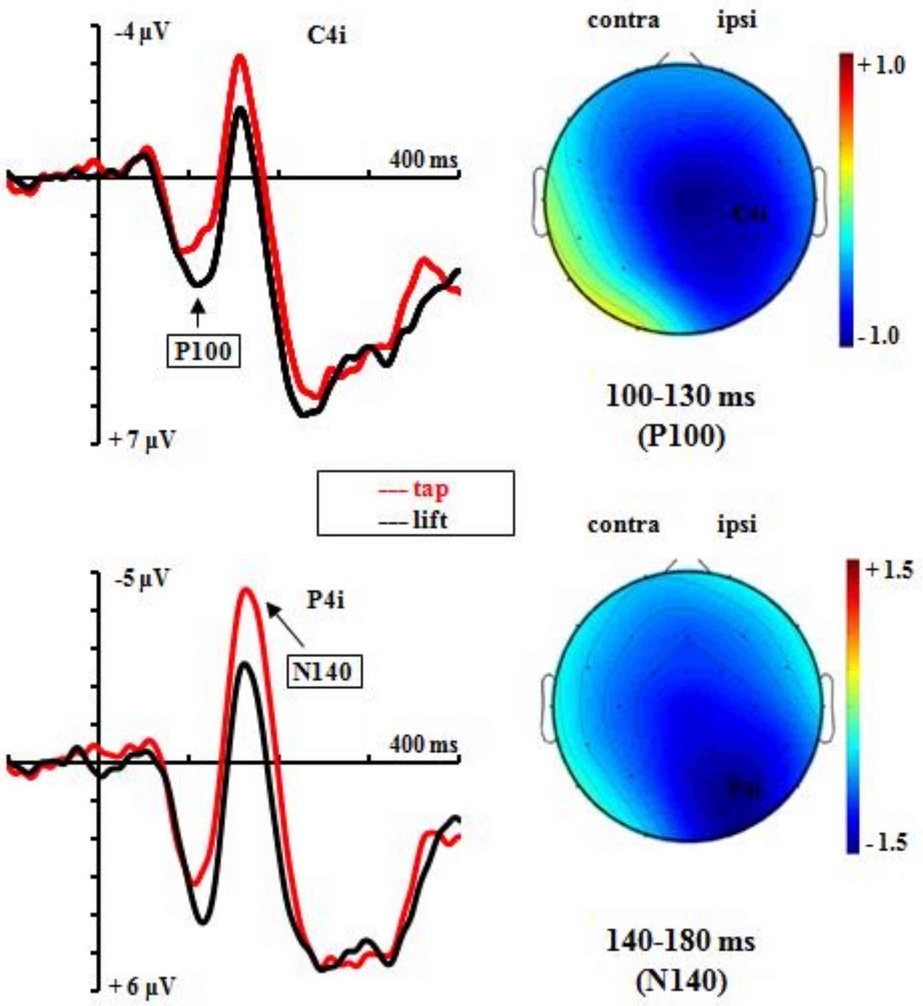
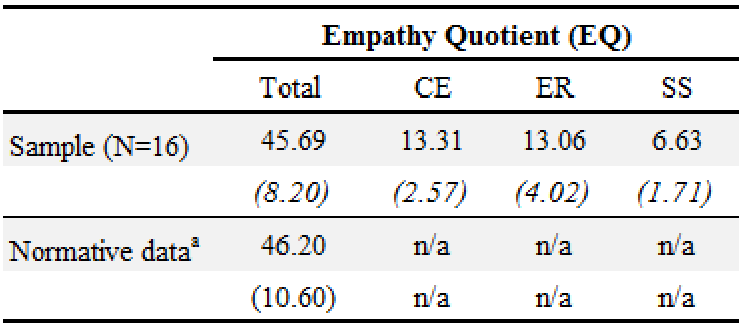


Fig. 3.1.c. Grand-averaged somatosensory ERP waveforms in response to task-irrelevant tactile stimuli to the left index finger tip during the observation of touch-related tapping movements (red line) and touch-free lifting movements (black line), at a representative central (C4i) and parietal (P4i) electrode over the hemisphere ipsilateral to the tactually stimulated hand. The scalp maps show the topographic distribution of the significant ERP amplitude difference for the two observational conditions in the 100-130 ms (P100) and 140-180 ms (N140) post-stimulus onset time epochs. Note that a negative difference indicates a decreased amplitude for the P100 component and an increased amplitude for the N140 component during the sight of touch.

Empathy correlations

Table 3.1.a shows the self-report measures of trait empathy obtained for this sample (N=16) by means of EQ questionnaire (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) administered at the end of the experiment.

Table 3.1.a. Mean scores and standard deviations for the self-report measures of dispositional empathy.



	Empathy Quotient (EQ)			
	Total	CE	ER	SS
Sample (N=16)	45.69	13.31	13.06	6.63
	(8.20)	*(2.57)*	*(4.02)*	*(1.71)*
Normative data[a]	46.20	n/a	n/a	n/a
	(10.60)	n/a	n/a	n/a

[a)] Normative data are derived from: Lawrence et al., 2004 (EQ).

EQ: CE = Cognitive Empathy ER = Emotional reactivity SS = Social skills

Maximal scores: Total score of EQ = 80; Cognitive empathy (EQ) = 22, Emotional reactivity (EQ) = 22, Social skills (EQ) = 12.

Systematic empathy-related correlations between the strength of the touch observation-induced SEP amplitude modulations and self-reported empathic dispositions could only be found for the modulated somatosensory P100 component, but not for the N140 (for the latter, all $p > .05$ except for two isolated frontal electrodes not reported here). At all five frontal and fronto-central electrodes sites within the anterior electrode cluster over the hemisphere contralateral to the task-irrelevant tactile stimulation, the extent of the observation-induced difference in P100 mean amplitude correlated significantly with the *emotional reactivity* subscale of the EQ (Fp1: $r_s(16) = -.531$; F3: $r_s(16) = -.600$; F7: $r_s(16) = -.593$; Fc1: $r_s(16) = -.554$; Fc5: $r_s(16) = -.701$; all $p \leq .05$). The higher participants scored on this empathy-related scale, the more likely they were to show a reduced P100 amplitude during the observation of tapping rather than lifting movements and the more pronounced this P100 effect was, respectively. Fig. 3.1.d visualises this relationship at a fronto-central electrode where the strongest correlation was found (Fc5; $r_s = -.701$).

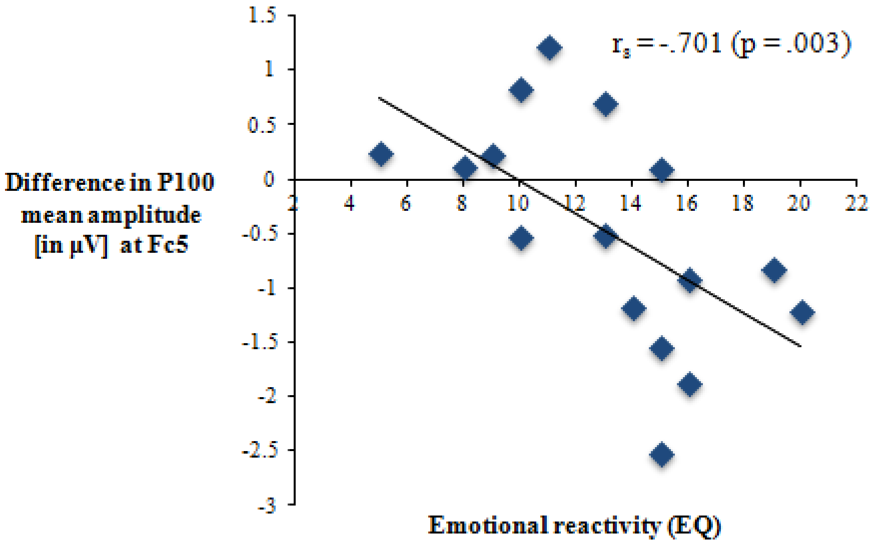


Fig. 3.1.d. Difference in mean P100 amplitude between the two types of observed tactile feedback (tapping vs. lifting) as a function of individuals' level of *emotional reactivity* (EQ) at a representative fronto-central electrode over the hemisphere contralateral to the tactile stimulation (Fc5c).

3.1.4 Discussion

The present study compared SEPs in response to tactile stimuli to the finger tip while a model's index finger was observed to perform either tapping movements (resulting in contact with the table top and thus a tactile sensation) or lifting movements. While early-latency SEP components (P50, N80) were found to be unaffected by the touch observation-related visual information, the type of observed tactile action feedback systematically modulated both the somatosensory P100 and N140 components.

The somatosensory P100 component is thought be generated in bilateral SII (Allison et al., 1992; Hämäläinen et al., 1990) while the somatosensory N140 is assumed to arise (at least in parts) from bilateral SII (Tarkka et al., 1996; Valeriani et al., 2001a; Allison et al., 1992, suggest, however, that the N140 is generated in the bilateral frontal lobes, presumably as a result of projections from the somatosensory cortices (Carmichael & Price, 1995)). The touch observation-related visual information thus modulated only higher-order somatosensory processing, leaving initial processing at primary levels unaltered. SII has previously been implicated not only in the internal simulation of the proprioceptive features of observed movements (Avikainen et al., 2002; Gazzola & Keysers, 2009) but also in the internal simulation of others' *passive* touch observations in the tactile mirror system (Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Schaefer et al., 2009). The present findings suggest that SII might also be involved in mirroring others' *active* touch sensations in the context of actions directed towards solid surfaces or objects, distinguishing the proprioceptive component associated with the observed movement as such from the tactile component associated with the cutaneous stimulation of the skin in the moment of contact.

SI, too, has been found to be active during the observation of others' (often object-directed) actions (Avenanti et al., 2007; Avikainen et al., 2002; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004; Raos et al., 2004; 2007; Voisin et al., 2011b), with a specific subregion, namely SI/BA 2, tending to respond particularly strongly to the sight of hand actions that involve manipulating and thus touching objects rather than merely pointing at them (Arnstein et al., 2011; Pierno et al., 2009; Turella et al., 2012) which is in line with the functional role of this area during the haptic exploration or manipulation of objects, integrating afferent tactile and proprioceptive information from the body (as relayed through BA 3a, BA 3b and BA 1) before passing it on to SII (Kaas, 1990). Based on this, Keysers et al. (2010) suggest that SI/BA2 might the region within the tactile mirror system that specifically resonates with observed "touching" rather than "being touched". The absence of any touch observation-related modulations for SEP components earlier than the P100 in the present study might, however, be an indication that *early* observation-induced SI activation might not yet clearly dissociate the tactile component of such observed hand actions from the movement-related proprioceptive component: The distinct SI activations during the sight of object-directed rather than non-object-directed and thus "touch-free" hand actions (Arnstein et al., 2011; Pierno et al., 2009; Turella et al., 2012) previously found by temporally poorly resolved fMRI studies might actually have been triggered by reentrant feedback from higher cortical areas such as SII *after* an initially unspecific SI resonance response. The lack of any early modulations in somatosensory processing as a function of the observed tactile action feedback in the present study could, however, also be due to the fact that the haptic component of the observed finger movements was relatively subtle and restricted, involving only a finger tip that briefly makes contact with a table, and not e.g. a full-hand grasp of an object (e.g. Pierno et al., 2009; Turella et al., 2012) where several fingers and parts of the palm are in contact with a surface. Especially during early-stage somatosensory processing, the internal simulation of the proprioceptive features of the observed lowering and lifting movements (Avenanti et al., 2007; Avikainen et al., 2002; Rossi et al., 2002) might have surpassed the comparatively subtle difference in the observed tactile component. The fact that the touch-related visual stimuli were actually task-irrelevant and participants were instructed to ignore them might also have contributed to the delay of a mirror touch response for observed *active* touch.

Interestingly enough, the strength of the presumably touch observation-related decrease in P100 amplitude correlated significantly with a self-report measures of empathy, namely the *emotional reactivity* subscale of the EQ (Lawrence et al., 2004). The more participants tended to report to respond emotionally to others' mental states (e.g. 'I tend to get emotionally involved with a friend's problems.', 'Seeing people cry does not really upset me.'), the more pronounced was the reduction in the SII-related P100 amplitude. Even though this subscale initially does not clearly differentiate between self- and other-oriented emotional responses, it is likely that it nevertheless measures other-related emotional empathy since no systematic correlations were found between this subscales and the *personal distress* subscale of the IRI (Lawrence et al., 2004). Intriguingly enough, mirror touch synaesthetes whose somatosensory system responds so strongly to the sight others' (passive) touch sensations (Blakemore et al., 2005) have been found to score particularly high on this very subscale. The present study indicates that also in non-synaesthetes, variations in dispositional (emotional) empathy are associated with differences in the strength of an automatic mirror touch response. Overall, this contributes to the growing empirical evidence that low-level mirror-matching mechanisms might be the neural basis of empathy (e.g. Gallese, 2003), at least as far as the empathic sharing of others' somatic experiences and feelings is concerned.

As far as the later-stage modulations in somatosensory processing are concerned (P100, N140), it is assumed that the revealed amplitude differences reflect the internal simulation of the observed "active" touch in the somatosensory system, above and beyond the proprioceptive features of the finger movements as such. Both components have, however, also been found to be sensitive to shifts in (primarily spatial but also non-spatial) selective attention to the tactually stimulated body part or the presented tactile stimuli as such (Eimer & Forster, 2003; Forster & Eimer, 2004; García-Larrea et al.,1995; Zopf, Giabbiconi, Gruber, & Müller, 2004). Behaviourally, there was indeed a slight reaction time effect in that participants were somewhat slower in detecting a colour change of the fixation cross when this colour change was accompanied by the sight of a tapping movement and faster when the respective colour change was accompanied by the sight of a lifting movement. The latter might suggest that participants tended to pay more attention to the lifting rather than the tapping movements, for instance because the lifting movements as such were more salient (simply lifting a finger into empty space might appear more unusual than tapping on table top) or because the incongruence between feeling a tap on one's finger while seeing a touch-free lifting movement enhanced their salience. Particularly the latter might, in turn, also have resulted in a transient shift of the attentional focus to the tactile stimuli presented to participants' own index finger during the observation of lifting movements. It should, however, be noted that participants were explicitly instructed that both the visual and the tactile stimuli were task-irrelevant and could be completely ignored. It seems unlikely that the proposed spontaneous shift in attention, if it occurred at all, could have been systematic enough – without any explicit instructions as to where to attend except for the fixation cross – to induce the observed P100 and N140 effects.

The described response time effect in the colour change detection task could simply be a result of the respective colour change being easier to detect in the “lift”-condition because the contrast between the purple fixation cross and the background was slightly better than in the “tap”-condition because a part of the fixation cross covered the dark shadow under the hand. It should also be borne in mind that this response latency effect was based on a very small percentage of catch trials and might thus not necessarily reflect a reliable difference in attention between the two observational conditions anyway. The finding that a subset of electrodes showed significant correlations between the strength of the P100 amplitude reduction and a measure of individuals’ trait empathy also associates the revealed modulations in somatosensory processing (at least for the P100) with a visuotactile mirror-matching mechanism for the observed touch component rather than with an attentional effect.

Nevertheless, the two types of finger movements presented in this study might not have been ideal. While the length of the movement trajectories and the displacement of the involved finger joint was comparable for both types of finger movements, the movement direction (up vs. down) was, however, not, possibly confounding the difference in observed tactile feedback (no touch vs. touch). That especially the lifting movements might have been perceived differently from the tapping movement, irrespective of the difference in associated tactile feedback, was indeed indicated not only by the slight reaction time difference discussed above but also by a (non-significant) trend for a response bias for the “lift-lift”-control trials in the behavioural Exp. 4.1.2 which was completely absent in the “tap-tap”-control trials.

To investigate whether the same pattern of modulated P100 and N140 revealed in this experiment would also been found if any differences between the movements other than whether or not they resulted in a tactile sensation for the agent were better controlled, a new set of visual stimuli was created for the subsequent Exp. 3.2. The new hand images showed an index finger elevated above a neutral object (a small red cardboard box). In the observational “touch”-condition, the index finger was then shown lowered down, touching the box. In the observational “no touch”-condition, the index finger was depicted hovering in the empty space next to the box. The amount of displacement of the finger was the same in both conditions. The only difference between the two observed movements was therefore whether or not the index finger contacted the object. Perceptually and proprioceptively (i.e. when actually performing the lowering movements), the two movements were thus as similar as possible.

In addition, tactile stimuli were not only presented to participants’ index finger tip but also to other finger locations across both hands to test whether any touch observation-related modulations in somatosensory processing depend on an anatomical congruence between the observed-to-touch and felt-to-be-touched finger.

Experiment 3.2

Finger-specificity of touch observation-related modulations in somatosensory processing in the context of observing others' haptic touch sensations (trial-by-trial manipulation of the concurrently stimulated finger location)

3.2.1 Introduction

Exp. 3.1 demonstrated that not only observing others' passive touch sensations but also observing their active touch sensations from making contact with a solid surface modulates ongoing somatosensory processing, independently from any somatosensory activations triggered by the sight of movements per se (Avikainen et al., 2002; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004; Raos et al., 2004; Rossi et al., 2002). While early somatosensory components (P50, N80) were unaffected, the sight of an index finger tapping down on a table top rather being lifted into empty space elicited a wide-spread decrease in P100 amplitude followed by an equally wide-spread increase in N140 amplitude.

There were, however, reservations that the observed SEP modulations in Exp. 3.1 might not have exclusively reflected the internal simulation of the tactile component associated with the tapping movements but might have been in parts be due to the simulation of the proprioceptive components of two movements that actually differed in movement direction (up vs. down): In two separately conducted behavioural studies (Exp. 4.1.1 and 4.1.2 in chapter 4), the sight of lifting rather than tapping movements was associated with some rather specific and unexpected response patterns which were ultimately interpreted as indication that the presence or absence of a tactile component might not have been the crucial difference between lifting and tapping movements. The present study thus utilised new stimulus images that further decreased the perceptual and proprioceptive difference between the two observed movements, ensuring as best as possible that they only differed to the effect that one movement resulted in a tactile sensation for the agent while the other one did not. The question of interest was whether the sight of touch associated with one of the movements would still induce a specific modulation in the somatosensory activity triggered by the presentation of task-irrelevant tactile stimuli to participants' hand(s).

In addition, the present experiment was to address a second research question regarding the possible differences between the observation of others' passive vs. active touch sensations. Exp. 2.3 in chapter 2 of this thesis suggested that the sight of somebody else's hand being passively touched modulates somatosensory processing of tactile stimuli presented to the onlooker's corresponding hand in a similar way, irrespective of whether the tactile stimuli are delivered to the anatomically congruent finger tip, an adjacent skin area on the same finger or to the finger tip of an adjacent finger. At least for different locations with one hand, touch observation-related somatosensory activity did thus not seem to represent very clearly which precise finger location was observed to be touched. It is, however, unclear whether the sight of somebody else's *active* touch sensations would result in a similarly location-unspecific somatosensory activity.

The unspecificity of the mirror touch response in Exp. 2.3 was attributed to the fact that the observation of *passive* touch on somebody else's hand might have activated the whole hand area in the onlooker's somatosensory cortex rather than merely the cortical representation of the observed-to-be-touched skin area or that the cortical representation of the respective finger location overlapped too much with those of the other stimulated finger locations to allow for a finger-specific touch observation effect for the index finger tip only. Notably, the most reliable SEP modulation in said Exp. 2.3 was a decrease in the P100 amplitude, a somatosensory component thought to be generated in bilateral SII (Allison et al., 1992; Hämäläinen et al., 1990) which has been shown to be generally less somatotopically organised than SI (e.g. Hari et al., 1993) and where the representations of individual digits tend to overlap considerably (Hoechstetter et al., 2001; Ruben et al., 2001; Simoes et al., 2001). While it is unclear to what extent somatosensory activations associated with the internal simulation of the proprioceptive features of observed fingers movements in particular (Avenanti et al., 2007; Avikainen et al., 2002; Gazzola & Keysers, 2009; Rossi et al., 2002) are clearly somatotopically organised[16], representing the different fingers of one hand, it is conceivable that the observation of the movements of a given finger simultaneously with a tactile sensation for that very finger might ultimately result in a stronger and more circumscribed activation of the somatosensory representation of that finger which, in turn, might facilitate a more restricted mirror touch response for the homologous finger only. Note that the internal simulation of the *efferent* (i.e. motor) components of observed movements has been found to be highly effector-specific, with the sight of e.g. index finger movements increasing the amplitude of concurrently TMS-induced motor evoked potentials (MEPs) only for hand muscles involved in actual index finger movements but not for hand muscles associated with actual movements of the little finger (Avenanti et al., 2007; Romani et al., 2005; Urgesi et al., 2006). Given the close interactions between motor and somatosensory areas during motor control of actually executed voluntary

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[16] With respect to full hand movements (as compared to the movements of separate fingers), a clear effector-specificity during action observation has indeed been found for the somatosensory cortices (Gazzola & Keysers, 2009; Oouchida et al., 2004). Similarly, Möttönen et al. (2005) demonstrated that viewing speech (i.e. mouth movements) modulates somatosensory processing of tactile pulses to the lip but not of median nerve stimulation of the hand.

movements based on reciprocal anatomical connections (cf. Gazzola & Keysers, 2009), it might be the case that the finger muscle-specific activations in motor areas are associated with similarly finger specific somatosensory activations also during mere observation.

Thus, participants in the present study observed a model's index finger perform uniform lowering movements during which the finger either briefly touched a small object or merely the empty space next to while tactile stimuli were delivered to four different finger locations (see also Exp. 2.3 in chapter 2) that differed in the extent to which they matched the precise skin area participants concurrently observed to come into contact with the surface of the object: To the tip of the left index finger as the anatomically congruent finger tip observed to touch the object, to the tip of the right index finger as the matching finger tip on the other, unobserved hand, to the bottom segment of the left index finger as a location on the anatomically congruent finger that is close to but not identical with the observed-to-touch finger tip and to the tip of the left middle finger as a matching finger location on the adjacent finger. Somatosensory-related ERPs elicited by the tactile stimuli were analysed with respect to possible modulations as a function of the observed tactile action feedback and the concurrently stimulated finger location to establish to what extent the exact location of the tactile component of the observed movements might be represented in the expected mirror touch response.

3.2.2 Methods

Participants. 16 neurologically unimpaired participants (8 females and 8 males) were recruited to participate in this study, ranging in age from 20 to 32 years (M = 25.9 years, SD = 4.1). All but three participants were right-handed and all reported to have normal or corrected-to-normal vision. Participants were naive as to the purpose of the study and gave written consent to participate after being informed in detail about all involved procedures. The experiment was approved by the local ethics committee and was conducted in accordance with the Declaration of Helsinki.

Stimuli. The task-irrelevant visual stimuli consisted of colour images of a left hand resting on a table next to a neutral object as seen from a egocentric first person perspective. The hand was shown in three different postures (see Fig. 3.2.a): In a neutral position with the index finger slightly elevated from the table top and "hovering" above the object (neutral) and in a lowered position in which the tip of the index finger either touched the top left corner of the neutral object (touch) or merely the empty space right next to it (no touch). By rapidly replacing the neutral position with one of the lowered positions and vice versa, the impression was created that the hand's index finger briefly moved downwards to touch the object or the empty space next to it and then resumed its neutral position. The trajectories of both lowering movements were of approximately the same length. The hand images “subtended” approximately 15° x 11° of visual angle and were presented on a black background.

A task-relevant orange fixation dot (slightly off-centre) was superimposed on all hand images slightly underneath the index finger when in neutral position. On approx. 17 % of the trials, the colour of the fixation dot changed briefly from orange to purple and participants were instructed to report each colour change by saying “pa!” as quickly as possible. Both the colours and the small size of the fixation dot were chosen to make the task demanding enough to ensure continuous fixation and close attention to the visual display. The slightly increased percentage of catch trials per block (in comparison to Exp. 3.1) was to engage participants more in the task and to help them maintain alertness. Vocal responses were recorded with a free-standing microphone.

To elicit somatosensory-evoked potentials, tactile stimuli that were presented using purpose-built 12-volt solenoids which drove a plastic rod with a blunt tip against participants’ skin whenever a current was passed through them. Using adhesive tape, tactile stimulators were attached to four different locations across both hands of the participants: i) The left index finger tip (i.e. same segment (tip), same finger, same hand), ii) the base segment of the left index finger (i.e. different segment, same finger, same hand), iii) the left middle finger tip (i.e. same segment (tip), adjacent finger, same hand) and iv) the right index finger tip (i.e. same segment, same finger, different hand)[17]. Thus, the extent to which the tactually stimulated body location of the observer matched the body location that was observed to contact the surface of the neutral object (left index finger tip) was manipulated. To mask any sounds made by the tactile stimulators, continuous white noise (65 dB SPL) was played through headphones.

The presentation of both the visual and the tactile events was controlled using E-Prime (Psychology Software Tools, Inc, version 1.1).

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[17] Initially, a fifth stimulator was attached to the back of the neck to investigate the possible effects of observing somebody else’s active touch sensations on somatosensory processing of stimuli presented to a non-lateralised non-hand body part. However, the task-irrelevant and thus unattended tactile stimuli to the neck failed to evoke any clearly distinguishable SEP components which is why this condition could not be analysed and will thus not be addressed here in any more detail for the sake of brevity.

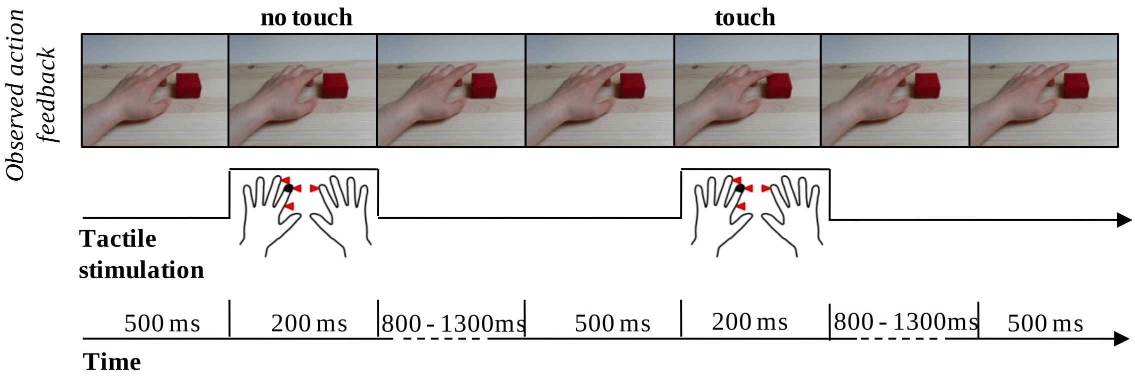


Fig. 3.2.a. Schematic representation of the typical sequence of visual and tactile events in *touch* and *no touch* trials, respectively. On each trial, a tactile stimulus was randomly presented to one of four different finger locations (indicated by red triangles). The anatomically congruent finger tip also observed to make contact with the object on *touch* trials is highlighted in black.

Procedure. Participants sat in a dimly lit sound-attenuated experimental chamber resting both arms on a table in front of the them, such that their hands were in a similar position to the observed hand, i.e. with the inside of the forearm and the palms facing down. The three tactually stimulated fingers were to be held in a slightly lifted position to prevent participants from (unwittingly) pressing down on the stimulators during the experiment. A wooden panel ensured that participants could not see their hands. A camera placed under the panel allowed the experimenter to continuously check for finger twitching indicating that participants imitated the finger movements they observed.

Participants were instructed to fixate on the orange fixation dot and to respond vocally by saying “pa!” as quickly as possible whenever the fixation dot’s colour changed from orange to purple. They were instructed to entirely focus on this task and to ignore the presented hand images and the tactile stimuli delivered to their body.

Each trial started with a presentation of a hand image with the index finger in a neutral position for 500 ms which was followed by the presentation of an image with the index finger lowered either touching the neutral object or the empty space next to it for 200 ms. The onset of this critical stimulus image was aligned with the presentation of a tactile stimulus to one of the five different locations for 200 ms. Subsequently, another presentation of the hand with the index finger in a neutral position was shown for a variable duration between 800 and 1300 ms, creating the impression of the index finger briefly moving downwards and then resuming its neutral position.

Both the observed tactile action feedback, i.e. whether or not the model’s index finger touched the object, and the site of concurrent tactile stimulation were manipulated on a trial-by-trial basis within each block. Each of the ten combinations of observed tactile action feedback and tactually stimulated body site was presented 5 times in random order. Randomly interspersed were an additional 10 catch trials for which the onset of the critical visual stimulus and the tactile stimulus was accompanied by a brief colour change of the fixation cross and a vocal response was required. Each experimental block thus comprised 60 trials in total and participants performed altogether 12 blocks. Participants were encouraged to take regular breaks to relax and move between the blocks to counteract tiredness and the associated increase in alpha waves, especially since this experiment required only very infrequently a response on the part of the participants.

Before the experiment was started, participants performed a short practice block (equivalent to an experimental block except for a reduced number of trials: 40 experimental trials, including 5 catch trials) to familiarise them with the colour change detection task at hand. Unlike in Exp. 3.1, participants were not initially required to briefly imitate the observed finger movements to experience the difference in tactile feedback associated with the two types of observed finger movements for themselves.

Recording and data. Continuous EEG was recorded with Ag-AgCl electrodes from 28 scalp sites following the 10-20 international system (midline electrodes: Fz, Fcz, Cz, Pz; electrodes over the right hemisphere: Fp2, F4, F8, Fc2, Fc6, C4, T8, Cp2, Cp6, P4, P8, O2 and the homologous electrode sites over the left hemisphere) using a Brain Vision 32 channel system. The vertical electrooculogram (VEOG) was recorded using an electrode below and above the right eye to detect vertical eye movements. All scalp electrodes were referenced to an electrode on the right ear lobe and re-referenced off-line to an average of both ear lobes for analysis. Electrode impedances were kept below 5 KΩ or 2KΩ, respectively, for the reference electrodes. The impedance of the earlobe electrodes was kept as equal as possible.

EEG and VEOG were sampled at a digitisation rate of 1000 Hz with a bandpass filter of 0.016 to 100 Hz and subsequently filtered off-line with a low pass filter of 30 Hz. In addition, a 50 Hz notch filter was applied to reduce line noise artifacts which were unexpectedly encountered during the course of running this experiment.

EEG data were analyzed using Brain Vision Analyzer software (version 1.05; Brain Products GmBH, Gilching, Germany). EEG and VEOG were segmented off-line into 500 ms epochs starting 100 ms before the onset of the tactile stimulus until 400 ms thereafter, epoched separately for all ten combinations of observed tactile action feedback (touch vs. no touch) and site of stimulation (left index finger tip, left index finger base segment, left middle finger tip, right index finger tip, neck). Trials with vertical eye movements (VEOG exceeding ± 30 µV relative to the 100 ms pre-stimulus baseline), eye blinks or other artifacts (voltage exceeding ±60 µV at any electrode relative to baseline) measured in this epoch were excluded from analysis. Trials in which a (correct or incorrect) vocal response occurred were also excluded. For the remaining trials, ERPs for tactile stimuli were averaged relative to a 100 ms pre-stimulus baseline for all ten combinations of observed tactile action feedback and site of stimulation.

Data analysis. ERP mean amplitudes for each of the eight conditions were computed for four latency windows centred around the discernible amplitude peaks of early somatosensory ERP components typically observed in response to tactile stimulation: P50 (35-55 ms post-stimulus onset), N80 (60-80 ms post-stimulus onset), P100 (90-110 ms post-stimulus onset) and N140 (140-170 ms post-stimulus onset). The choice of the time epochs was based on the visual inspection of the peak latencies in the grand average ERP waveforms elicited by tactile stimuli averaged across all experimental conditions at posterior electrode sites over the hemisphere contralateral to the stimulated finger locations.

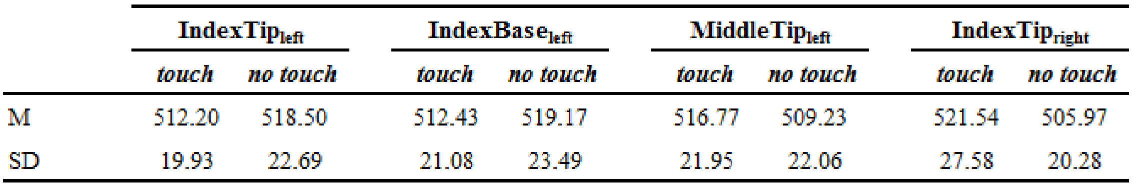
Statistical analyses were then conducted on the default subsets of electrodes sites described for Exp. 2.1 in chapter 2. Mean ERP amplitudes for a given latency window were analysed by means of 2x2x4x2x5 repeated measures ANOVAs with the within-subject factors *hemisphere* (ipsilateral vs. contralateral), *anterior-posterior* (anterior vs. posterior), *site of stimulation* (left index finger tip, base segment left index finger, left middle finger tip, right index finger tip), *observed tactile action feedback* (touch vs. no touch) and *electrode site* to investigate whether the observation of an action resulting in a touch sensation modulates somatosensory processing of a concurrently delivered tactile stimulus and whether any such modulation might be contingent upon a close anatomical congruency between observed and stimulated finger location. Greenhouse-Geisser adjustments to obtained p-values were applied where appropriate. An alpha level of .05 was used for all statistical tests.

3.2.3 Results

Behavioural performance

As instructed, participants paid close attention to the infrequent colour changes of the fixation dot, accurately detecting 96.8 % of them and producing only very few false alarms (< 1 %). The response times for correctly detecting a colour change of the fixation dot did not systematically differ as a function of the observed tactile action feedback (F(1,15) = .302; p = .591, η^2_p = .020), the concurrently stimulated finger location (F(3,45) = .100; p = .959, η^2_p = .007) or an interaction of both factors (F(3,45) = 1.085; p = .352, η^2_p = .067), suggesting that attention to the visual display was generally similar in all conditions. Table 3.2.a summarises the respective response times.

Table 3.2.a. Means and standard deviations of response times in colour change detection task (in ms) as a function of *observed tactile action feedback* and *site of tactile stimulation.*



	IndexTip$_{left}$		**IndexBase$_{left}$**		**MiddleTip$_{left}$**		**IndexTip$_{right}$**	
	touch	***no touch***	***touch***	***no touch***	***touch***	***no touch***	***touch***	***no touch***
M	512.20	518.50	512.43	519.17	516.77	509.23	521.54	505.97
SD	19.93	22.69	21.08	23.49	21.95	22.06	27.58	20.28

Electrophysiological data

The effects of observing somebody else’s active touch sensations on somatosensory processing were determined by comparing ERPs obtained when tactile stimulation was accompanied by observing the index finger of a left hand touch a neutral object vs. the empty space right next to it. Figures 3.2.b-e show the obtained grand-averaged ERP waveforms elicited for the two observational conditions at all analysed electrode sites separately for the four different tactually stimulated finger locations while Fig. 3.2.f directly contrasts the respective waveforms for all four stimulated finger locations at two representative electrodes.

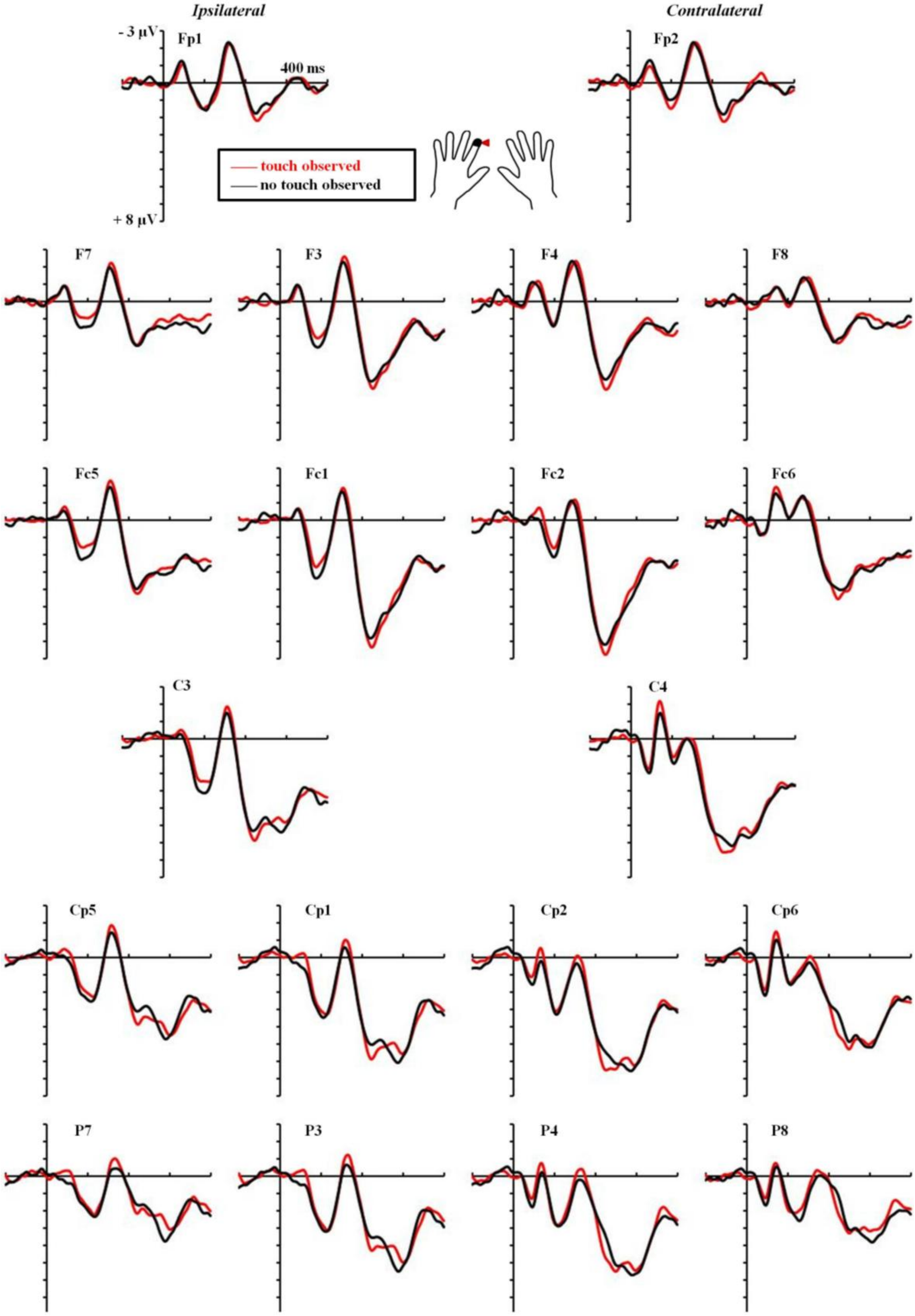


Fig. 3.2.b. Grand-averaged ERP waveforms in response to tactile stimuli to the left index finger tip (IndexTip$_{left}$) during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

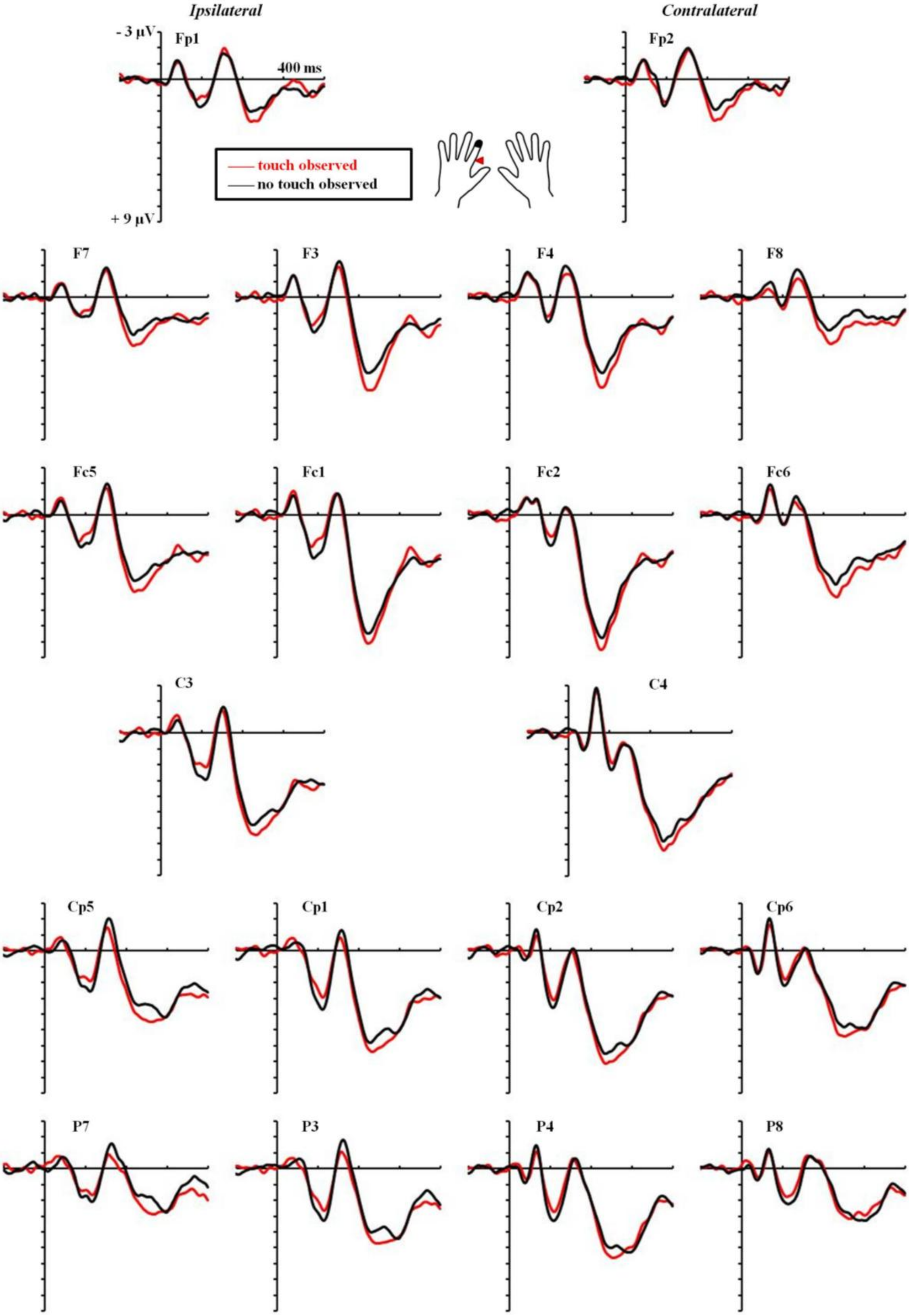


Fig. 3.2.c. Grand-averaged ERP waveforms in response to tactile stimuli to the base segment of the left index finger (IndexBase$_{left}$) during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

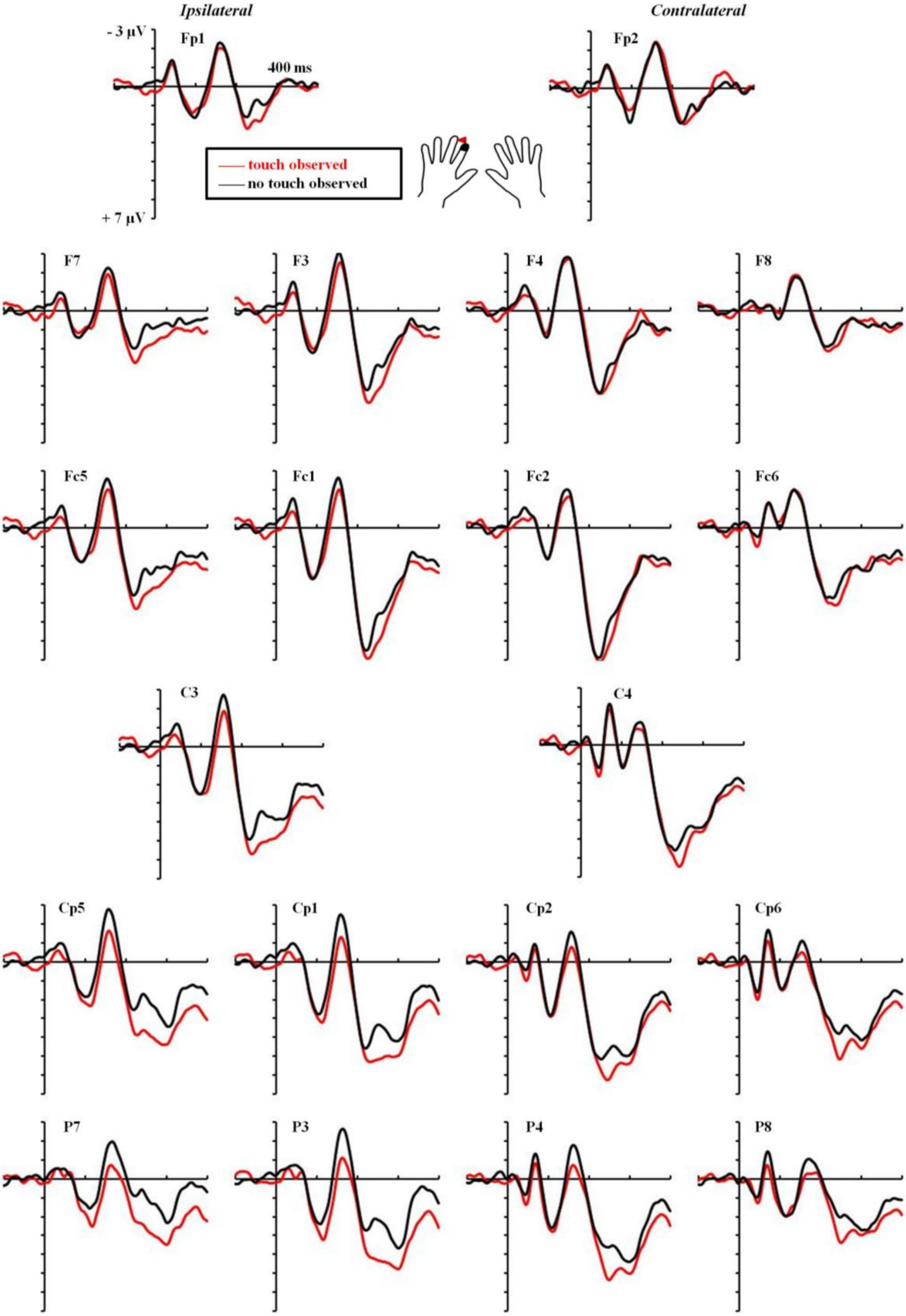


Fig. 3.2.d. Grand-averaged ERP waveforms in response to tactile stimuli to the left middle finger tip (MiddleTip$_{left}$) during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

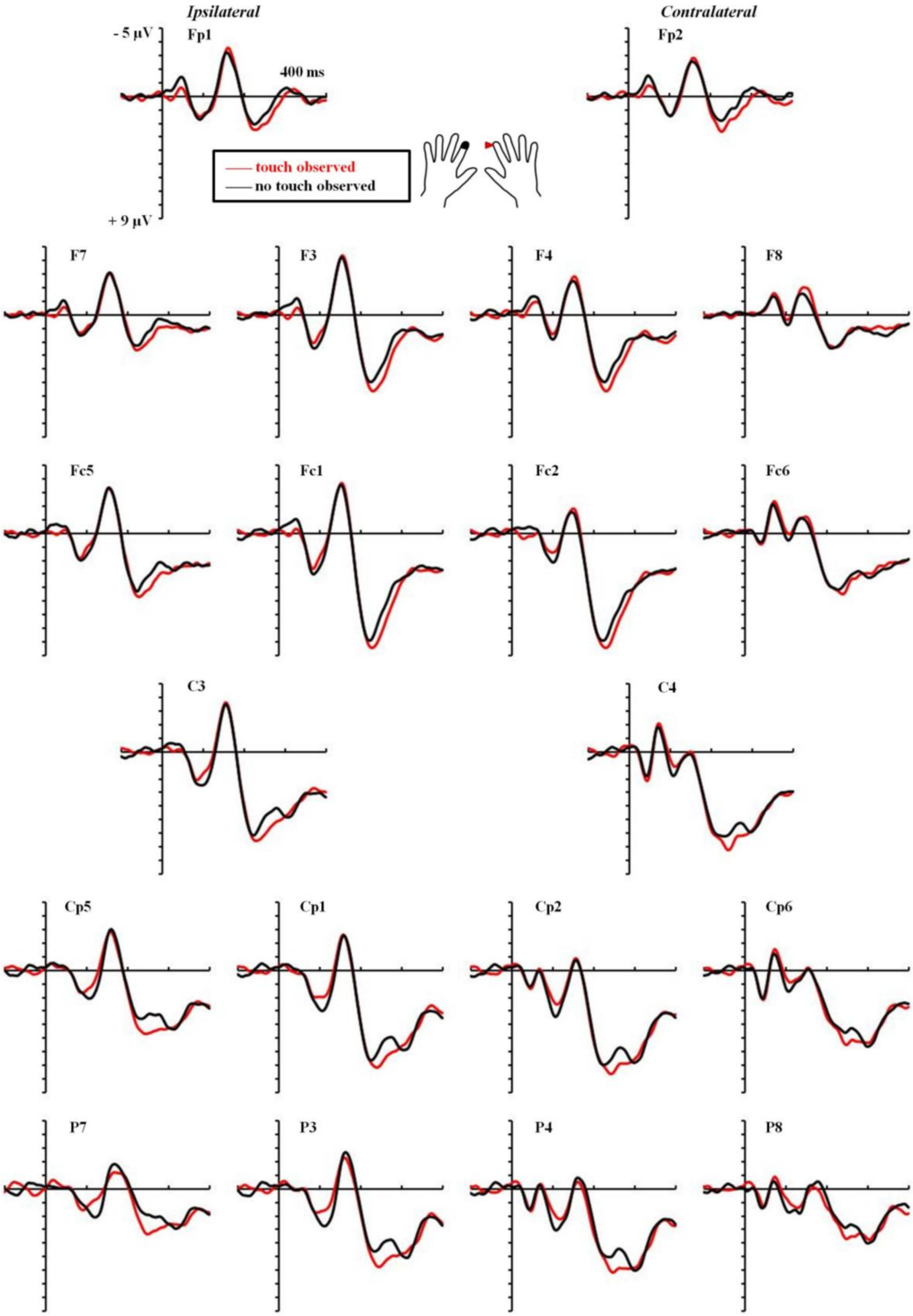


Fig. 3.2.e. Grand-averaged ERP waveforms in response to tactile stimuli to the right index finger tip (IndexTip$_{right}$) during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

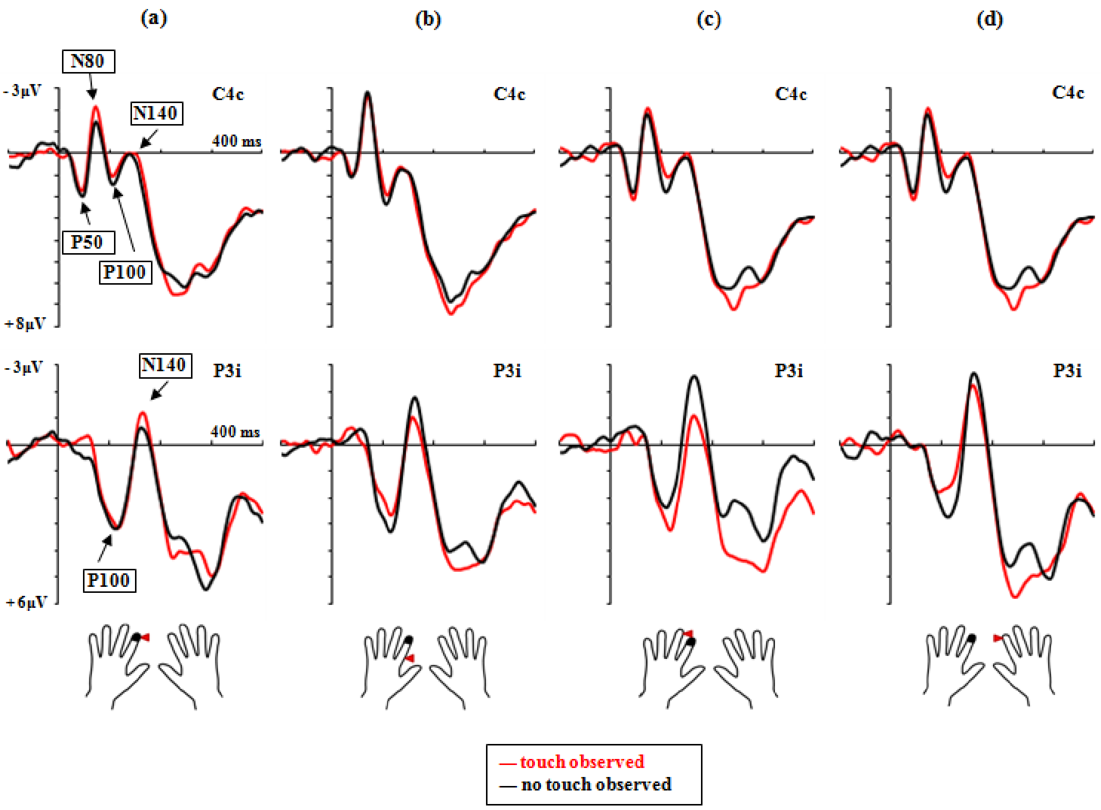


Fig. 3.2.f. Grand-averaged ERP waveforms in response to tactile stimuli to the (a) anatomically congruent index finger tip, (b) the base segment of that same index finger, (c) the adjacent middle finger tip or (d) the homologous index finger tip of the other unobserved hand during the observation of a model's index finger touch either an object (red line) or merely the empty space next to it (black line). Waveforms are shown at a representative contralateral central (C4c; top panel) and ipsilateral parietal electrode (P3i; bottom panel).

In the early and mid-latency ranges (35-55 ms post-stimulus onset (P50), 60-80 ms post-stimulus onset (N80) and 90-110 (P100)), no effects at all of the *observed tactile action feedback* on concurrent somatosensory processing could be found, neither in the form of unspecific modulations across all stimulated finger locations (all $F < 1.819$, $p > .197$, $\eta^2_p < .108$) nor in the form of any kind of location-specific modulation (all $F < 2.641$, $p > .061$, $\eta^2_p < .150$).[18]

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[18] To allow for a more direct comparison between the present study and the preceding experiment 3.1 with respect to possible modulations in somatosensory processing when the observed-to-touch and the tactually stimulated finger match, the analysis of the present data was re-run for tactile stimuli presented to the left index finger tip only. No significant effects of the observed action feedback were found for any of the four analysed latency windows. At some central and frontocentral electrodes over the hemisphere ipsilateral to the stimulated hand (C3i, Fc1i, Fc5i, F3i, F7i), the P100 amplitude appeared to be similarly reduced as in Exp. 3.1 and a significant *hemisphere* by *observed action feedback*-interaction ($F(1,15) = 8.057$, $p = .012$) for the 90-110 ms latency range pointed to this, but post hoc analyses for the two separate hemispheres did not yield significant results (both $F(1,15) \leq 1.021$, $p \geq .328$).

For the late peaking somatosensory N140 component (140-170 post-stimulus onset), follow-up analyses of a significant *hemisphere* by *observed tactile action feedback*-interaction (F(1,15) = 5.060, p = .040, η^2_p = .252) with separate *anterior-posterior* (2) by *site of stimulation* (4) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs did not yield a significant touch observation-related effect for neither of the two hemispheres (for both hemispheres, F(1,15) < 3.916, p > .066, η^2_p < .207). There was, however, also a significant four-way interaction between hemisphere, anterior-posterior, stimulated finger location and observed tactile action feedback (F(3,45) = 4.223, p = .019, η^2_p = .220). Simple effects analyses of the effect of the observed tactile action feedback on the mean SEP amplitude in this time window based on *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs conducted separately for all combinations of hemisphere, anterior-posterior and stimulated finger location revealed that the sight of a model's left index finger move and touch an object modulated concurrent somatosensory processing only at the posterior electrode cluster (C3, Cp1, Cp5, P3, P7) over the ipsilateral hemisphere and, crucially, only for tactile stimuli to the left middle finger tip (F(1,15) = 11.789, p = .004, η^2_p = .440). For tactile stimuli presented to this finger location, the mean N140 amplitude was significantly smaller ipsilateral-posteriorly when the model's index finger was observed to actually touch the object rather than merely move through the empty space next to it (see electrode P3i in panel c of Fig. 3.2.f). Interestingly enough, no systematic enough modulation in SEP amplitude could be found for tactile stimuli delivered to the finger location that actually corresponded to where the observed model experience a tactile sensation from briefly tapping on the object, i.e. for tactile stimuli delivered to the left index finger tip (for all four analysed electrode clusters for the left index finger tip, all F(1,15) < .326, p > .577, η^2_p < .021). Similarly, there were no reliable visually-induced N140 modulations in any of the analysed electrode clusters for tactile stimuli delivered to a different location on the anatomically congruent finger location ($\text{IndexBase}_{\text{left}}$: all F(1,15) < 3.535, p > .080, η^2_p < .191) or to the homologous finger tip of the other, unobserved hand ($\text{IndexTip}_{\text{right}}$: all F(1,15) < .901, p > .358, η^2_p < .057). Fig. 3.2.g shows the topographic distribution of the touch observation-related mean difference in SEP amplitude in the 140-170 ms latency range for the left middle finger tip with its clear (and significant) maximum over the ipsilateral-posterior scalp region.

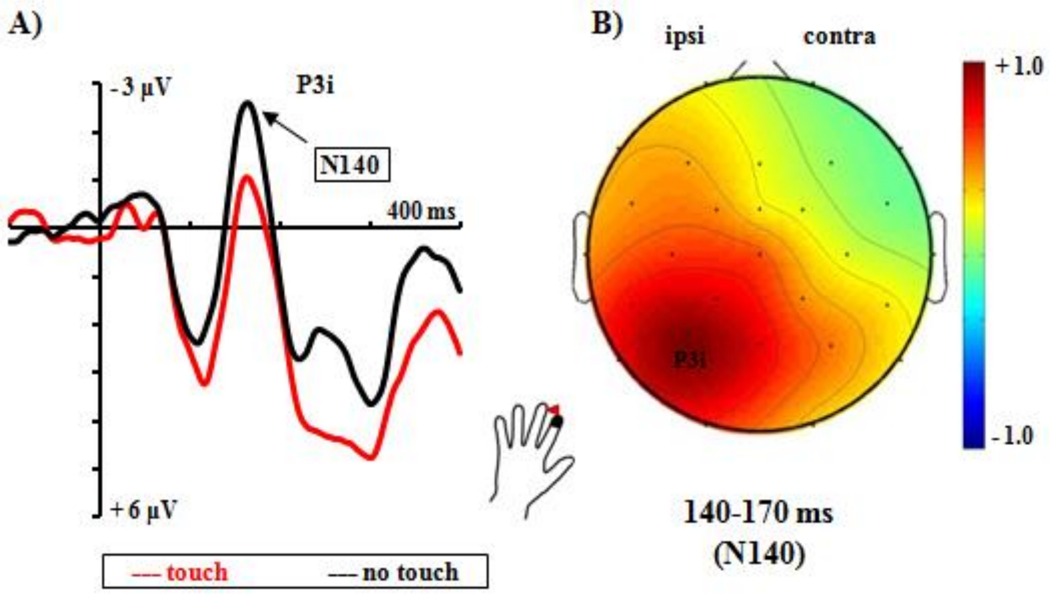

Fig. 3.2.g. A) Grand-averaged ERP waveforms in response to tactile stimuli to the left middle finger tip ($\text{MiddleTip}_{\text{left}}$) during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line), at a representative parietal electrode (P3i) over the hemisphere ipsilateral to the stimulated finger. **B)** Topographic distribution of the difference in SEP mean amplitude for the two observational conditions for the 140-170 ms post-stimulus latency range during tactile stimulation of the left middle finger tip. Note that a positive difference indicates a decreased N140 amplitude during the sight of touch.

In addition, there was also a significant *anterior-posterior* by *stimulated finger location* – interaction (F(3,45) = 4.891, p = .013, η^2_p = .246) for the N140, with pairwise post hoc comparisons between the different tactually stimulated finger locations based on separate *hemisphere* (2) by *stimulated finger location* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for the anterior and posterior electrode cluster indicating that, anteriorly, the cortical response to the presented stimuli deviated somewhat for stimuli delivered to the base of the left index finger as compared to the left middle finger tip and the right index finger tip, respectively (F(1,15) = 6.093, p = .026, η^2_p = .289 and F(1,15) = 8.461, p = .011, η^2_p = .361, respectively; for all other comparisons, p > .05) while posteriorly and more interestingly, the N140 amplitude was significantly decreased for tactile stimuli presented to the left index finger tip as compared to the adjacent middle finger tip (F(1,15) = 8.716, p = .010, η^2_p = .368; for all other comparisons, p > .05). This posterior effect as a function of whether the anatomically congruent left index finger tip or the adjacent left middle finger tip were stimulated is of particular interest given the revealed touch observation-related effect for the middle but not the index finger. Fig. 3.2.h shows the respective ERP waveforms elicited by tactile stimuli to the two finger tips, irrespective of the concurrently observed tactile action feedback, at a representative electrode (C4c), as well as the bilateral posterior scalp distribution of the difference in mean amplitude for the N140 (140-170 ms post-stimulus onset).

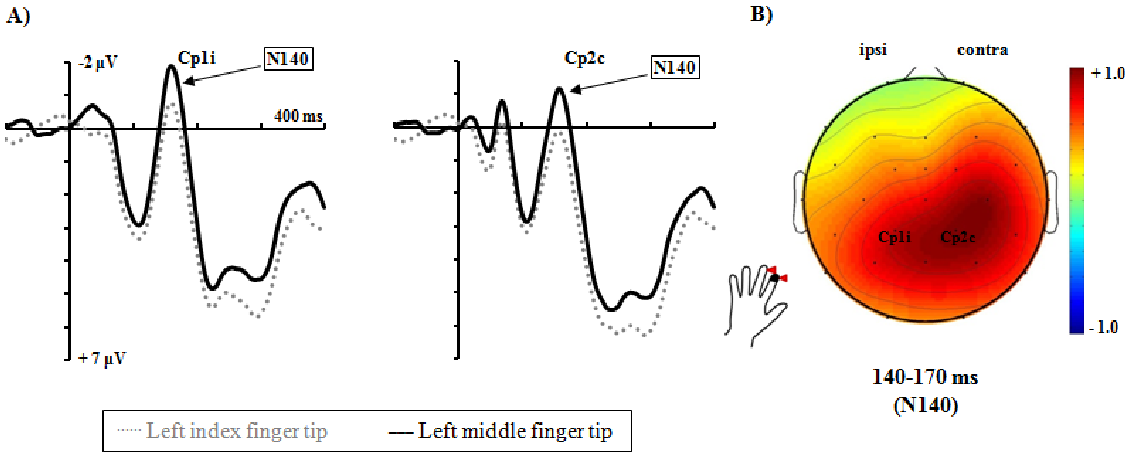

Fig. 3.2.h. A) ERP waveforms in response to tactile stimuli presented to the left index finger tip (dotted grey line) and the adjacent left middle finger tip (black solid line), respectively, at two representative centroparietal electrodes over the hemispheres contralateral (Cp2c) and ipsilateral (Cp1i) to the tactually stimulated hand. **B)** Scalp distribution of the mean difference in ERP mean amplitude in the 140-170 ms post-stimulus latency range (N140) for tactile stimuli presented to the left index finger tip and the left middle finger tip (mean $\text{amplitude}_{\text{index finger tip}}$ – mean $\text{amplitude}_{\text{middle finger tip}}$). Note that a positive difference indicates a decreased N140 amplitude during index finger stimulation.

3.2.4 Discussion

The aim of this experiment was two-fold: Firstly, it was to be determined whether the sight of somebody’s index finger touch a solid surface rather than merely move through empty space modulates somatosensory processing of tactile stimuli presented to the onlooker’s corresponding index finger also when perceptual and proprioceptive features of the associated movements were better controlled than in Exp. 3.1. Secondly, it was to be investigated whether the observation of others’ *haptic* touch sensations modulates somatosensory processing for tactile input from different finger locations in a similarly unspecific way as does the observation of others’ passive touch sensations (see Exp. 2.3 in chapter 2). To this purpose, tactile stimuli were delivered not only to the tip of the left index finger as the anatomically congruent finger tip observed to touch an object but also to three additional finger locations that, crucially, differed in the extent to which they matched the precise skin area participants concurrently observed to come into contact with the surface of the box: To the tip of the right index finger as the matching finger tip on the other, unobserved hand, to the bottom segment of the left index finger as a location on the anatomically congruent finger that is close to but not identical with the observed-to-touch finger tip and to the tip of the left middle finger as a matching finger location on the adjacent finger.

The absence of any systematic touch observation-related ERP modulations during tactile stimulation of the anatomically congruent index finger tip

Unexpectedly, somatosensory-related ERP responses within the first 200 ms after the onset of the tactile stimuli were found to be almost entirely unmodulated by the touch-related visual input (for an unexpected exception, see below). The strong and wide-spread ERP modulations during index finger stimulation evoked by the observation of index finger tapping and lifting movements for the mid- and late-latency P100 and N140 components in Exp. 3.1 could not be replicated, neither in the overall analysis nor when analysing the ERPs in response to tactile stimuli to the anatomically congruent left index finger tip separately. While this might be interpreted as an indication that the somatosensory system does not tend to dissociate between the tactile and proprioceptive components of observed haptic actions or that, what is more likely, the mirror response to the observed tactile component was too subtle to stand out from the somatosensory activity triggered by the automatic internal simulation of the proprioceptive component of the observed movements (Avikainen et al., 2002; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004; Raos et al., 2004; Rossi et al., 2002), it should be noted that the present experiment and the preceding Exp. 3.1 differed with respect to the used stimulus material as well as to several other methodological aspects:

First of all, the visual stimuli in the present study depicted index finger movements that were more comparable with respect to movement trajectory, joint displacement and, crucially, movement direction than those used in Exp 3.1, ensuring that the only difference between the observed movements was whether or not they resulted in a tactile sensation for the model. The improved control of the features of the visual stimuli might, however, have rendered this crucial difference (i.e. did the finger touch the object or not?) too subtle to induce reliable ERP modulations, even more so since participants in this study were not asked to casually imitate the observed movements prior to the experiment (see Exp. 3.1). Participants thus might have not been fully aware of the difference in associated tactile consequences of the two types of observed movements, especially considering that they were instructed to ignore the visual stimuli anyway.

More importantly, the finger location to which a tactile stimulus was presented to on a given trial was manipulated on a trial-by-trial basis rather than block-wise (see Exp. 2.3 in chapter 2), with stimuli being delivered equiprobably and in random order to one of the four designated locations in each block. Touch observation-related modulations in somatosensory processing from observing a given finger touch an object might, however, depend on a more repetitive rather than a transient activation of the associated cortical finger representation of the concurrently tactually stimulated finger, especially when the presented tactile stimuli are task-irrelevant and are thus not being attended to. Alternatively, since participants could not anticipate where the next tactile stimulus would be delivered due to the random presentation order, the presentation of a tactile stimulus in an unexpected location might all the more have exogenously drawn attention to the concurrently stimulated finger location, interfering with the instruction to ignore them and also drawing attention away from the visual stimulus display. Given that there was no significant difference in response latencies in the colour change detection task, the latter appears, however, unlikely.

The presence of unexpected touch observation-related ERP modulations during tactile stimulation of the adjacent but not the anatomically congruent finger

Somatosensory processing was also not entirely unaffected by the observation of an index finger either touch or not touch an object. A subset of posterior electrodes over the hemisphere ipsilateral to the tactile stimulation did show a significant change in N140 amplitude during the sight of touch. Unexpectedly, this modulation was, however, not found for the somatosensory processing of stimuli delivered to the anatomically congruent left index finger tip but for stimuli presented to the adjacent middle finger tip. In addition, rather than an increase in N140 amplitude (see Exp. 3.1), the sight of touch was associated with decrease in N140 amplitude, possibly pointing two different cognitive mechanisms being at work when the observed-to-touch and the tactually stimulated finger are not the same.

The more crucial question is, however, why and how the observation of an index finger touch an object failed to modulate somatosensory processing for index finger stimuli yet did alter somatosensory processing for middle finger stimuli. The methodological differences between the present study and Exp. 3.1 discussed above might explain the absence of significant ERP modulations for the index finger, yet they cannot explain why middle finger-related somatosensory processing should be altered instead. Importantly, the mere observation of others' actions has been found to induce activity in a wide-spread network of frontoparietal motor areas (Buccino et al., 2001; Chong et al., 2008a; Kilner et al., 2009; Rizzolatti et al., 1996b; Shmuelof & Zohary, 2006; 2007) as well as somatosensory areas (Avenanti et al., 2007; Avikainen et al., 2002; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004; Raos et al., 2004; 2007; Rossi et al., 2002) as part of an automatic internal simulation of the observed movements as such. For both such motor and somatosensory activations during action observation, there is evidence for a somatotopic organisation of the triggered activity, i.e. which body part is involved in the observed movements is represented in the vicarious mirror response

(Buccino et al., 2001; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004). While it still unclear how fine-grained specifically the observation-related *somatosensory* activations might be when it comes to the observation of movements of immediately adjacent fingers rather than whole body parts, it is at least clear that the automatic simulation of the motor aspects of seen finger movements has been found to be highly finger-muscle specific (Avenanti et al., 2007; Romani et al., 2005), which might suggest that also somatosensory activations during finger movement observation might to some degree represent which finger is concurrently observed to be in motion, given the close links between motor and somatosensory areas during actual movement execution (cf. Gazzola & Keysers, 2009). Considering the possible finger-specificity of somatosensory activations related to resonating with the proprioceptive features of the observed movements of a given finger, it is conceivable that the processing of tactile stimuli concurrently presented to the homologous finger might be more affected than the processing of tactile stimuli delivered to the adjacent finger. In this context, SEP modulations in response to the observed tactile component of the seen movements might simply have been obscured by the simultaneously occurring simulation of the kinematic index finger movement features during tactile stimulation of the anatomically congruent finger. During tactile stimulation of the adjacent finger, on the other hand, the (possibly less somatotopically fine-grained) mirror response (see Exp. 2.3) triggered by the sight of touch might have been easier to detect given that it had to "compete" to a lesser degree with proprioceptive simulation processes.

EPR modulations as a function of the concurrently stimulated finger location, irrespective of the observed tactile action feedback

Of particular interest with respect to the just discussed effects of merely observing finger movements, irrespective of whether or not they were associated with a haptic sensation, was the finding that, at least over posterior electrode sites, somatosensory processing in the N140 latency range appeared to be modulated during index finger tip as compared to middle finger tip stimulation, irrespective of whether a haptic sensation was observed or not. While the index and middle finger of hand do differ from each other with respect to e.g. their tactile sensitivity (Vega–Bermudez & Johnson, 2001) and also the size of their cortical representations in SI (Duncan & Boynton, 2007), there are currently no studies that suggest that the (separate) tactile stimulation of these two digits is associated with differences in SEP amplitude (Franzén & Offenloch, 1969, compared SEPs in response to index and middle finger stimulation and did not find any significant differences). Instead, it could be speculated that the deviant cortical response to the tactile stimulation of the index finger tip and the adjacent middle finger tip might indeed be associated with the fact that the index finger stimulation was accompanied by the observation of somebody else’s *corresponding* finger in motion which might have triggered a finger-specific vicarious activation in the somatosensory system, modulating the somatosensory processing of tactile stimuli presented to the very same finger (see above). Middle finger stimulation, too, was accompanied by the sight of “a” moving finger but since it was not the corresponding finger, the somatosensory processing of tactile stimuli to the middle finger was less affected.

Interestingly, said N140 amplitude was found to be *attenuated* during index as compared to middle finger stimulation, prompting speculations as to whether the mere sight of movements might induce a suppression of somatosensory processing of tactile stimuli concurrently presented to the homologous finger in the absence of any actual movements of that finger. Importantly, the actual execution of voluntary movements (such as index finger flexions) has been found to result in a suppressed processing of afferent input from the moving body part, most likely induced by central signals from motor areas in the context of movement preparation (Haggard & Whitford, 2004; Jiang, Chapman, & Lamarre, 1990; Voss, Ingram, Haggard, & Wolpert, 2006; see, however, Chapman & Beauchamp, 2006, on the possible role of reafferent peripheral input in sensory suppression). This suppression of tactile input gradually decreases with the distance from the moving body part (Williams, Shenasa, & Chapman, 1998) and has been found to show a high degree of specificity even across the fingers of one hand in that it is maximal if e.g. the thumb moves while it is electrically stimulated but decreases significantly if it is not the thumb but the adjacent index or middle finger that moves (Rushton, Rothwell, & Craggs, 1981). Since the neural processes during the mere observation of movements seem to resemble in so many ways those during the actual execution of corresponding movement (with respect to both the motor and proprioceptive components of motor planning and execution), one might speculate if not also movement observation might induce to a certain degree a suppression of tactile stimuli concurrently delivered to the observer’s body which might be most pronounced for the corresponding finger, i.e. the index finger, and whether such a general attenuation of somatosensory processing might also have obscured the mirror touch response triggered by the sight of touch. In contrast to Avikainen et al. (2002) and Rossi et al. (2002) whose findings indicated that the mere sight of movements increases the somatosensory excitability, Voisin et al. (2011b) recently demonstrated that the mere observation of others’ actions can indeed result in a reduced responsiveness of the somatosensory system, possibly mimicking sensory suppression during actual movement execution. It is, however, important to note that Voisin et al. (2011b) analysed EEG-(rather than MEG) recorded steady-state somatosensory responses and thus observed the reported reduction in somatosensory excitability in the context of continuous rather than transient (electrical) stimulation with the two types of stimulation being possibly associated with different dipole sources in SI (Nangini, Ross, Tam,

& Graham, 2006). Apart from the fact that the present study also involved transient rather than continuous somatosensory stimulation, there are several other factors that shed doubt on whether the decrease in N140 amplitude during transient index finger stimulation as compared to middle finger stimulation really reflects a movement observation-related sensory suppression-like effect for the anatomically congruent finger: First of all, actual movement execution has been found to modulate primarily early-latency SEP components such as the N20 (Huttunen & Hömberg, 1991) or the P45 (Cohen & Starr, 1987; Rushton et al., 1981; see, however, Cheron & Borenstein, 1987) but not SEPs as late as the N140[19]. While merely observing rather than executing movement might, of course, delay a sensory suppression effect, this nevertheless casts doubts on whether sensory suppression might really be an appropriate explanation for the finger-specific N140 effect and the absence of a mirror touch response for the anatomically congruent index finger. It should also be noted that while mean ERP amplitudes at the posterior recording sites differed significantly during index finger tip vs. middle finger tip stimulation, there was no significant difference when comparing the waveforms in response to middle finger tip stimulation to those for tactile stimuli presented to the base segment of the index finger and also no significant difference when comparing the waveforms in response to index finger tip stimulation to the waveforms elicited by tactile stimulation of the base segment of the very same finger or the corresponding finger tip of the other hand. While null effects are always difficult to interpret, their presence still raises doubts as to a whether a finger-specific movement observation-related suppression effect on somatosensory activity is an appropriate explanation for the unexpected middle finger modulation. On the one hand, it would be expected that somatosensory processing is attenuated for the whole index finger, i.e. for both the tip and the adjacent base segment, since it is whole finger that is observed move, on the other hand, it would be expected that a direct comparison between the left and the right index finger tip might yield a similarly significant effect as the comparison between the left index finger and the left middle finger, assuming that somatosensory processing would be unaffected by the observation of movements of the *other* hand, in line with the finding that the somatosensory response to the stimulation of a given finger is *not* attenuated by actual movements of the homologous finger of the other hand (Rushton et al., 1981). Finally and specifically with respect to the lack of a detectable mirror touch response for the anatomically congruent finger, one would assume that given the similarity between the two types of observed movements, any movement observation-related

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[19] Both Cheron and Borenstein (1987) and Lee and White (1974) found a significant enhancement of a late negative SEP peak during movement execution but the latency of this peak was approx. 130 ms and thus somewhat earlier than the 140-180 ms post-stimulus range analysed here.

suppression of somatosensory processing should be about the same for the two observational conditions so that the cortical response would be attenuated but the difference in somatosensory activity as a function of whether or not the observed movement had a tactile component might still be measurable.

An alternative speculation regarding the described N140 modulation concerns the fact that the somatosensory N140 is an SEP component that has particularly often been found to be sensitive to whether or not participants attend to tactile stimulation (Eimer & Forster, 2003; Forster & Eimer, 2004; García-Larrea et al., 1995; Zopf et al., 2004). The posterior difference in N140 mean amplitude for the two adjacent finger tips could be seen as an indication that participants for some reason paid either more attention to tactile stimuli delivered to their middle finger tip or less attention to tactile stimuli delivered to their index finger tip. As mentioned above, participants' attention might automatically have shifted to the location of the tactile stimulus on each trial despite the instruction to ignore the tactile stimulation. While tactile stimulation to the index finger (especially the tip) might have been perceived as more congruent with what participants concurrently observed, namely an index finger move and touch, tactile stimulation to the middle finger might have been more salient since it might have been conceived as somewhat incongruent given that is only the index but never the middle finger of the observed hand that was seen to move and touch (in particularly so because the middle finger was the immediately adjacent finger to the index finger). Eventually, this increased attention to tactile stimuli to the middle finger in the context of perceiving the incongruency with the observed finger might also have "boosted" the processing of the different tactile consequences of the observed index finger movements (touch vs. no touch), resulting in a visuotactile mirror response for the middle finger but not the anatomically congruent finger. Alternatively, participants might have perceived the observed index finger movements in combination with concurrent tactile stimulation to the very same finger as particularly distracting and tried to more actively ignore both (in accordance with the instruction to ignore both the visual and the tactile stimuli), thus inhibiting also the processing of the tactile component of the observed movements, while no such "active ignoring" was necessary during middle finger stimulation.

All in all, the findings of the present experiment did not allow to draw any reliable conclusions as to whether or not the sight of others' active touch sensations modulates somatosensory processing above and beyond the somatosensory response triggered by the automatic internal simulation of the proprioceptive features of observed movements. Unlike in Exp. 3.1, no significant ERP modulations at all were found for the anatomically congruent index finger tip, possibly due to the combination of a more subtle touch-related difference in the hand images, the trial-by-trial manipulation of the tactile stimulus location and the fact that the different tactile consequences of the observed movements were not demonstrated to the participants prior to the experiment. An unexpected touch observation-related N140 effect for the adjacent middle finger tip also pointed to the possibility that the absence of any modulations during the tactile stimulation of the index finger might have been the result of a general attenuation of somatosensory processing during the observation of index finger movements. Alternatively, the latter effect might have been associated with an unexpected systematic difference in the extent to which attention was paid to index finger stimulation as compared to middle finger stimulation. Given the relatively small sample size, the observed N140 might, however, simply have been an artifact that happened to reach statistical significance.

Experiment 3.3

Finger-specificity of touch observation-related modulations in somatosensory processing in the context of observing others' haptic touch sensations (blocked manipulation of the concurrently stimulated finger location)

3.3.1 Introduction

In the previous Exp. 3.2, the observation of a model's index finger being lowered down to either touch an object or merely the empty space next to it failed to induce any significant modulations in the somatosensory processing of tactile stimuli delivered to the anatomically congruent index finger tip, contrary to Exp. 3.1 where the sight of tapping rather than lifting movements systematically altered how tactile stimuli presented to the matching finger were processed, as indicated by wide-spread P100 and N140 amplitude changes. The absence of any significant somatosensory-related ERP modulations might suggest that the expected somatosensory mirror touch activations in response to the sight of touch (Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012; 2009; Wood et al., 2010) might not have been strong enough to stand out from the somatosensory activations due to the automatic simulation of the proprioceptive features of the observed finger movements (Avikainen et al., 2002; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004; Raos et al., 2004; Rossi et al., 2002) when using the more strongly controlled visual stimuli, especially since participants were not presented with a demo of the difference in tactile consequences of the observed (but later task-irrelevant) finger movements prior to the experiment.

It is, however, also conceivable that the deviation in how repeatedly the cortical representations of the skin areas in question were triggered by the presented tactile and hand-related visual stimuli might have made it difficult to detect a mirror touch response: Assuming that the sight of touch, too, activates somatosensory representations, at least in parts, in a similarly somatotopically organised fashion (Blakemore et al., 2005), the visually-induced somatosensory activations, were, thus, very sustained, given that participants continuously observed a left index finger move and touch throughout the experiment. Which finger location was concurrently tactually stimulated was, however, manipulated on a trial-by-trial basis in Exp. 3.2, resulting in rather transient activations of the respective cortical representations of the respective finger locations. In the present study, the stimulated finger location was therefore manipulated block-wise so that one and the same finger location was stimulated for several consecutive blocks (see also Exp. 2.3) to trigger a sustained tactually-induced activation of the respective cortical representation. That the touch-related difference between the two types of observed lowering movements as such might indeed have been strong enough to induce a somatosensory mirror touch response is suggested by the (unexpected) N140 effect for the adjacent middle finger tip. The sight of a model's index finger being lowered down to either touch an object or merely the empty space did evoke a modulation in somatosensory processing in Exp. 3.2, just not for the anatomically congruent finger but the adjacent one.

The aim of the present study was thus two-fold: Firstly, it was to be tested whether index finger-related ERP modulations might be found after all if the stimulated finger location was manipulated block-wise to allow for a more sustained activation of the cortical representations of the corresponding finger locations and if participants were made more aware of the fact the two types of observed movements differed as to whether or not they resulted in a tactile sensation for the agent. Secondly, it was of particular interest if somatosensory processing of tactile stimuli delivered to the adjacent rather than the anatomically congruent finger tip would again result in strong(er) ERP modulations, given that it cannot be ruled out that the middle finger-specific N140 effect in Exp. 3.2 was a statistical fluke due to the small sample size. In addition, participants were again asked to complete standard empathy questionnaires at the end of the experiment to allow to test whether the strength of touch observation-related SEP modulations co-varies with interindividual differences in trait empathy.

3.3.2 Methods

Participants. Seventeen neurologically normal volunteers took part in the experiment. One had to be excluded due to excessive alpha activity. Thus, sixteen participants (8 males and 8 females), aged between 20 and 35 years (mean age: 25.9 years; SD = 4.1) remained in the sample. Participants were naive as to the purpose of the experiment and gave informed consent to participate after a detailed explanation of the involved procedures. Two participants were left-handed and all had normal or corrected-to-normal vision by self-report. Participants were paid £ 7/h for their participation in the study. The procedures were approved by the local ethics committee.

Stimuli. The visual and tactile stimuli presented during the experiment were exactly the same as during Exp. 3.2. The tactually stimulated body locations were also the same except that no tactile stimuli were presented to the back of the neck after this had failed to elicit clear, discernible SEPs in the previous experiment.

Procedure. The experimental procedure and task were the same as in Exp. 3.2 with the following exceptions: Rather than manipulating the tactually stimulated finger location on a trial-by-trial basis within each block, it was manipulated block-wise: Participants were stimulated at one and the same finger site for three consecutive blocks whereupon the next location was stimulated for three consecutive blocks etcetera. Again, 12 experimental blocks were performed in total with the order in which the four different sites were stimulated being randomised across participants using a random number generator.

The observed tactile action feedback, on the other hand, was again manipulated on a trial-by-trial basis: On 25 trials each per block, the observed index finger was seen to be lowered to either touch the neutral object or the empty space right next to it. In an additional 9 trials of each block, the lowering movement of the index finger was accompanied by a colour change of the fixation dot and a vocal response was required (catch trials; approx. 15 % of trials). Each experimental block thus consisted of 59 trials in total, presented in random order. The sequence and timing of the visual and tactile events during each trial was the same as in Exp. 3.2 except that the variable delay of 800 – 1300 ms between the end of one trial and the beginning of the next was automatically prolonged by 500 ms for all trials in which a correct or incorrect (false alarm) vocal response occurred to avoid any contamination of ERPs with response-related artifacts.

In addition, participants were presented with a brief demo of the upcoming visual stimuli (7 trials in each observational condition, presented in random order) prior to the experiment, assuming that difference in associated tactile feedback between the two observed finger movements might be too subtle for participants to be aware of spontaneously. A piece of cardboard holding the red box from the hand images was placed in front of them and participants were asked to imitate the movement seen on a given demo trial with their index finger. No explanation was given to participants as to why they were to do this.

Finally, participants were asked to complete the 60-item EQ questionnaire (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) which was presented in a computerised form using E-Prime, Version 1.1 at the end of the experiment.

Recording and data. The procedures for recording, pre-processing and segmenting the obtained EEG data as well as the criteria for artifact rejection were exactly the same as for Exp. 3.2 except that no notch filter had to be applied to the raw data prior to segmenting the time epochs.

Data analysis. ERP mean amplitudes were computed for each condition for four latency windows centred around the amplitude peaks of the following four SEP components: P50 (35-55 ms post- stimulus onset), N80 (60-90 ms post-stimulus onset), P100 (100-120 ms post-stimulus onset) and N140 (140-180 ms post-stimulus onset). The approximate peak latencies of each component were identified visually at posterior electrode sites over the hemisphere contralateral to the stimulated finger locations.[20] The statistical analysis was the same as for Exp. 3.2. Greenhouse-Geisser adjustments to obtained p-values were applied where appropriate. An alpha level of .05 was used for all statistical tests.

In addition, correlational analyses using Spearman's rank correlation coefficients were run on the difference in SEP mean amplitude between the two observational conditions and participants' trait empathy measures for any time epoch for which a significant effect to the observed tactile action feedback on concurrent somatosensory processing was indicated.

3.3.3 Results

Behavioural performance

The mean accuracy rate in the colour change detection task was 96.3 % with only very few false alarms (< 1%), indicating that participants paid close attention to the visual display. The response times for correctly detecting a colour change of the fixation dot did not differ as a function of the observed tactile action feedback ($F(1,15) = .629$; $p = .440$, $\eta^2_p = .040$), the concurrently stimulated finger location ($F(3,45) = .228$; $p = .876$, $\eta^2_p = .015$) or an interaction of both factors ($F(3,45) = .694$; $p = .560$, $\eta^2_p = .044$), suggesting that attention to the visual display was similar in all conditions. Table 3.3.a summarises the respective response times.

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[20] It should be noted that the SEP waveforms for stimuli delivered to both the left index and middle finger tip showed a strikingly early onset of a difference between the waveforms for the sight of touch vs. no touch, even earlier than the analysed P50 (see, for instance, electrode C4 in Fig. 3.3.a and Fig. 3.3.c). This modulation could, however, not be assigned to a specific SEP component. Tactile stimuli delivered to the left middle finger tip ($\text{MiddleTip}_{\text{left}}$) might possibly have induced a very early negative deflection in the latency range of about 15 – 25 ms at contralateral posterior electrode sites which might have corresponded to the somatosensory N20 component which is, however, commonly observed only in response to electrical rather than mechanical stimulation (e.g. Bufalari et al., 2007). This peak was, however, rather obscure and very small in comparison to the following P50. Stimuli to the left index finger tip ($\text{IndexTip}_{\text{left}}$) did not elicit such an early negative peak at all. Therefore, an analysis for a not clearly and reliably discernible "N20" did not seem appropriate. In addition, a close visual inspection of the SEP waveform revealed that the onset of this early modulation actually coincided with the onset of the tactile stimulus ($\text{IndexTip}_{\text{left}}$) or started even before the tactile stimulus was presented ($\text{MiddleTip}_{\text{left}}$). Given the relatively small sample size and the relatively small number of experimental trials for each participant, the early differentiation in the SEP waveforms as a function of the observed visual input, especially for the middle finger, might be associated with the noisiness of the baselines. If it was associated with some sort of expectation effect (as to whether or not the observed finger would touch the object on a given trial), it seems unclear why such an effect was not observable for all four stimulus locations or why it was not at least as pronounced for the anatomically congruent index finger tip as it was for the adjacent middle finger tip.

Table 3.3.a. Means and standard deviations of response times in colour change detection task (in ms) as a function of *observed tactile action feedback* and *site of tactile stimulation.*

	IndexTip$_{left}$		**IndexBase$_{left}$**		**MiddleTip$_{left}$**		**IndexTip$_{right}$**	
	touch	*no touch*	*touch*	*no touch*	*touch*	*no touch*	*touch*	*no touch*
M	542.76	541.90	554.33	542.47	543.80	543.65	545.71	544.82
SD	54.12	61.32	52.43	45.45	51.31	59.11	51.62	56.27

Electrophysiological data

Visually-induced effects of observing somebody else's touch sensations on somatosensory processing were determined by comparing ERPs obtained when tactile stimulation was accompanied by observing the index finger of a left hand touch a neutral object versus the empty space right next to it. Figures 3.3.a-d show the obtained grand-averaged ERP waveforms elicited for the two observational conditions at all analysed electrode sites separately for the four different tactually stimulated finger locations while Fig. 3.3.e contrasts the respective waveforms for the different finger locations directly at two representative electrodes.

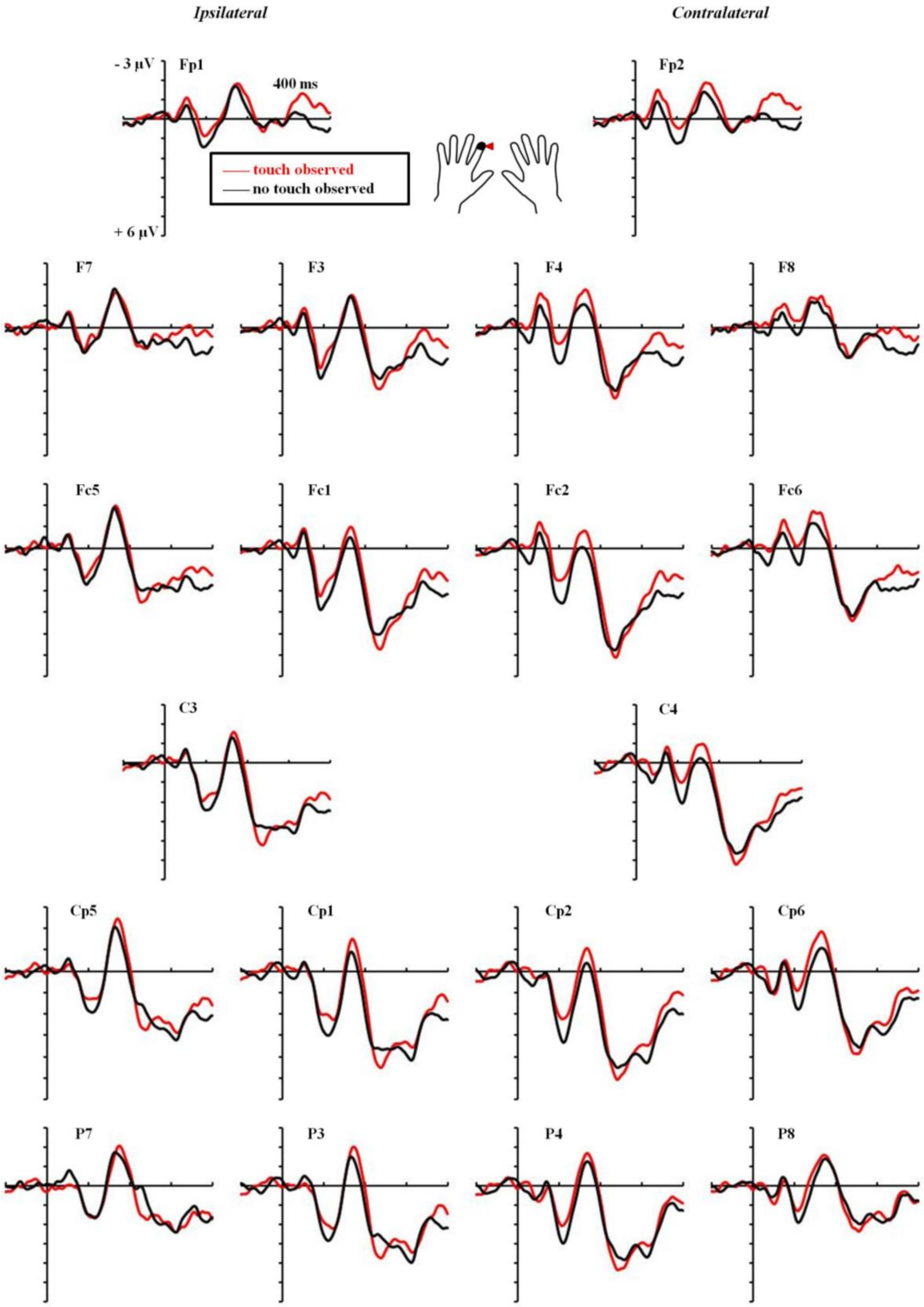


Fig. 3.3.a. Grand-averaged ERP waveforms in response to tactile stimuli to the left index finger tip (IndexTip$_{\text{left}}$) during the observation of the model’s index finger tip touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

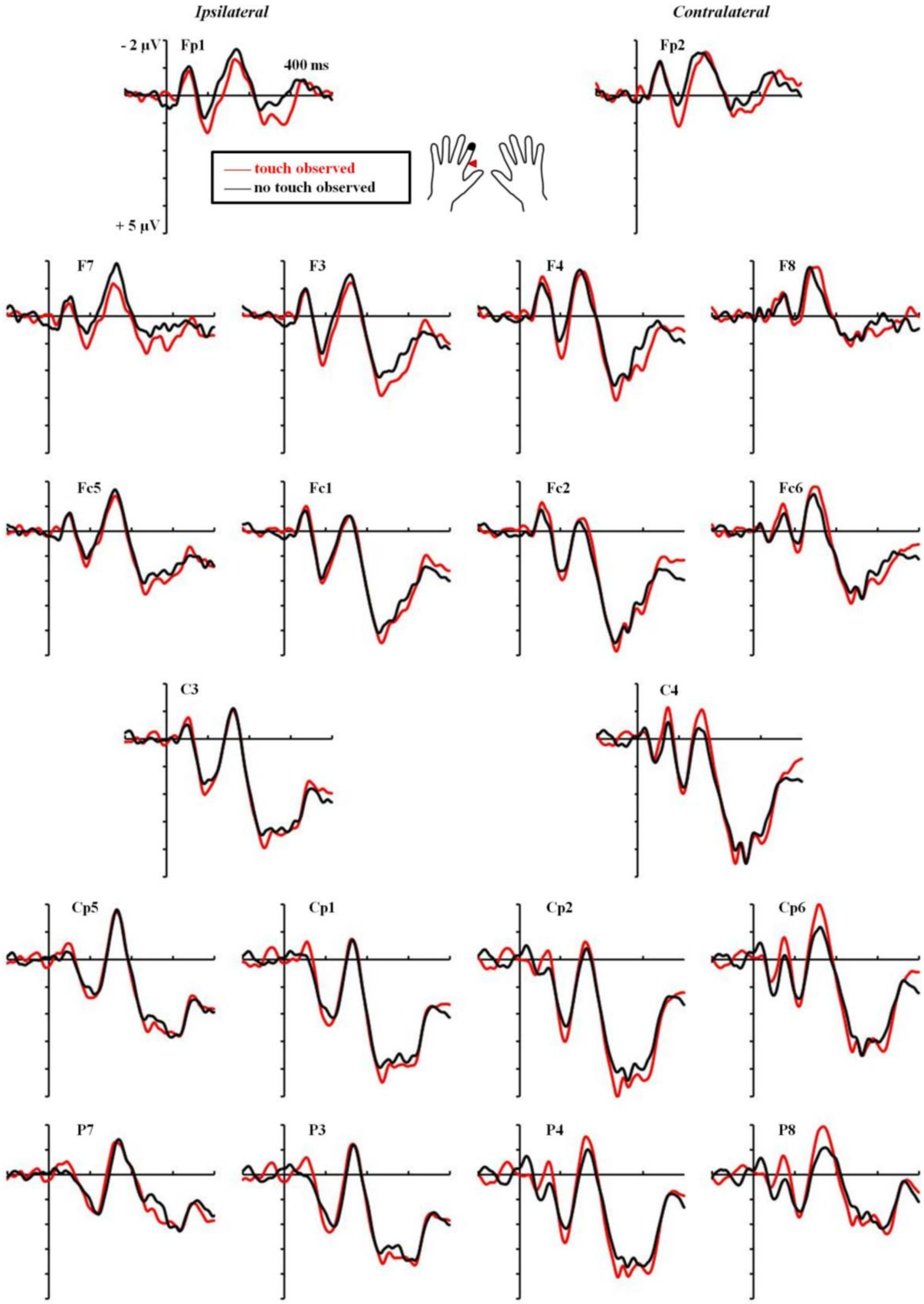


Fig. 3.3.b. Grand-averaged ERP waveforms in response to tactile stimuli to the base segment of the left index finger (IndexBase$_{left}$) during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

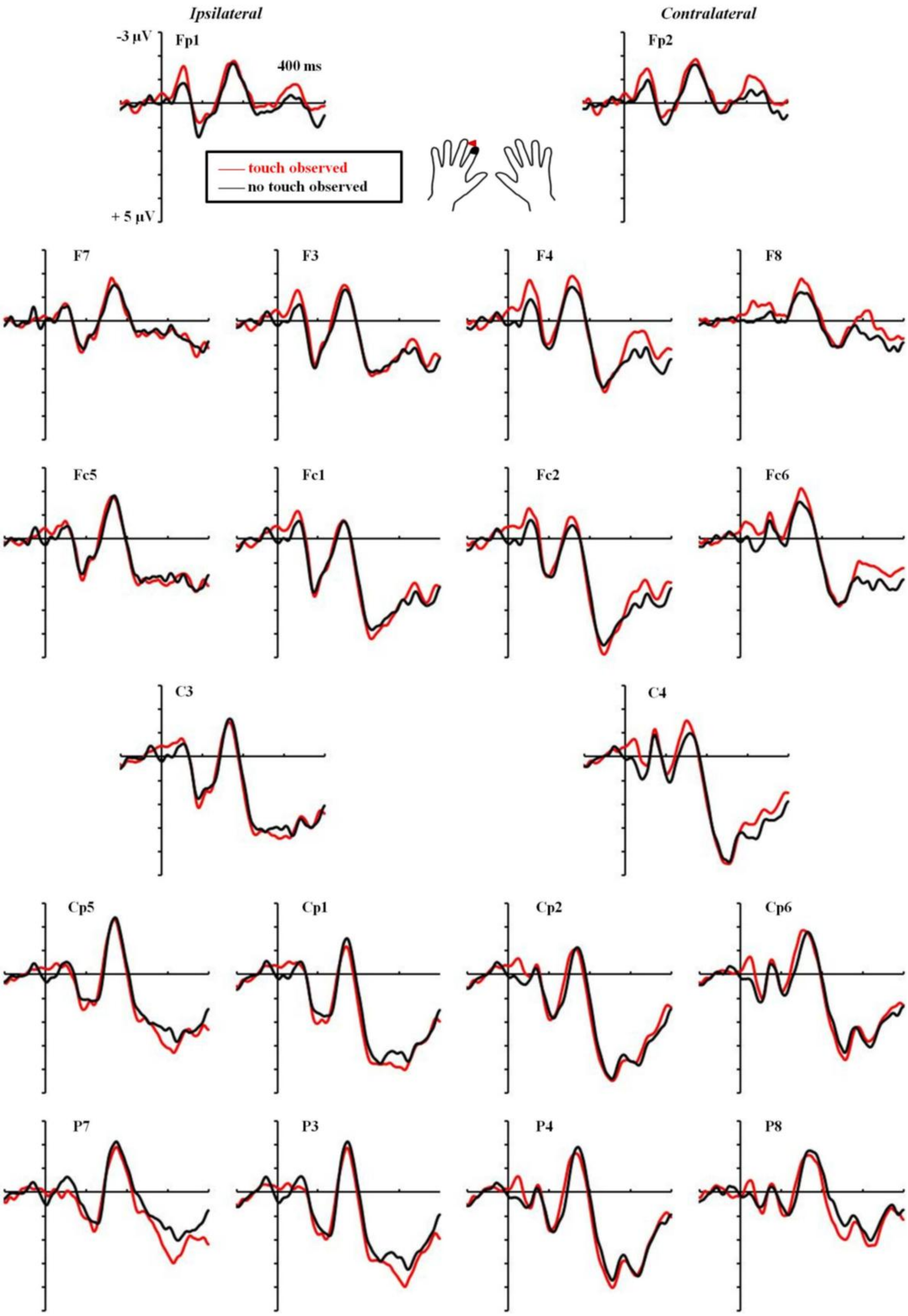


Fig. 3.3.c. Grand-averaged ERP waveforms in response to tactile stimuli to the left middle finger tip (MiddleTip$_{left}$) during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

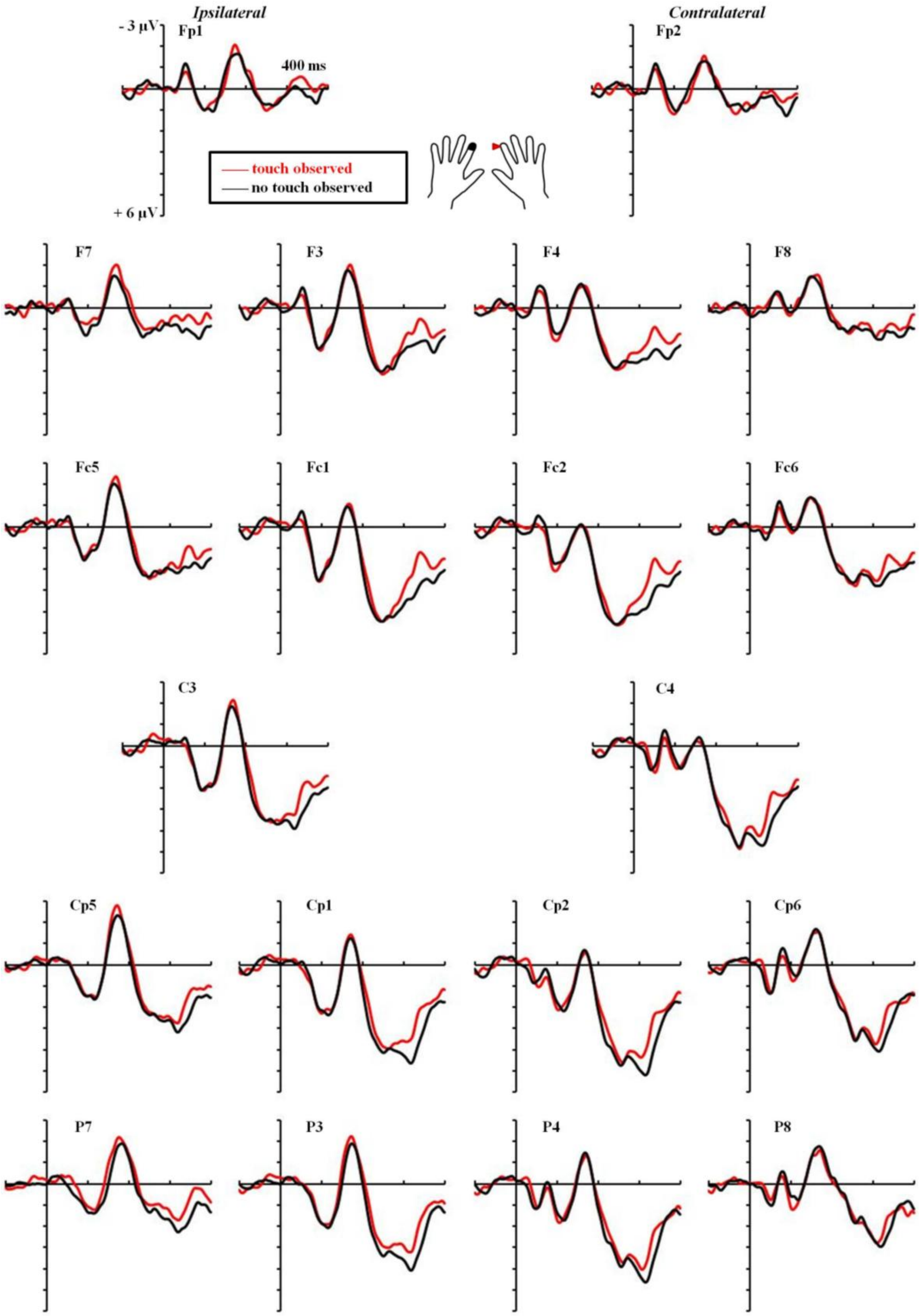


Fig. 3.3.d. Grand-averaged ERP waveforms in response to tactile stimuli to the right index finger tip (IndexTip$_{right}$) during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

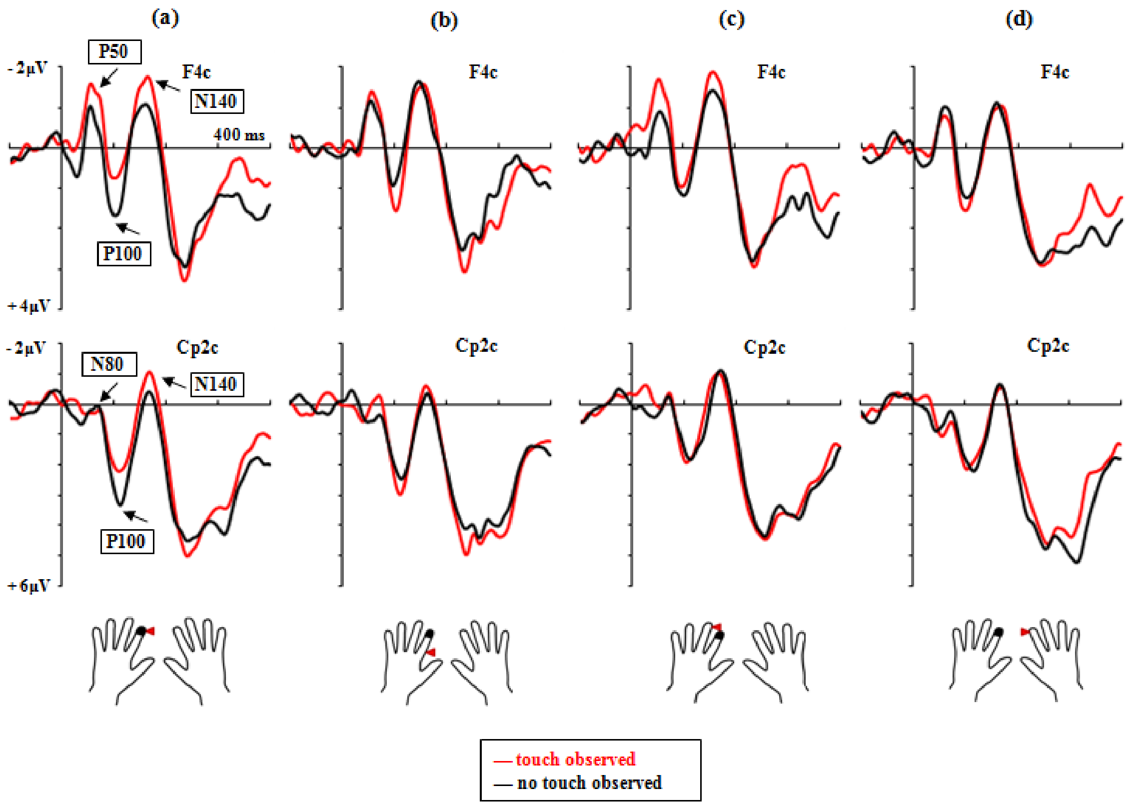


Fig. 3.3.e. Grand-averaged ERP waveforms in response to tactile stimuli to **(a)** the anatomically congruent index finger tip, **(b)** the base segment of that same index finger, **(c)** the adjacent middle finger tip or **(d)** the homologous index finger tip of the other unobserved hand during the observation of a model's index finger touch either an object (red line) or merely the empty space next to it (black line). Waveforms are shown at a representative frontal (F4c; top panel) and centro-parietal electrode (Cp2c; bottom panel).

Epoch 35-55 ms post-stimulus onset (P50)

For the somatosensory P50 component (35-55 ms post- stimulus onset), the analysis and interpretation of touch observation-related SEP modulations was complicated by two concurrently present but somewhat contradictory interactions, namely a significant *hemisphere* by *observed tactile action feedback*-interaction ($F(1,15) = 6.416$, $p = .023$, $\eta^2_p = .300$) along with an also significant *anterior-posterior* by *site of stimulation* by *observed tactile action feedback*-interaction($F(3,45) = 3.122$, $p = .035$, $\eta^2_p = .172$).

The former, first of all, suggested a significant P50 modulation at electrode sites over the contralateral hemisphere irrespective of which exact finger location was actually stimulated when followed up with separate *anterior-posterior* (2) by *site of tactile stimulation* (4) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for the two hemispheres (contralateral: $F(1,15) = 5.504$, $p = .033$, $\eta^2_p = .268$; ipsilateral: $F(1,15) = .073$, $p = .791$, $\eta^2_p = .005$). Statistically, this two-way interaction was clearly not further modulated by the *site of* *tactile stimulation* (*hemisphere* by *site of tactile stimulation* by *observed tactile action feedback*: F(3,45) = .425, p = .736, η^2_p = .028). A close visual inspection of the SEP modulations in the P50 latency range for the four different stimulated finger locations (see Figures 3.3.a-d and 3.3.e) and of the corresponding topographical distribution of the mean SEP amplitude difference, however, seemed to suggest that the contralateral P50 modulations were mostly driven by modulations for the left index and middle finger tips at frontal and fronto-central electrode sites (see Figures 3.3.a and c) as well as somewhat smaller modulations for the bottom segment of the left index finger at fronto-central and more posterior electrode sites (see Fig. 3.3.b). For the homologous right index finger tip, the SEP amplitudes appeared barely altered by the observation of the homologues finger of the other hand experiencing a tactile sensation (see Fig. 3.3.d). Overall, the touch observation-induced P50 effect thus seemed to be driven primarily by modulations for the left index and middle finger tips with the modulations being most pronounced at anterior electrode sites.

The aforementioned significant *anterior-posterior* by *site of stimulation* by *observed tactile action feedback*-interaction seems to substantiate this observation in parts. Follow-up comparisons of the effect of the sight of the finger touch the object rather than merely move through empty space on somatosensory processing separately for the four different tactually stimulated finger locations and the anterior and posterior electrode cluster (based on separate *hemisphere* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs) indicated that significant SEP modulations could be found only anteriorly and only for the adjacent middle finger tip (F(1,15) = 5.486, p = .033, η^2_p = .268). Note that the somatosensory P50 component tends to reverse its polarity at anterior electrode sites where it then appear as a negative rather than a positive deflection (Hämäläinen et al., 1990). Here, the mean amplitude of this anteriorly negative peak elicited by tactile stimuli to the left middle finger tip was significantly larger when the observed index finger moved to touch the object rather than the empty space next to it. The anteriorly located P50 modulations for the left index finger tip describe above, on the other hand, turned out to be not as reliable as the ones for the adjacent middle finger tip and thus failed to reach significance (F(1,15) = 1.583, p = .228, η^2_p = .095). Also for the remaining two stimulated finger locations, somatosensory processing remained unaffected the observation of an index finger touch an object, at anterior as well as posterior electrode sites ($\text{IndexBase}_{\text{left}}$: F(1,15) < 1.441, p > .249, η^2_p < .088; $\text{IndexTip}_{\text{right}}$: F(1,15) < .206, p > .657, η^2_p < .014).

Epoch 60-90 ms post-stimulus onset (N80)

While somatosensory processing in the early P50 latency range was thus mainly modulated for tactile stimuli presented to the adjacent rather than the anatomically congruent finger tip, the subsequent somatosensory N80 component (60-90 ms post-stimulus onset) did show a modulatory effect specific for the left index finger tip only, i.e. for the finger location anatomically congruent to the one observed to experience a tactile sensation: Following-up a significant *anterior-posterior* by *site of stimulation* by *observed tactile action feedback*-interaction (F(3,45) = 3.546, p =.022, η^2_p = .191), a systematic and moderately strong modulation of the N80 mean amplitude could only be found for the left index finger tip at anterior electrode sites (F(1,15) = 14.071, p = .002, η^2_p = .484; for all remaining finger locations (for anterior as well as posterior electrode clusters): F(1,15) < 1.858, p > .193 , η^2_p < .110; see the 3-way interaction for the P50 component above for details on the conducted follow-up ANOVAs). The mean SEP amplitude in response to tactile stimuli to the left index finger was significantly more negative-going in this time range when the observed index finger actually touched the object rather than the empty space next to it.

Epoch 100-120 ms post-stimulus onset (P100)

The somatosensory P100 component showed a similarly finger-specific effect for the anatomically congruent left index finger tip like the N80, however, for this mid-latency component, the effect was more wide-spread and not restricted to anterior electrode sites: Post hoc analyses of a significant interaction between the *site of stimulation* and the *observed tactile action feedback* (F(3,450 = 3.029, p = .039, η^2_p = .168) with separate *hemisphere* (2) by *anterior-posterior* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for each stimulated finger location revealed that the P100 mean amplitude was significantly smaller in response to seeing the model's index finger touch the object rather than merely move through empty space, but significantly so only for tactile stimuli to the anatomically congruent index finger tip (F(1,15) = 6.015, p = .027, η^2_p = .286).

It should, however, be mentioned that following-up the aforementioned *site of stimulation* and the *observed tactile action feedback*-interaction revealed, in addition, a marginally significant trend for a P100 effect for the bottom segment of the left index finger (F(1,15) = 4.181, p = .059, η^2_p = .218). In comparison to the modulations for the tip of this finger, the effect at its base was somewhat smaller and, crucially, reversed: The mean P100 amplitude was larger (rather than smaller) for the sight of the model's index finger tip touching.

Epoch 140-180 ms post-stimulus onset (N140)

For all four stimulated finger locations, the grand-averaged waveforms revealed a N140 component that peaked relatively late across most analysed electrode sites. Consequently, a late and broad time epoch of 140-180 ms after stimulus onset was chosen for the analysis. While the visual inspection of the evoked ERP waveforms in Figures 3.3.a-d seemed to suggest that the sight of touch tended to result in a larger N140 mean amplitude for all stimulated finger locations on the left (i.e. the observed) hand – mostly anteriorly for the left index and middle finger tips, mostly posteriorly for the bottom segment of the left index finger – , the statistical analyses did not confirm a reliable presence of such an effect. A significant *hemisphere* by *site of stimulation* by *observed tactile action feedback*-interaction ($F(3,45) = 2.984$, $p = .041$, $\eta^2_p = .166$) generally pointed to the contralateral hemisphere as the scalp area where the N140 modulations might be clearest but post hoc conducted comparisons remained inconclusive (for all separately conducted *anterior-posterior* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for the eight combinations of the factor levels of *hemisphere* and *site of stimulation*, $F(1,15) < 2.477$, $p > .136$, $\eta^2_p = .142$). The touch-related visual information thus did not reliably modulate concurrent somatosensory processing in this late latency range.

Fig. 3.3.f summaries the touch observation-related findings of the present study, showing the early-latency P50 modulation during middle finger stimulation at a representative frontal electrode (where the P50 appeared reversed to a negative peak) as well as the subsequent N80 and P100 modulations at representative frontal and centroparietal electrodes. The latter SEP modulations were specific in that the sight of somebody else's index finger modulated somatosensory processing only for tactile stimuli that were presented to the observer's anatomically congruent finger tip but not for any of the other three tactually stimulated finger locations.

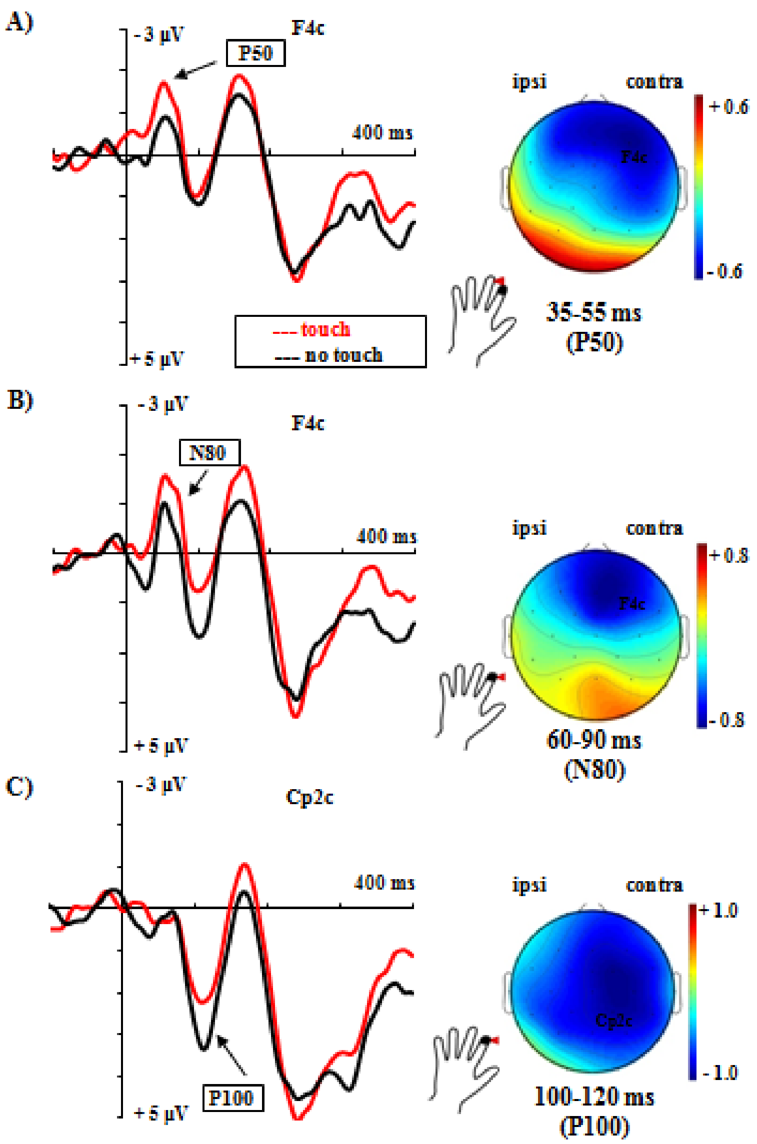


Fig. 3.3.f. A) Grand-averaged ERP waveforms in response to tactile stimuli presented to the adjacent middle finger tip during the observations of a model's index finger either touch an object (red line) or merely the empty space next to it (black line) at a representative frontal electrode (F4c), along with the topographic distribution of the significant difference in SEP mean amplitude in the P50 latency range in this condition. **B)** and **C)** Grand-averaged ERP waveforms in response to tactile stimuli presented to the anatomically congruent index finger tip for the two types of observed tactile feedback at a representative frontal (F4c) and centroparietal (Cp2c), respectively, along with the topographic distribution of the significant difference in SEP mean amplitude in the N80 **(B)** and P100 **(C)** latency range, respectively, in this condition. Note that a negative difference indicates an increased amplitude for the N80 and N140 component and a decreased amplitude for the P100 component during the sight of touch.

With respect to possible differences in somatosensory processing as a function of the concurrently stimulated finger location, irrespective of the observed tactile action feedback (see Exp. 3.2), it was found that the P100 latency range was the only time epoch for which such a modulation was indicated. Post hoc analyses of a significant *anterior-posterior* by *site of* *stimulation*-interaction (F(3,45) = 3.840, p = .016, η^2_p = .204) indicated that, posteriorly only, the mean P100 amplitude in response to tactile stimuli to the left index finger tip was significantly larger than that in response to tactile stimuli to the (left) middle finger tip (F(1,15) = 5.179, p = .038, η^2_p = .257); for all comparisons between the remaining finger locations (for both the posterior and anterior electrode cluster separately), all $p \geq .157$; the follow-up analyses of the effect of the stimulated finger location as a function of the anterior-posterior electrode location here were conducted by entering each possible combination of two finger locations into a separate *hemisphere* (2) by *site of stimulation* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVA for the two electrode clusters). Fig. 3.3.g shows the respective difference in ERP amplitude during tactile stimulation of the left index and the middle finger tips, along with its scalp distribution with a clear posterior-parietal maximum.

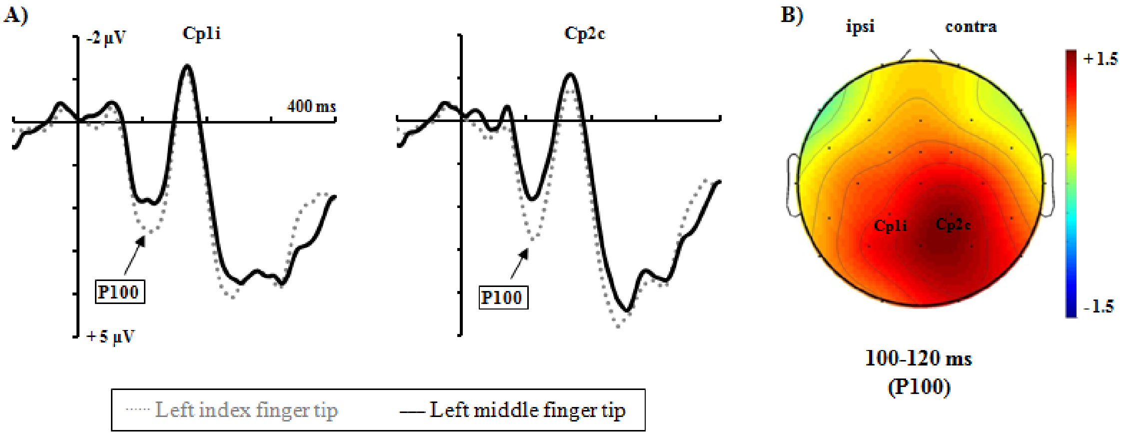
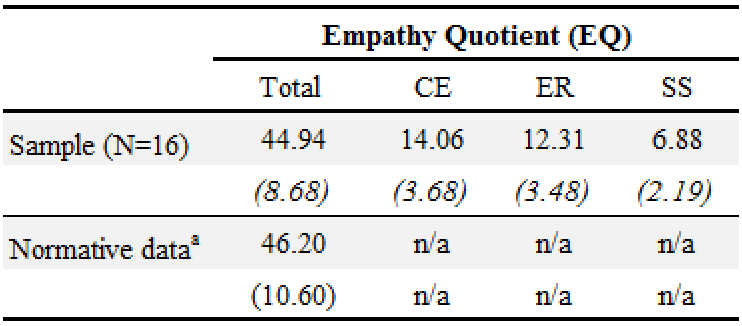


Fig. 3.3.g. A) Grand-averaged ERP waveforms in response to tactile stimulation of the left index finger tip and the left middle finger tip, respectively, irrespective of the concurrently observed tactile action feedback, at two representative centroparietal electrodes over the hemisphere contralateral (Cp2c) and ipsilateral (Cp1i) to the stimulated finger. **B)** Topographic distribution of the difference in ERP mean amplitude during index vs. middle finger tip stimulation in the 100-120 post-stimulus onset latency range (P100). Note that a positive difference indicates an increased amplitude for the P100 component during index finger stimulation.

Empathy correlations

Table 3.3.b shows the self-reported trait empathy measures for the present sample as obtained by administering the EQ questionnaire (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) at the end of the experiment.

Table 3.3.b. Mean scores and standard deviations for the self-report measures of dispositional empathy (EQ only).



	Empathy Quotient (EQ)			
	Total	CE	ER	SS
Sample (N=16)	44.94	14.06	12.31	6.88
	(8.68)	*(3.68)*	*(3.48)*	*(2.19)*
Normative data[a]	46.20	n/a	n/a	n/a
	(10.60)	n/a	n/a	n/a

[a)] Normative data are derived from: Lawrence et al., 2004 (EQ).

EQ: CE = Cognitive Empathy ER = Emotional reactivity SS = Social skills

Maximal scores: Total score of EQ = 80; Cognitive empathy (EQ) = 22, Emotional reactivity (EQ) = 22, Social skills (EQ) = 12.

To investigate whether the touch observation-induced SEP modulations found for the somatosensory P50, N80 and P100 component here might vary in strength as a function of individual levels of empathic skills, the mean difference in SEP amplitude between the two observational conditions (mean amplitude$_{touch}$ – mean amplitude$_{notouch}$) was computed for the finger location and electrode clusters for which somatosensory processing was found to be significantly modulated by the touch-related visual input and correlated with total score of the EQ as well as with its three subscales. Note that significant correlations are only reported here if they were found at least 3 electrodes within a given electrode cluster that has been found to show significant touch-observation induced modulations.

No reliable empathy-related correlations were found for the early-latency somatosensory P50 and N80 components (all $p > .05$). For the somatosensory P100, however, whose mean amplitude was significantly smaller for the sight of touch rather than no touch but only for concurrent tactile stimuli presented to the anatomically congruent left index finger tip, several fronto-central, central and centro-parietal electrode sites over the contralateral hemisphere showed significant correlations with the EQ's *social skills* subscale (Fc2: $r_s(16) = -.593$; Fc6: $r_s(16) = -.551$; C4: $r_s(16) = -.527$; Cp2: $r_s(16) = -.533$; Cp6: $r_s(16) = -.501$; all $p \leq .05$). The higher participants scored on this subscale, the more pronounced was their P100 effect (see Fig. 3.3.h).

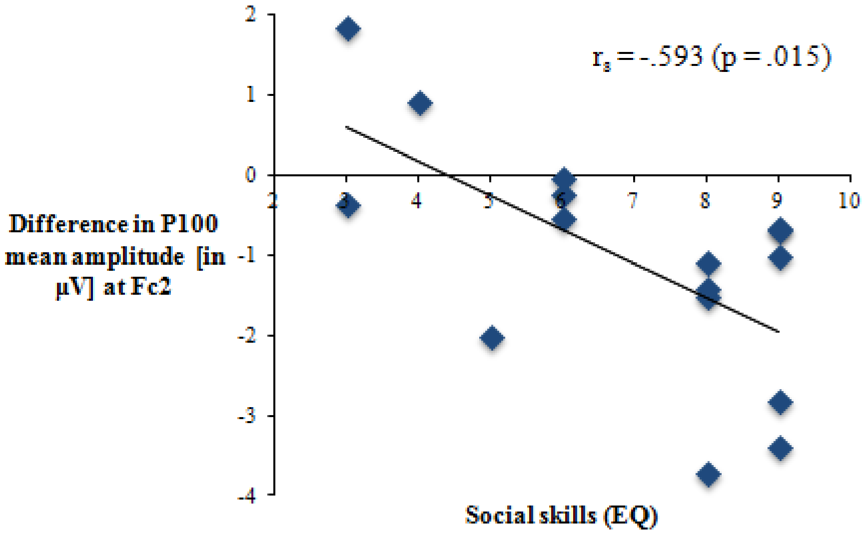


Fig. 3.3.h. Difference in somatosensory P100 mean amplitude for the two types of observed tactile action feedback for tactile stimuli delivered to the anatomically congruent left index finger tip as a function of individuals' self-reported *social skills* (EQ).

Unlike in Exp. 3.1, the strength of the touch observation-induced SEP modulations did not significantly correlate at any electrode site with the *emotional reactivity* subscale of the EQ (all $p > .05$). A correlational analysis of the relationships between the EQ subscales showed that the *social skills* subscale was in fact associated with the *cognitive empathy* subscale ($r_s(16) = .661$; $p = .005$) rather than with the *emotional reactivity* subscale ($r_s(16) = .372$; $p = .156$).

3.3.4 Discussion

Participants in the present study observed the same visual stimuli (i.e. a model's index finger performing lowering movements that either resulted in the finger tip touching a small box or merely moving through empty space) as in Exp. 3.2 while they were presented with tactile stimuli to either their anatomically congruent (left) index finger tip, the base segment of same index finger, the adjacent middle finger tip or the index finger of the unobserved right hand. Crucially, which finger location was concurrently tactually stimulated was manipulated block-wise rather than on a trial-by-trial basis (see Exp. 3.2), with the same finger location being stimulated continuously for three consecutive blocks.

Index-finger specific touch observation-related somatosensory-related ERP modulations

First and foremost, the sight of an index finger touch an object rather than the empty space next to it was associated with systematic ERP mean amplitude changes for the evoked N80 (60-90 ms post-stimulus onset) and P100 (100-120 ms post-stimulus onset) components which are thought to be generated in contralateral SI and bilateral SII, respectively (Allison et al., 1992; Hämäläinen et al., 1990; see, however, Tomberg et al., 2005), and which have recently been implicated in shared neural representations for experienced and observed (passive) touch (Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012; 2009; Wood et al., 2010).

While the revealed enhancement of the N80 mean amplitude during the sight of actual touch was restricted to the anterior electrode cluster over the hemisphere contralateral to tactile stimulation, being maximal at medial frontal electrodes, the subsequent P100 effect was found to be much more wide-spread. Similarly to Exp. 3.1, the ERP mean amplitude in the P100 latency range was significantly decreased whenever the model's index finger was seen to actually touch the object. The topographic distribution of the revealed difference in ERP mean amplitude was also very similar to the one found in Exp. 3.1, indicating that the touch observation-related reduction in P100 mean amplitude was most pronounced over fronto-central, central and centro-parietal electrodes over the contralateral hemisphere and thus at electrode sites over and close to the somatosensory cortex. Importantly, both the N80 and the P100 component were found to be modulated only for the anatomically congruent index finger tip, suggesting that the mirror touch response triggered by observing the tactile component of somebody else's actions might quite clearly represent which part (tip or bottom segment?) of which finger (index or middle finger?) was observed to come into contact with the object, in marked contrast to the location-unspecific N80/P100 modulations during the observation of passive touch found in Exp. 2.3. The sight of an index finger moving (irrespective of whether it then touched the object or not) most likely induced activity in both SI and SII due to the automatic simulation of the proprioceptive features of observed movements (e.g. Avikainen et al., 2002; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004; Raos et al., 2004; Rossi et al., 2002). While it is unclear how fine-grained the somatotopic organisation of such movement observation-related somatosensory activity actually is, i.e. to what extent cortical representations of specific fingers rather than e.g. the whole hand are triggered (it does show a somatotopic organisation for different body parts (Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004), it is conceivable that, if it is indeed sufficiently somatotopically organised, this might have boosted the touch observation-induced activation of shared neural representations for felt and observed touch specifically on the index finger tip. Considering the close links between the motor and the somatosensory system (cf. Gazzola & Keysers, 2009) and the finding that the *motor* component of observed finger movements is internally simulated in a highly muscle-specific way within a given hand (Avenanti et al., 2007; Romani et al., 2005; Urgesi et al., 2006), it might very well be that also the somatosensory activations during the observation of finger movements might, too, represent quite clearly which finger was observed in motion, along with the location of any associated haptic sensations.[21]

The somatosensory-related ERP modulations in the 60-90 ms (N80) and 100-120 ms (P100) latency range discussed so far thus suggest that the internal simulation of the haptic consequences of others' movements occurs in a very fine-grained fashion, involving exclusively the finger (tip) that is observed to move and touch (and possibly adjacent skin areas on that very same finger; see footnote 21). There was, however, also an even earlier ERP modulation, namely in the 35-55 ms (P50) time window, which was unexpectedly only significant for the adjacent middle finger tip but not for the anatomically congruent index finger tip. This will be discussed subsequently.

Unexpected early touch observation-related middle-finger specific somatosensory-related ERP modulations

For the anterior electrode cluster over the hemisphere contralateral to the stimulated hand, the mean P50 amplitude appeared to be larger during the sight of the model's index finger actually touch the object rather than the empty space next to it in response to tactile stimuli delivered to the anatomically congruent index finger tip as well as the adjacent middle finger tip. The statistical analysis indicated, however, that the respective modulation was only

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[21] The inevitable sight of finger movements during the observation of others' active touch sensations might boost the somatosensory activity triggered by the sight of touch specifically for the observed finger due to the somatosensory activity triggered by the described internal simulation of the proprioceptive movement component but since the observed movement involved the whole finger rather than just its tip, one might expect that also somatosensory processing of stimuli presented to the base segment of the index might then also be modulated. There was indeed a marginally significant trend for a wide-spread P100 modulation during the tactile stimulation of the base segment of the left index finger. Unlike during the observation of passive touch for which the P100 amplitude was found to be reduced in a similar way for the tip as well as the base segment of the left index finger (see Exp. 2.3), the P100 effect here was reversed for the base segment as compared to the tip of the index finger. The P100 mean amplitude tended to be enlarged rather than diminished when tactile stimuli were presented to the bottom segment of the index finger while the tip of that finger was observed to make contact with the object. Since no such reversal was indicated by the findings in Exp. 2.3, it appears unlikely that this reversed effect merely reflected differences in e.g. the regularity with which the respective locations are involved in brief touch sensations in daily life. Instead, it is more likely that this deviating pattern between two adjacent location within one finger was related to the specific type of observed movements performed by that very finger: During this kind of movement (hand rests relaxed on a table top with middle finger, ring finger and little finger being curled up slightly while the index finger performed lowering movements), the base segment of the index finger could never come into contact with a surface in a plausible way. The reversed P100 effect (and also the delay since the N80 did not show any modulation for the base segment) during the tactile stimulation of that very finger location might somehow reflect this incongruency and it would be interesting to compare somatosensory-related ERP modulations during tactile stimulation of both the index finger tip and the base segment during the observation of index finger movements that result in a tactile sensation at the base of the index finger rather than the tip.

significant for the middle finger but not for the index finger. Unlike in Exp. 3.2 where the late-latency N140 component showed an unexpected middle finger-specific modulatory effect of the observed tactile action feedback for the ipsilateral-posterior electrode cluster, the middle finger effect here was found not only with a different scalp distribution (contralateral-anterior) but also in a much earlier latency range (35-55 ms (P50)). In addition, the effect resembled the (non-significant) trend for the anatomically congruent index finger tip rather than being reversed as found in the previous experiment. In Exp. 3.2, the attenuation of somatosensory processing during the actual performance of movements (Cheron & Borenstein, 1987; Cohen & Starr, 1987; Haggard & Whitford, 2004; Huttunen & Hömberg, 1991; Rushton et al., 1981) but possibly also during the observation of others' actions (Voisin et al., 2011b) was discussed as a possible explanation as to why observing the tactile component of a given finger movement might be associated with a detectable mirror touch response for the adjacent but not the anatomically congruent finger tip. Interestingly, a direct comparison of the ERP mean amplitude (at posterior electrode sites) showed that the N140 amplitude during index finger stimulation was significantly reduced as compared to the N140 amplitude during middle finger stimulation in Exp. 3.2. In the present experiment, the only component for which a significant effect of the stimulated finger location as such was found was the SII-associated P100 component whose mean amplitude at posterior electrode sites was enlarged during the tactile stimulation of the index finger tip rather than the middle finger tip which might point to the boosting effect observing somebody else move the same finger might have on the excitability of the somatosensory system (Avikainen et al., 2002; Rossi et al., 2002). Interestingly enough, the actual *execution* of movements (or maintenance of a muscular contraction) has been found to be associated with an enhanced sensory response *specifically* in SII (Forss & Jousmäki, 1998; Huttunen, Wikström, Korvenoja, Seppäläinen, & Aronen, 1996; Lin, Simoes, Forss, & Hari, 2000). At least during early stages in somatosensory processing (note that the P50 is thought to arise from contralateral SI; Allison et al., 1992; Hämäläinen et al., 1990), the additional movement observation-related somatosensory activity might, however, induce more "somatosensory noise" and obscure the mirror touch response related to the concurrently observed tactile component, especially when the observed movements involve the same finger. Note that, other than in Exp. 3.2, the anterior P50 effect did show a similar (if somewhat smaller and less wide-spread) touch observation-induced amplitude increase for both stimulated finger tips but for the index finger, this difference was just not reliable enough to be significant (due to a larger standard error of the mean difference).

Variations in touch observation-related modulations in somatosensory processing as a function of interindividual differences in trait empathy

The strength of the revealed index finger-specific P100 modulation was found to be related to the observer's empathic traits, with significant positive correlations between the strength of the visually induced SEP modulations and the *social skills* subscale of the EQ (Lawrence et al. 2004) for several contralateral fronto-central, central and centroparietal electrodes where the P100 effect was also largest. The higher participants scored on this subscale, the more pronounced was the difference in mean P100 amplitude between the two observational conditions. Self-rated individual differences in empathic skills have previously been linked to differences in vicarious *somatosensory* activity in response to perceived actions and touch sensations of others, linking it with either emotional (Banissy & Ward, 2007) or cognitive components (Gazzola et al., 2006; Schaefer et al., 2012) of empathy. While the ERP studies on passive touch observation in the present thesis tended to show that the strength with which touch observation-related ERP modulations was primarily associated participants' self-reported dispositions to respond emotionally to others' negative experiences (see Exp.s 2.1, 2.2 and 2.3; see Exp. 2.4 for an exception), the present study on active touch observation points to an empathy scale that is more likely to be related to, if anything, cognitive rather than emotional aspects of empathy (Lawrence et al., 2004). Items of this subscale such as "I often find it difficult to judge whether something is rude or polite." or "I consciously work out the rules of social situations." mostly seem to actually tap, however, the ability to respond spontaneously in social situations rather than to rely or depend too much on social rules, casting doubt on whether or not this subscale actually measures empathy at all. Especially due to the small sample size, the revealed empathy correlations with this particular subscale have to be interpreted with caution (until replicated).

Summary and limitations

Overall, the sight of somebody else's index finger touch an object rather than merely the empty space next to it modulated somatosensory processing in the early 35-55 ms latency range unexpectedly for the adjacent middle finger tip only while somatosensory processing in the subsequent 60-90 ms and 100-120 ms latency ranges differed exclusively for tactile stimuli delivered to the anatomically congruent finger tip only (and possibly also during tactile stimulation of the base segment of the very same finger, but only in the 100-120 time epoch). An important limitation with respect to the index finger-specific effects was, however, that the different tactile consequences (touch or no touch) of the observed finger movements had been demonstrated to participants solely for their corresponding index finger by having asked them to briefly imitate the later-to-be-seen finger movements prior to the experiment. The aim of the subsequently reported Exp. 3.4 was therefore to test the finger-specificity of the N80/P100 effect after ensuring that participants actually “performed” the observed movements with both their index and middle finger tip before the experiment was started. In addition, participants were asked to casually “try out” the presented movements for themselves after passively observing a short presentation of the involved visual stimuli rather than to explicitly “imitate” and observe them at the same time. This was to ensure that participants were somewhat aware of the subtle difference in tactile feedback to the two types of index finger movements without interfering too much with subsequent instruction to ignore the visual stimuli during the experiment. Only participants’ left index and middle finger tip were to be stimulated during Exp. 3.4 to allow for a more direct comparison between these two finger locations and to determine whether the unexpected P50 during middle finger stimulation could be replicated.

Experiment 3.4

Finger-specificity of touch observation-related modulations in somatosensory processing in the context of observing others' haptic touch sensations (direct comparison between index and middle finger)

3.4.1 Introduction

In the preceding Exp. 3.3, the sight of somebody else's index finger touch an object rather than merely the empty space next to it was found to be associated with significant modulations of the N80 and P100 mean amplitude during tactile stimulation of participants' anatomically congruent index finger tip. While there were no significant alterations in somatosensory processing for any of the other tactually stimulated finger locations in these two latency ranges, it had at the same time been solely the left index finger with which participants imitated the observed tapping movements on the object prior to the experiment. It could therefore not been ruled out that the seemingly index finger-specific N80/P100 effect was confounded by this asymmetric pre-exposure to what it actually feels like to touch the object in the observed way. The finding that the early-latency P50 component, on the other hand, was modulated by the observed tactile action feedback exclusively during tactile stimulation of the adjacent middle finger tip and thus a finger location for which there had been no pre-exposure to what it actually feels like to tap on the object seems to somewhat dissipate this concern, but since the P50 possibly reflects an entirely different stage of somatosensory processing, the significance of having explicitly been made aware of the difference in tactile consequences associated with the observed movements is nevertheless unclear. For this reason, the present study aimed to compare touch observation-related ERP modulations in response to tactile stimulation to either the left index finger or middle finger tip when participants were asked to casually "try out" tapping on and next to the object a couple of times prior to the experiment with both their own index and middle finger tip.

3.4.2 Methods

Participants. The sixteen participants recruited to participate in this experiment were the same who also took part in Exp. 2.3 and 3.5 within the same EEG recording session since no major practice or carry-over effects were expected for the task-irrelevant visual and tactile stimuli and since each study in itself was relatively short. The order in which the participants went through the different experiments was randomised and participants were encouraged to take sufficiently long break between the studies.

Stimuli. The visual and tactile stimuli presented during the experiment were exactly the same as during Exp.s 3.2 and 3.3. However, only two finger locations were tactually stimulated here: The left index finger as the anatomically congruent finger also observed to touch the object during the experiment and the left middle finger as the immediately adjacent finger.

Procedure. The experimental procedure was in large parts identical to the one in Exp. 3.3 with the following modifications: With only two different finger locations to tactually stimulate, the total number of experimental blocks for each participant was six. The order in which the two fingers were successively stimulated was counterbalanced: For 50 % of the participants, the index finger was stimulated first for three consecutive blocks and for the other 50 % of the participants, the middle finger was stimulated first for three consecutive blocks. The observed tactile action feedback was again manipulated on a trial-by-trial basis within each experimental blocks, with 25 trials each for the two observational conditions, presented in random order. An additional 9 trials (approx. 15 % of all trials) were catch trials, resulting in a total number of 59 trials per block.

The initial demo of the visual stimuli and the difference in the tactile feedback associated with the observed finger movements was simplified: Rather than having participants imitate the observed movements *while* watching the visual stimuli, they instead first passively observed the two types of finger movements on the screen (12 trial in total, presented in random order) and were only afterwards asked to casually “try out the seen movements for themselves” a couple of times by either tapping on the object positioned on a piece of cardboard in front of them or merely moving their finger through the empty space next to the object. To ensure that both fingers received an equal amount of pre-experimental exposure to what it feels like to actually touch the object in the seen way, participants were instructed to perform with observed movements not only with their index finger, but also with their middle finger.

Data recording. The procedures for recording, pre-processing and segmenting the obtained EEG data as well as the criteria for artifact rejection were exactly the same as for Exp. 3.2.

Statistical analyses. ERP mean amplitudes were computed for each combination of observed tactile action feedback and concurrently stimulated finger location for four latency windows centred around the amplitude peaks of the following four SEP components: P50 (35-55 ms post- stimulus onset), N80 (65-85 ms post-stimulus onset), P100 (100-120 ms post-stimulus onset) and N140 (140-170 ms post-stimulus onset). The approximate peak latencies of each component were identified visually at posterior electrode sites over the hemisphere contralateral to the tactually stimulated left hand. The mean ERP amplitudes for each latency window were then subjected to 2x2x2x2x5 repeated measures ANOVAs with the within-subject factors *hemisphere* (ipsilateral vs. contralateral), *anterior-posterior* (anterior vs. posterior), *site of stimulation* (index finger vs. middle finger), *observed tactile action feedback* (touch vs. no touch) and *electrode site* to investigate whether the observation of an action resulting in a touch sensation modulates somatosensory processing of a concurrently delivered tactile stimulus. It was of particular interest whether the unexpected pattern of early-latency SEP modulations for the adjacent rather than the anatomically congruent finger (P50 effect for middle finger in Exp. 3.3) followed by mid-latency SEP modulations that were indeed specific to the anatomically congruent index finger would be replicated here, having assured that it was not only the anatomically congruent finger with which the observed movements were tried out prior to the experiment. Greenhouse-Geisser adjustments to obtained p-values were applied where appropriate. An alpha level of .05 was used for all statistical tests.

3.4.3 Results

Behavioural performance

Even though the reduced size of the fixation dot made it somewhat more difficult to perceive its infrequent and rapid colour changes, participants still managed to accurately detect them on 96.8 % of the catch trials with a false alarm rate of less than 1 %.

The response times for correctly detecting such a colour change of the fixation dot did not systematically differ as a function of the observed tactile action feedback (F(1,15) = 4.026; p = .063, η^2_p = .212), the concurrently stimulated finger location (F(1,15) = .119; p = .735, η^2_p = .008) or an interaction of both factors (F(1,15) = .024; p = .879, η^2_p = .002), suggesting that attention to the visual display was generally similar in all conditions. Table 3.4.a summarises the respective response times.

Table 3.4.a. Means and standard deviations of response times in colour change detection task (in ms) as a function of *observed tactile action feedback* and *site of tactile stimulation.*

	IndexTip		**MiddleTip**	
	touch	***no touch***	***touch***	***no touch***
M	583.00	576.40	579.21	573.68
SD	74.41	68.67	51.65	49.02

Electrophysiological data

Visually-induced effects of observing somebody else's active touch sensations on somatosensory processing were determined by comparing ERPs obtained when tactile stimulation was accompanied by observing the index finger of a left hand touch a neutral object versus the empty space right next to it. Figures 3.4.a and 3.4.b show the obtained grand-averaged ERP waveforms elicited for the two observational conditions separately for the left index finger tip and the adjacent left middle finger tip.

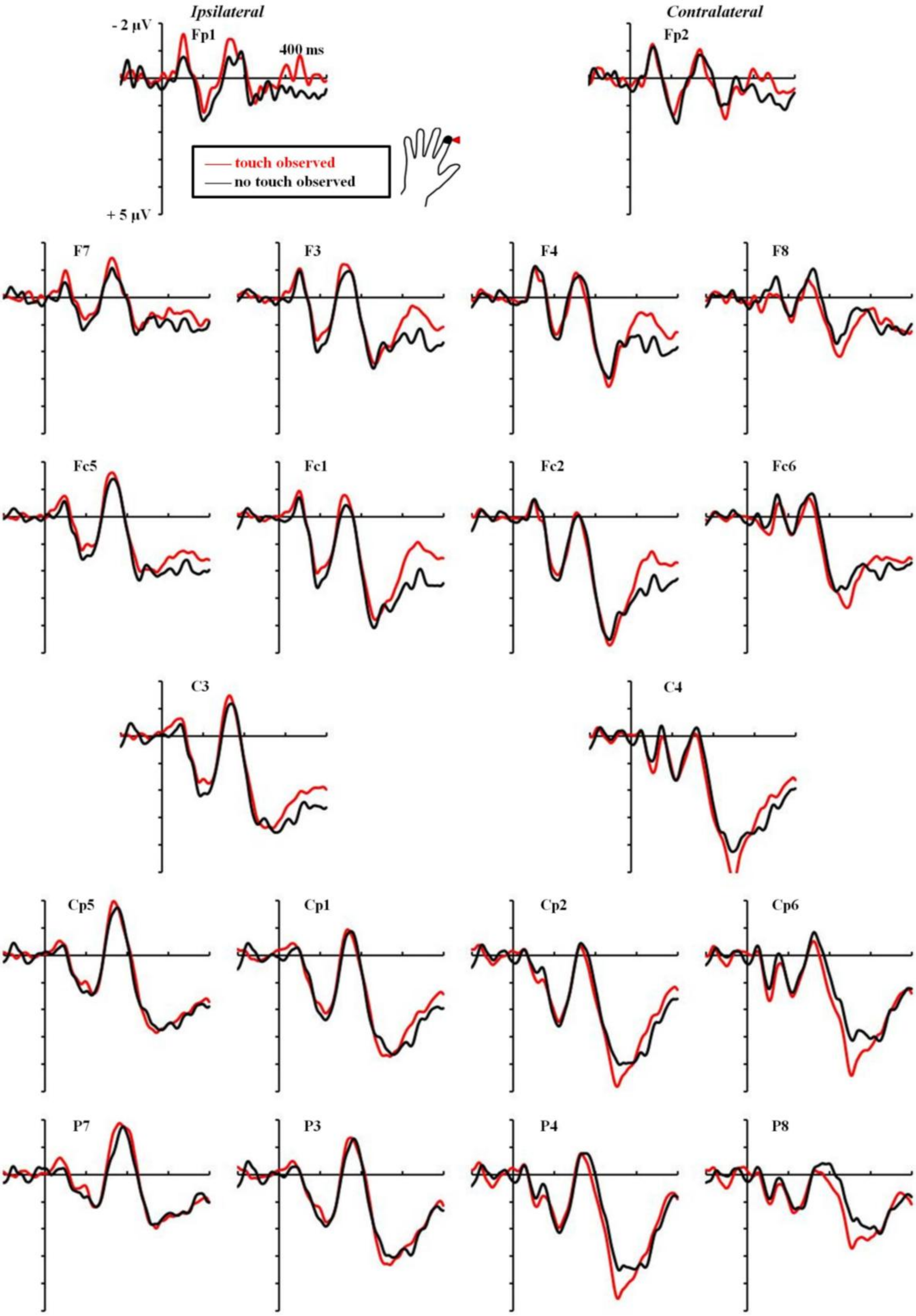

Fig. 3.4.a. Grand-averaged ERP waveforms in response to tactile stimulation of the index finger (IndexTip) during the observation of the model's index finger touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

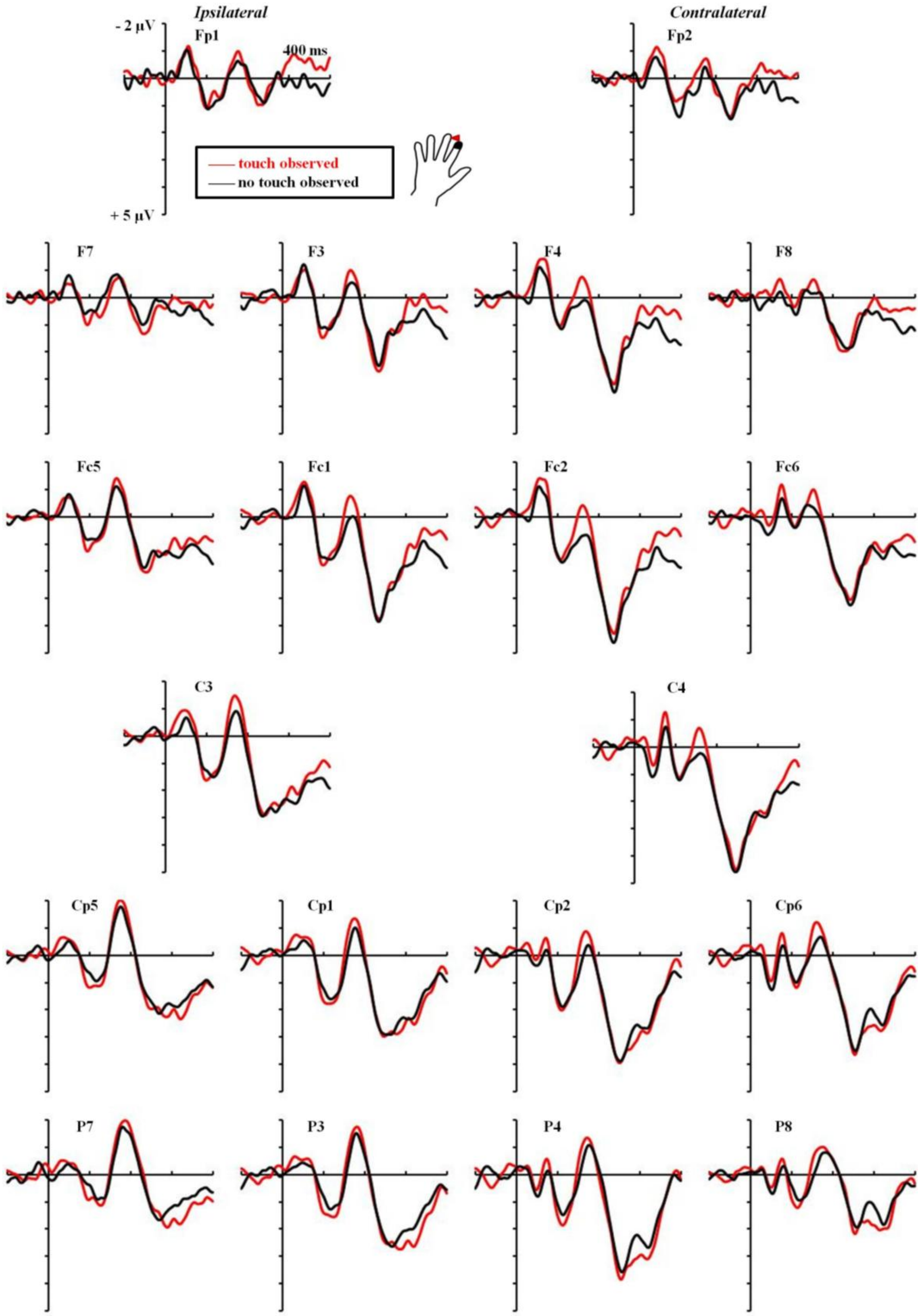

Fig. 3.4.b. Grand-averaged ERP waveforms in response to tactile stimulation of the middle finger (MiddleTip) during the observation of the model's index finger touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

The visual inspection of the SEP waveforms in response to tactile stimuli to left index finger tip suggested that the observation of somebody else's index finger touch an object induced at least at some ipsilateral electrode sites a reduction in P100 mean amplitude, less widespread but yet similar to the one observed in Exp.s 3.1 and 3.3 for the anatomically congruent finger location (see, for instance, F3, Fc1, Fc5 and C3 in Fig. 3.4.a). For the somatosensory processing of tactile stimuli to the left middle finger tip, on the other hand, the observation of an index finger make contact with an object quite clearly seemed to alter, mostly contralaterally from frontal to centro-parietal electrode sites, the mean amplitude of the N140 component, in addition to possibly earlier but less pronounced modulations of the somatosensory P50 (see Exp. 3.3) and/or N80 components.

The statistical analyses of the specified latency ranges, did, however, not confirm any of these observations. While the 35-55 ms post-stimulus latency range (P50) as well as in the 65-85 ms post-stimulus (N80) were found to show significant *hemisphere* by *site of stimulation* by *observed tactile action feedback*-interactions as the only significant effects involving the factor *observed tactile action feedback* at all (P50: F(1,15) = 6.888, p = .019, η^2_p = .315; N80: F(1,15) = 9.345, p = .008, η^2_p = .384), respective follow-up analyses based on separate *anterior-posterior* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for the four different combinations of the levels of the factors *hemisphere* and *site of stimulation* failed to reveal any significant SEP modulations for either of the two stimulated finger locations in these early time epochs (P50: all F(1,15) < 1.546, p > .233, η^2_p < .093; N80: all F(1,15) < 2.467, p > .137, η^2_p < .141). For the somatosensory P100 component for which the ERP waveforms seemed to suggest at several contralateral electrode sites an opposite effect of the sight of touch on concurrent somatosensory processing at the index vs. the middle finger tip (compare, for instance, Fc5 in Figures 1 and 2), the *hemisphere* by *site of stimulation* by *observed tactile action feedback*-interaction failed to reach significance (F(1,15) = 4.005, p = .063, η^2_p = .211).

The somatosensory N140 component whose amplitude appeared, especially contralaterally, so strongly modulated for tactile stimuli to the middle finger tip, did show a significant *hemisphere* by *site of stimulation* by *observed tactile action feedback*-interaction (F(1,15) = 12.816, p = .003, η^2_p = .461). Simple effects analyses (see 3-way ANOVAs described above) of the effect of the sight of an index finger touch an object separately for the two hemispheres and the two stimulated finger tips, however, did not confirm this seemingly strong N140 effect for the middle finger tip, neither contralaterally (F(1,15) = 1.555, p = .232, η^2_p = .094) nor ipsilaterally (F(1,15) = .313, p = .584, η^2_p = .020). Instead, the, in comparison to the ones at the middle finger, small N140 modulations over the ipsilateral hemisphere for the left index finger tip turned out to be marginally significant (ipsilateral: F(1,15) = 4.385, p = .054, η^2_p = .226; contralateral: F(1,15) = .056, p = .816, η^2_p = .004). Fig. 3.4.c shows the mean SEP difference (mean amplitude$_{touch}$ – mean amplitude$_{notouch}$) over the two hemispheres for both the index and middle finger tip, along with the associated standard error. While the observation of the model's index finger touch the object rather than the empty space next to it clearly induced the largest modulations over the contralateral hemisphere when the middle finger tip was concurrently tactually stimulated, the, by comparison, more pronounced inter-individual variability for the middle finger effects rendered them not reliable enough to be significant for neither hemisphere.

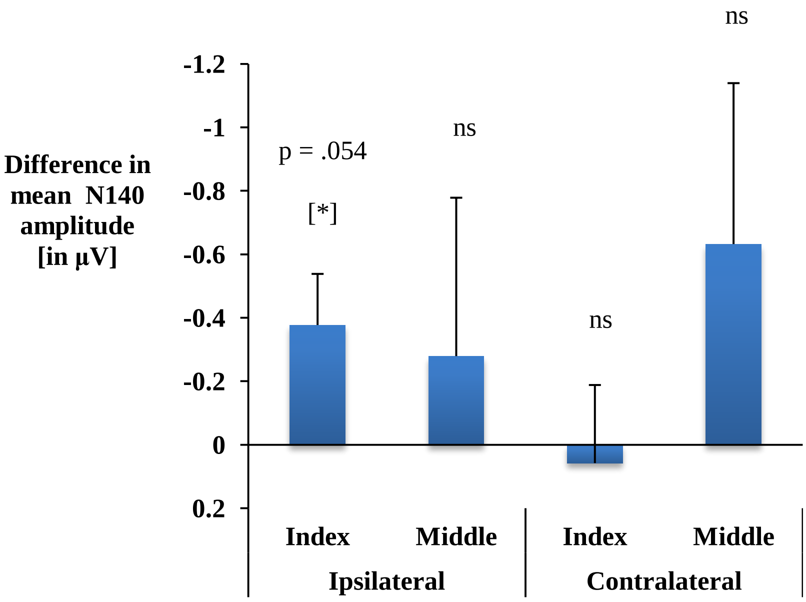

Fig. 3.4.c. Touch observation-induced mean difference in N140 amplitude (touch – no touch) as a function of hemisphere and tactually stimulated finger location.

In both the 65-85 ms (N80) and the 140-170 ms (N140) post-stimulus latency range, somatosensory processing was found to differ between the two stimulated finger tips, irrespective of the observed tactile action feedback. For the former time epoch, a significant main effect of the *site of stimulation* (F(1,15) = 11.544, p = .004, η^2_p = .435) indicated that the mean N80 amplitude was less negative-going and thus reduced in response to tactile stimuli to the index finger than in response to ones to the middle finger. An also significant *anterior-posterior* by *site of stimulation*-interaction (F(1,15) = 6.064, p = .026, η^2_p = .288) confirmed that the respective difference was present in a wide-spread fashion over both anterior (F(1,15) = 5.911, p = .028, η^2_p = .283) and posterior electrode sites (F(1,15) = 13.034, p = .003, η^2_p = .465; follow-up analyses of this interaction were based on separate *hemisphere* (2) by *site of stimulation* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for the anterior and posterior electrode cluster) but more strongly so posteriorly. For the N140 component, this difference in amplitude was reversed: Here, following-up a significant *hemisphere* by *anterior-posterior* by *site of stimulation*-interaction (F(1,15) = 5.087, p = .039, η^2_p = .253) by means of separate *site of stimulation* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for the four different electrode clusters indicated that the mean N140 amplitude was significantly more negative-going and therefore larger in response to tactile stimuli to the index rather than the middle finger, at least at ipsilateral-anterior electrode sites (F(1,15) = 5.284, p = .036, η^2_p = .261; for the remaining three electrode clusters, all F(1,15) < 1.801, p > .200, η^2_p < .107). Fig. 3.4.d shows the revealed ERP mean amplitude differences during index as compared to middle finger stimulation at a representative electrode each, along with the corresponding scalp distribution of the ERP amplitude difference in the 65-85 ms (N80) and the 140-170 ms (N140) post-stimulus latency range.

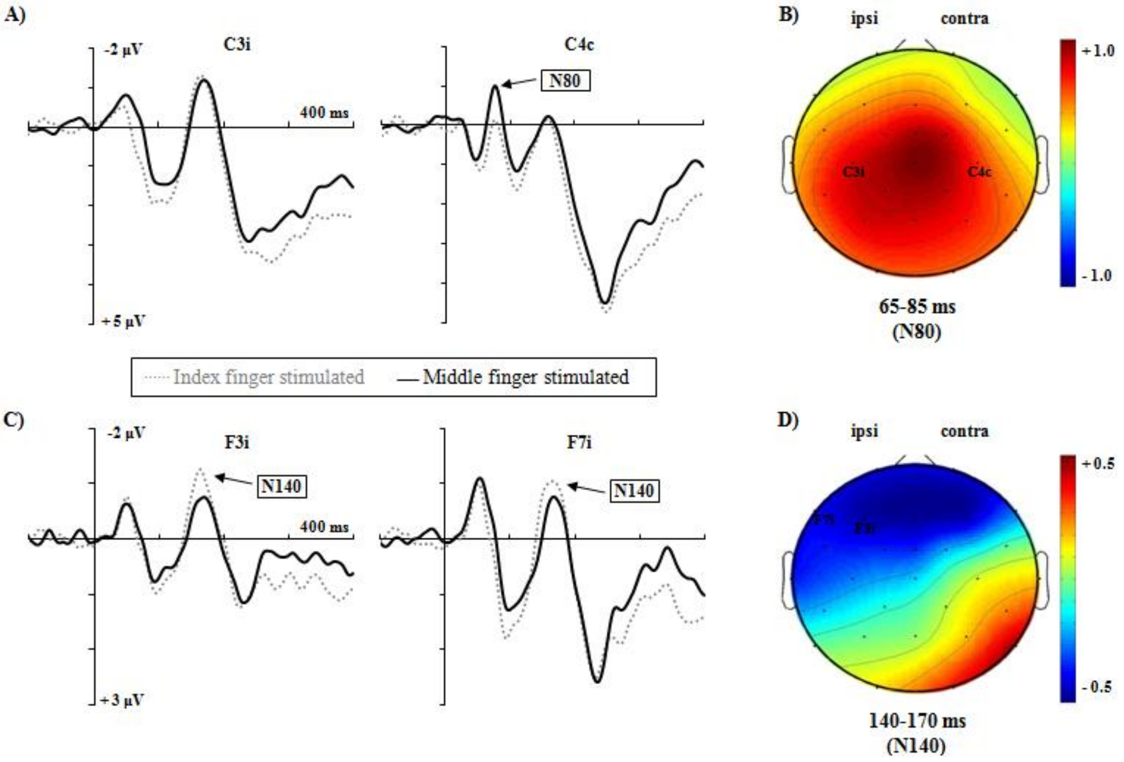

Fig. 3.4.d. A) Grand-averaged ERP waveforms in response to tactile stimuli presented to the index and middle finger tip, respectively, at two representative central electrodes (C3i/C4c), irrespective of the concurrently observed tactile action feedback, along with the scalp distribution of the corresponding ERP amplitude difference in the 65-85 ms post-stimulus latency window (N80). Note that a positive difference indicates a decreased N80 amplitude during index finger stimulation. **B)** Grand-averaged ERP waveforms in response to tactile stimuli presented to the index and middle finger tip, respectively, at two representative frontal electrodes (ipsilateral F3 and F7), along with the scalp distribution of the corresponding ERP amplitude difference in the 140-170 ms post-stimulus latency window (N140). Note that a negative difference indicates an increased N140 amplitude during index finger stimulation.

3.4.4 Discussion

Participants in this study observed a model's left index finger either touch an object or merely the empty space next to it while they were presented with tactile stimuli to either their homologous left index finger tip or the adjacent left middle finger tip. Crucially, it was made sure that participants tried out the later-to-be-observed movements involving either touching the object or not for themselves with both their index and middle finger prior to the experiment to make sure they briefly experienced what tapping on the object in the observed way actually feels like.

Unlike in the preceding Exp. 3.3 where the sight of the model's index finger touch the object was found to evoke a complex pattern of somatosensory-related ERP modulations in three different latency ranges during middle and index finger stimulation (P50 and N80/P100, respectively), in the present study, the type of observed tactile action feedback had, statistically, no reliable effect at all on somatosensory processing in the analysed latency ranges (similar to Exp. 3.2). Solely the late 140-170 ms post-stimulus time window showed at least a marginally significant trend for an ipsilaterally enhanced N140 amplitude, unexpectedly, though, not during middle finger but during index finger stimulation: The visual inspection of the ERP waveforms for the two different finger locations seemed to suggest quite clearly an primarily contralaterally enlarged N140 amplitude when the index finger was observed to touch the object while participants' *middle* finger was tactually stimulated but a pronounced inter-individual variability in the data appeared to render this modulation insignificant. For the anatomically congruent index finger, on the other hand, (ipsilateral) N140 modulations seemed much smaller but were obviously more consistent across participants and thus approached (but did not reach) statistical significance.

Interestingly, the observation of index finger movements as such, irrespective of whether they resulted in touch on the object or not, seemed to influence somatosensory processing much more reliably than the observed tactile action feedback, differently so, however, depending on whether the anatomically congruent index finger or the adjacent middle finger was stimulated*:* A subset of ipsilateral-anterior electrodes showed a significant enhancement in N140 amplitude during index as compared to middle finger stimulation, irrespective of whether the observed index finger touched the object or not, possibly reflecting that the somatosensory response associated with observing others' movements (Avikainen et al., 2002; Rossi et al., 2002) might not only be sufficiently somatotopically organised to represent the moving body part as such (Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004) but also to distinguish even between different fingers of one hand. The earlier peaking N80, on the other hand, showed a wide-spread reduction in mean amplitude during index as compared to middle finger stimulation which might suggest that even the mere sight of a moving index finger might initially attenuate somatosensory processing (see Voisin et al., 2011b) of tactile stimuli concurrently presented to the observer's homologous finger (as compared to the observer's adjacent finger), just as the actual execution of such finger movements would do, just with a delay since reduced SEP amplitudes during movement execution are usually found at latencies earlier than the N80 (e.g. P22, P27/P30, N30 and/or N60; Cheron & Borenstein, 1987; Shimazu et al., 1999). It should, however, be noted that due to a lack of a baseline condition during which somatosensory-evoked potentials were recorded in the absence of any observed finger movements, it is unclear whether the difference in N80 and N140 mean amplitudes, respectively, during index as compared to middle finger stimulation genuinely reflect enhanced or attenuated somatosensory processing.

That no reliable ERP modulations as a function of the observed tactile action feedback were found specifically during tactile stimulation of the anatomically congruent index finger (except for the merely marginally significant trend in the N140 latency range) might corroborate the aforementioned possibility that the index finger-specific N80/P100 modulations in Exp. 3.3 might have emerged in the context of having repeatedly imitated the two types of movements with the index finger prior to the experiment. When reducing the amount of pre-experiment exposure to what it actually feels like to perform the observed movements from simultaneous and explicit imitation to "casually trying out" tapping on the object after having seen a brief demo of the visual stimuli, the respective ERP modulations could not be replicated. As to *how* the amount of "pre-experiment exposure" might influenced how reliably the observation of touch affected somatosensory processing in particular of tactile stimuli presented to the anatomically congruent finger tip, several mechanisms are conceivable: First of all, watching and simultaneously imitating the index finger movements prior to the experiment might have strengthened existing visuotactile associations between the sight of somebody else's index finger move and touch (or of one's own index finger move and touch, for that matter) and the actual experience of touch when tapping on a surface with the finger tip in a way that merely casually trying the movements out in the present study did not manage to achieve to the same extent. This explanation seems, however, unlikely for several reasons*:* Firstly, even the more stringent "observe and imitate at the same time"-protocol used in Exp. 3.3 did still not involve such an excessive amount of self-felt "touch on the object" during the imitation phase that the revealed index finger-specific N80/P100 modulations were more likely to draw entirely on a *newly* learned visuotactile association between the sight of touch on an object and the concurrent feeling of touch on one's own finger rather than to reflect the automatic activation of an *existing* visuotactile mirror mechanism in response to the sight of others' tactile sensations (see e.g. Heyes, 2010 on the emergence of mirror-matching mechanisms based on associative learning in the context of a life-long experience of correlated multisensory events such as seeing one’s own body being touched and simultaneously feeling that touch). The number of trials on which participants not only observed but also imitated the index finger movements was small and the fact that both Exp. 3.2 (no prior imitation/”trying out” at all for any of the involved finger locations) and Exp. 3.3 (prior imitation only for the left index finger) showed middle fingers-specific EPR modulations even though participants were not exposed to what it feels like to tap on the object with the middle finger tip also indicates that self-experiencing what it actually feels like to perform the involved movements as such might not be the crucial factor in determining whether the sight of an index finger touch an object modulates somatosensory processing (during tactile stimulation of the anatomically congruent finger tip).

Alternatively, having imitated the involved index finger movements, including the tap on the object, prior to testing might have predisposed participants in Exp. 3.3 to imaging themselves touching the object (with their homologous finger tip but not e.g. with the adjacent one) during the actual experiment, especially since participants were to simultaneously imitate the index finger movements while they also observed them. Tactile mental imagery as such has been found to activate both SI and SII (Yoo, Freeman, McCarthy III, & Jolesz, 2003) and might thus have further boosted the activity in somatosensory areas related to the passive observation of the tactile component of the seen movements. While tactile imagery is generally difficult to rule out, it nevertheless seems unlikely that participants systematically did so during Exp. 3.3, given that participants were instructed to ignore the hand movements and the object and given that there was no instruction to engage in mental imagery of any kind.

The third and most compelling appearing explanation as to why somatosensory processing was found to be modulated in Exp. 3.3 (differentially during index as compared to middle finger stimulation) but not in the present study is that the explicit and more extensive imitation of the later-to-observed index finger movements in Exp. 3.3 might generally have enhanced the attention to the visual stimuli and the fact that one of the movements was associated with a tactile sensation for the observed agent. The effects of observing others’ touch sensations are often studied in the context of instructions that explicitly draw participants’ attention to the occurrence of touch, such as instructions to focus on what the other person might be feeling (Bufalari et al., 2007), to keep track of the number of times a brush touches a hand (Schaefer et al., 2009), to rate the intensity of the observed touch (Blakemore et al., 2005) or to at least observe the visual touch stimuli carefully (Keysers et al., 2004). In all previously reported studies in the present thesis (see Exp. 2.2 for an exception), participants were, however, explicitly instructed to ignore the actual visual stimuli and to focus entirely on reporting infrequent colour changes of the fixation cross, i.e. the touch-related visual input was completely task-irrelevant. While this was to allow to investigate the completely automatic and involuntary response to the sight of others' touch, even if no attention is paid to it, this might eventually also have made it more difficult to find systematic modulatory effects if the difference in observed tactile feedback is subtle and additionally embedded in simultaneously observing somebody else's movements which, in itself, is likely to induce somatosensory activity (Avenanti et al., 2007; Avikainen et al., 2002; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004; Raos et al., 2004; Rossi et al., 2002) that might consequently obscure the mirror touch response for the observed tactile component.

To investigate whether somatosensory-related ERP modulations in response to the sight of somebody else's index finger touch an object as compared to merely the empty space next to it might thus modulate somatosensory processing more reliably if the touch-related visual input is made more relevant, participants in the subsequently reported Exp. 3.5 were given a new task: Rather than respond to infrequent colour changes of the fixation cross, participants were instructed to indicate on each and every trial whether the observed index finger touched the object or not.

Experiment 3.5

Finger-specificity of touch observation-related modulations in somatosensory processing in the context of observing others' task-relevant haptic touch sensations

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3.5.1 Introduction

In experiment 3.4, the sight of somebody else's index finger touch an object rather than the empty space to it did not result in any reliable modulations in somatosensory processing, neither during tactile stimulation of the anatomically congruent index finger tip nor during tactile stimulation of the adjacent middle finger tip. In the light of the index finger-specific N80/P100 modulations and the preceding middle finger-specific P50 modulations previously found in Exp. 3.3, it was speculated that the brief imitation protocol at the beginning of Exp. 3.3 might have facilitated touch observation-related ERP effects in a way that a more casual experience of what it feels like to touch the object in Exp. 3.4 did not sufficiently achieve. The explanation deemed most likely was that having observed and concurrently imitated the involved movements repeatedly prior to testing might not only have made participants more aware of the different tactile consequences of the seen movements but might also have generally enhanced their attention to the observed visual stimuli and their tactile consequences despite their task-irrelevant nature. Given that the to-be-observed tactile component was very subtle and embedded in the observation of rather similar appearing finger movements, an entirely passive observation of the touch-related visual stimuli might not have been sufficient to induce reliable SEP modulations. The facilitating effect of a pre-experimental imitation protocol, however brief it might be, could, however, also be seen as a contingency of touch observation-related ERP modulations on having previously performed the touch-related index finger movements oneself to a sufficient extent, an interpretation which would raise the question of whether the respective modulations then indeed index a genuine mirror touch response triggered by the sight of *somebody else's* touch sensation (e.g. Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004) or whether they merely reflect e.g. the activation of visuotactile association learned at the beginning of the experiment.

It has generally be found that the *automatically* triggered matching of e.g. executed and observed actions can nevertheless be modulated by the amount of attention directed to the observed movements as such or to certain action features (e.g. Bach, Peatfield, & Tipper, 2007; Chong, Cunnington, Williams, & Mattingley, 2009; Chong, Williams, Cunnington, & Mattingley, 2008b) and in most studies on the effects of observing others' touch, the provided experimental instructions ensure that participants pay sufficient attention to the occurrence of touch in the visual display, e.g. by asking them to focus on what the other person might be feeling (Bufalari et al., 2007), to keep track of the number of times a brush touches a hand (Schaefer et al., 2009) or to rate the intensity of the observed touch (Blakemore et al., 2005). Accordingly, the aim of the present study was to investigate whether simply enhancing participants' attention to the occurrence of touch during the observation of the previously used index finger movements by making it task-relevant might be more effective in evoking touch observation-related SEP modulations in comparison to mere passive observation as in Exp. 3.4. To this end, participants were to report on each and every trial whether or not the model's index finger touched the object. Crucially, the pre-experimental exposure to what it feels like to actually perform the movements in questions was restricted to a very casual "trying out" prior to Exp. 3.4 without any "refresher" prior to the subsequently conducted Exp. 3.5.

3.5.2 Methods

Participants. The sixteen participants recruited to participate in this experiment were the same who also took part in Exp. 3.4. All participants participated in Exp. 3.4 first and then in Exp. 3.5 to avoid carry-over effects from an experimental task in which the observed finger movements were task-relevant (Exp. 3.5) to a task in which they were not and participants were merely to respond to a colour change of the fixation cross (Exp. 3.4).

Stimuli. The visual and tactile stimuli presented during the experiment were exactly the same as during Exp.s 3.2 - 3.4. Again, only the left index finger as the anatomically congruent finger also observed to touch the object during the experiment and the left middle finger as the immediately adjacent finger were tactually stimulated.

Procedure. The experimental set-up was similar to the one in Exp. 3.4 with the crucial modification that the observed finger movements and their relations to the nearby object were made task-relevant by introducing a visual discrimination task in which participants had to indicate on each trial whether the observed index finger touched the red box or not. Participants were instructed to hold the concurrently tactually stimulated finger of their left hand in a neutral position while the index and middle of their other hand rested on two dedicated response keys labelled "1" and "2" on standard computer keyboard used to collect the responses.

Participants were instructed to focus on the fixation cross while monitoring the hand closely and responding on each trial as quickly as possible. To avoid drawing participants' attention one-sidedly to the occurrence of touch rather than no touch simply through the semantics of the task instruction, two different instructions were provided: Half of the participants were instructed to indicate on each trial whether the observed index finger landed *on* the object or not while the other half of the participants were instructed to indicate on each trial whether the observed index finger landed *next to* the object or not. For each type of instruction, the response key assignment was counterbalanced across participants. Half of the participants were to press “1” to indicate that the finger landed *on* or *next to*, respectively, the object and “2” otherwise while the other half of the participants had the reversed response key assignment.

Sequence and timing of both the visual and tactile events on each trial was identical to in Exp. 3.4 except that a new trial began as soon as a response key was pressed. Each block contained again 59 trials in total, 25 trials each for the two types of observed tactile action feedback and, to maintain comparability across the ERP studies in this thesis, 9 trials on which the onset of the critical visual stimulus and the concurrent tactile stimulus was accompanied by a brief colour change of fixation cross which was, however, to be ignored by the participants here. Participants performed four consecutive blocks for each tactually stimulated finger, with the order with which the two finger locations were stimulated being counterbalanced across participants, resulting in a total number of eight experimental blocks in this study. An additional block for each finger location was added to counteract the general increase in noise due to the fact that a motor response was required on each and every trial. At the end of each block, participants were provided with feedback regarding their overall accuracy and average response latency in the visual discrimination task.

Prior to the actual experiment, participants performed a practice block (equivalent to an experimental block except for a reduced number of trials: 15 trials for each observational condition presented in random order, plus two randomly interspersed trials with colour change of the fixation cross, resulting in a total number of 32 trials) to familiarise them with the discrimination task at hand.

At the end of the experimental session, participants completed the 60-item EQ questionnaire (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) as well as the 28-item IRI by Davis (1983).

Data recording. The procedures for recording, pre-processing and segmenting the obtained EEG data as well as the criteria for artifact rejection were exactly the same as in previous experiments of this chapter.

Statistical analysis. Collapsing across the two types of instructions, ERP mean amplitudes were computed for each combination of observed tactile action feedback and concurrently stimulated finger location for four latency windows centred around the amplitude peaks of the following four SEP components: P50 (40-60 ms post- stimulus onset), N80 (65-85 ms post-stimulus onset), P100 (95-115 ms post-stimulus onset) and N140 (140-200 ms post-stimulus onset). The approximate peak latencies of each component were identified visually at posterior electrode sites over the hemisphere contralateral to the tactually stimulated left hand. Similarly to Exp. 3.4, the calculated mean ERP amplitudes for each latency window were then subjected to 2x2x2x2x5 repeated measures ANOVAs with the within-subject factors *hemisphere* (ipsilateral vs. contralateral), *anterior-posterior* (anterior vs. posterior), *site of stimulation* (index finger vs. middle finger), *observed tactile action feedback* (touch vs. no touch) and *electrode site*.

In addition, correlational analyses using Spearman's rank correlation coefficients were run on the difference in SEP mean amplitude between the two observational conditions and participants' trait empathy measures (EQ and IRI) for any time epoch for which a significant effect to the observed tactile action feedback on concurrent somatosensory processing was indicated.

3.5.3 Results

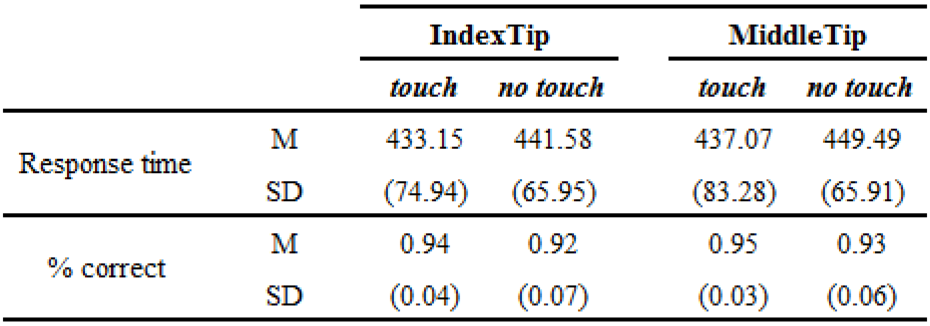
Behavioural performance

Due to a programming error, response times and accuracy data were not logged in the E-Prime files during stimulation of the middle finger for three participants in the "next to object"-group. Therefore, the overall sample size for the analysis of the behavioural task was reduced to N=13, with 8 participants in the "on the object"-group and 5 in the "next to object"-group.

Participants discriminated on average 93.5 % of the observed finger movements correctly (SD = 4.3 %). While there seemed to be a tendency for participants in the "next to object"-group to be both slower and less accurate in their responses, neither the overall response times ($\text{Mdn}_{\text{next to object}}$ = 467.2 ms ; $\text{Mdn}_{\text{on the object}}$ = 415.67 ms; U = 11.00, p = .188) nor the overall response accuracy ($\text{Mdn}_{\text{next to object}}$ = 92.5% ; $\text{Mdn}_{\text{on the object}}$ = 96.6 %; U = 8.00, p = .079) was found to differ significantly as a function of the provided instruction. Therefore, data were collapsed across the two types of instructions for further analyses.

The response times for discriminating whether the observed index finger touched the object or not did not systematically differ as a function of the observed tactile action feedback (F(1,12) = 1.593; p = .231, η^2_p = .117), the concurrently stimulated finger location (F(1,12) = 1.296; p = .277, η^2_p = .097) or an interaction of both factors (F(1,12) = .230; p = .640, η^2_p = .019). The response accuracy was also not affected by neither the observed tactile action feedback, nor by the concurrently stimulated finger location or an interaction between the two factors (all F(1,12) < 2.725, p > .125, η^2_p < .003). Table 3.5.a shows the response times and accuracy as a function of observed tactile action feedback and stimulated finger location, collapsed across type of instruction.

Table 3.5.a. Mean response times (in ms) and discrimination accuracy as a function of observed tactile action feedback and concurrently stimulated finger.



		IndexTip		MiddleTip	
		touch	*no touch*	*touch*	*no touch*
Response time	M	433.15	441.58	437.07	449.49
	SD	(74.94)	(65.95)	(83.28)	(65.91)
% correct	M	0.94	0.92	0.95	0.93
	SD	(0.04)	(0.07)	(0.03)	(0.06)

Electrophysiological data

For the analysis of the electrophysiological data, the full sample of N = 16 was used. Visually-induced effects of observing somebody else’s active touch sensations on somatosensory processing were determined by comparing ERPs obtained when tactile stimulation was accompanied by observing the index finger of a left hand touch a neutral object vs. the empty space right next to it. To increase the attention paid to those finger movements, participants were instructed to report (via a key press) on each trial whether the observed index finger actually made contact with the object or not. Figures 3.5.a and 3.5.b show the obtained grand-averaged ERP waveforms elicited for the two observational conditions separately for the left index finger tip and the adjacent left middle finger tip.

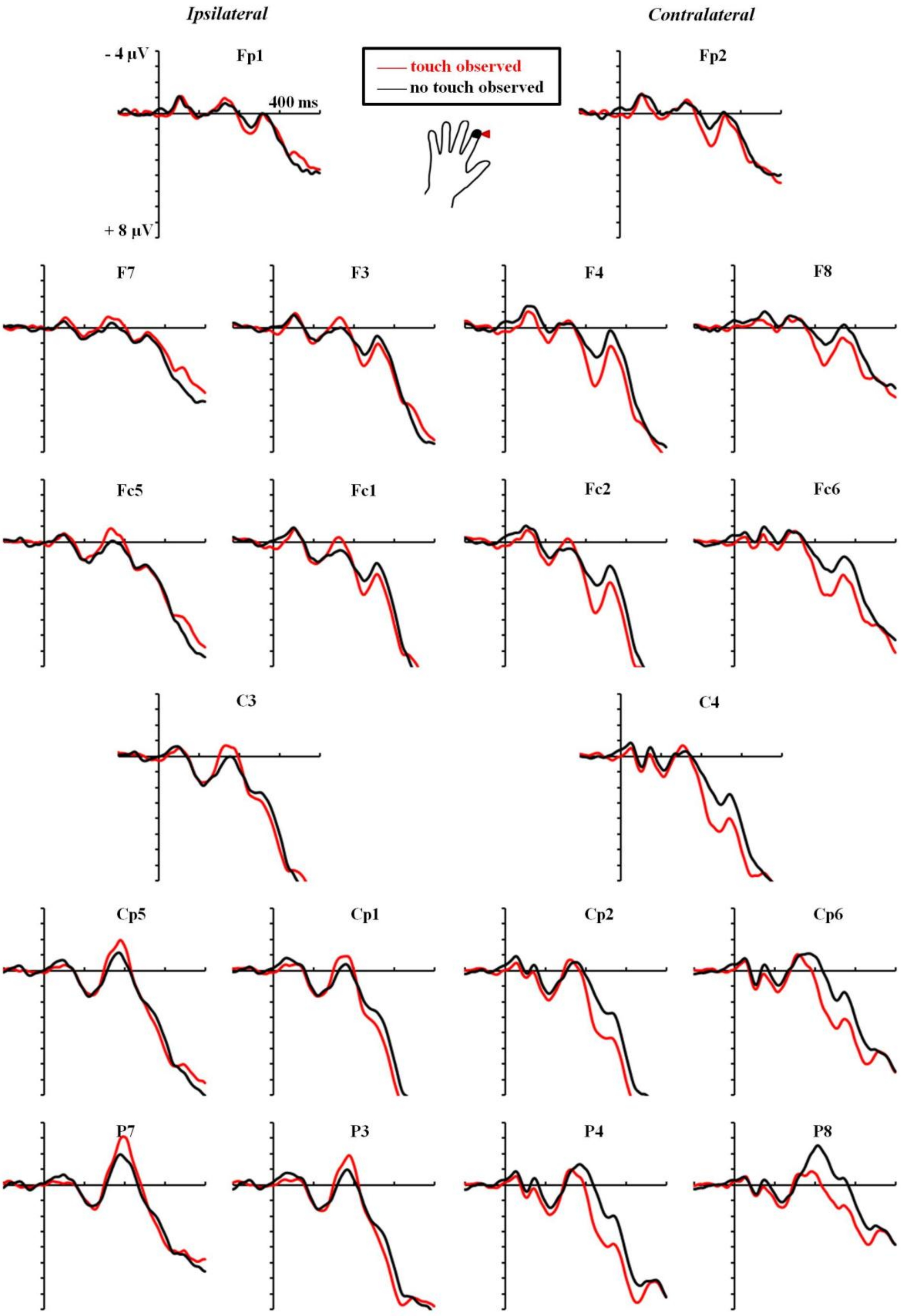


Fig. 3.5.a. Grand-averaged ERP waveforms in response to tactile stimuli to the left index finger tip during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

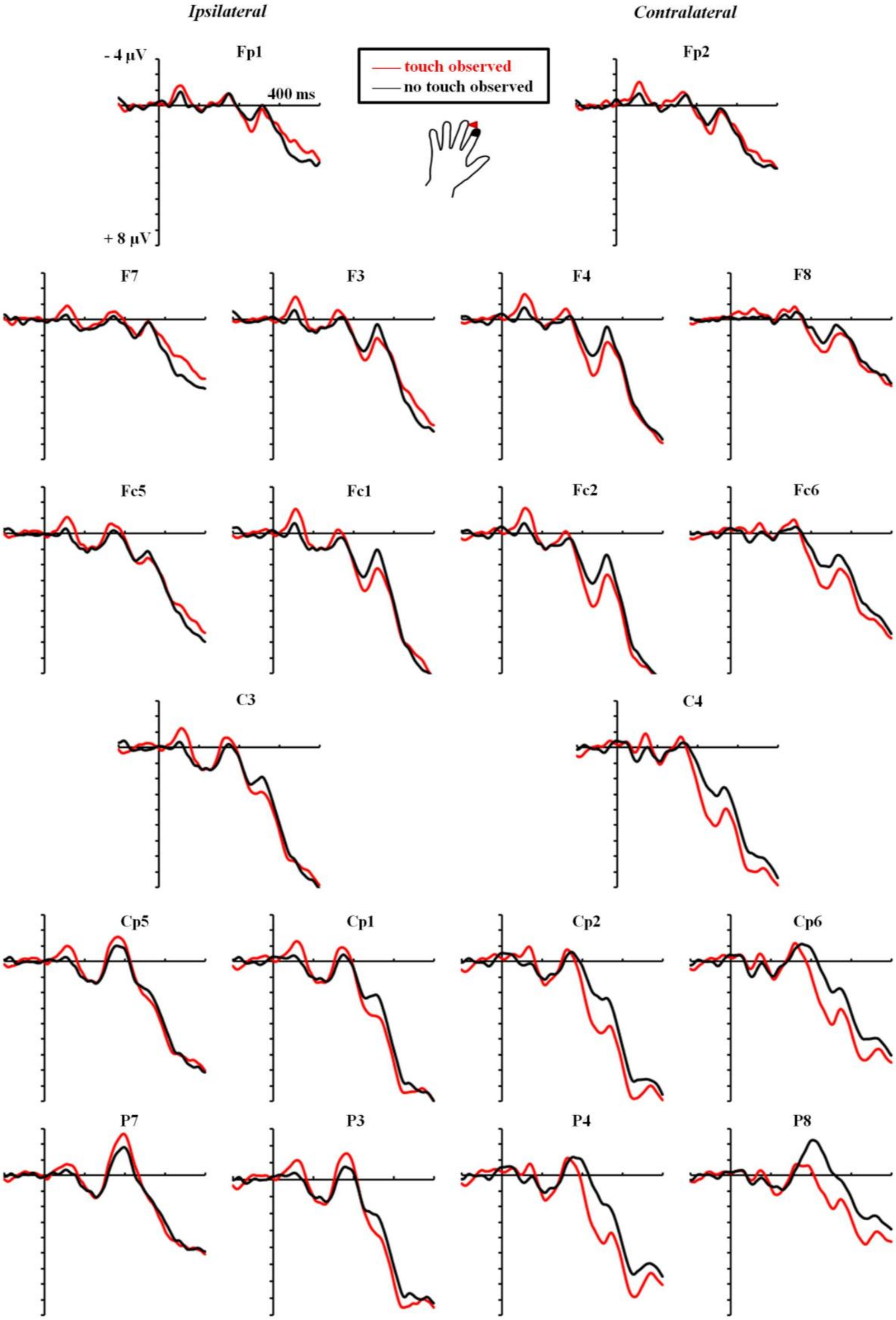


Fig. 3.5.b. Grand-averaged ERP waveforms in response to tactile stimuli to the left middle finger tip during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

In the previously collected ERP data sets in this thesis, the somatosensory N140 component was usually followed by a large positivity at a latency (at central electrodes) of approx. 220-250 ms post-stimulus onset after which the EPR amplitude slowly returned towards the baseline. Here, the tactile stimuli delivered to the index and middle finger of the left hand while participants were instructed to report on each trial whether the model's index finger actually touched the object or not, too, elicited a post-N140 positive peak (peak at approx. 225 ms) but this positive deflection was followed, especially at more anterior electrode sites, by a small negative one (approx. peak at 260-270 ms) after which the positivity of the ERP amplitude seemed to increase again (see Fig.s 3.5.a and b). This late and pronounced positivity was likely to be related to the choice response required at the end of each trial and might reflect a P3, an endogenous ERP component associated with attention, stimulus categorisation and decision-making elicited typically at latencies between 250 and 500 ms (cf. Polich, 2007). Importantly, a visual inspection of Figures 3.5.a and 3.5.b suggested that, at least contralaterally, the P225-N265 complex seemed to be strongly affected by the type of observed tactile action feedback. However, since the main focus of this thesis was the effects of touch-related visual information on *early* somatosensory processing in SI and SII within the first 200 ms after tactile stimulus onset, these modulations were not statistically analysed.

Systematic effects of the observed tactile action feedback on the mean ERP amplitudes of the *early* somatosensory components investigated in this thesis, on the other hand, were found for the P50, N80 and N140 components. There was a significant *hemisphere* by *observed tactile action feedback*-interaction ($F(1,15) = 10.116$, $p = .006$, $\eta^2_p = .403$) for the P100 component but post hoc analyses with two separate *anterior-posterior* (2) by *site of stimulation* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs did not confirm a reliable visually-induced modulation over either hemisphere ($F(1,15) < 1.407$, $p > .254$, $\eta^2_p < .086$).

For the early somatosensory P50 and N80 components, touch observation-induced SEP modulations were yet again primarily found for the middle finger tip rather than the anatomically congruent index finger tip: While a just significant main effect of the *observed tactile action feedback* ($F(1,15) = 4.864$, $p = .043$, $\eta^2_p = .245$) suggested a wide-spread enhancement of the P50 amplitude for the sight of the model's index finger actually touch the object rather than the empty space next to it, simple effects analyses following up on an also significant *hemisphere* by *anterior-posterior* by *site of stimulation* by *observed tactile action feedback*-interaction ($F(1,15) = 5.096$, $p = .039$, $\eta^2_p = .254$) indicated that this main effect was primarily driven by SEP modulations at anterior electrode sites over both hemispheres for concurrent tactile stimuli to the middle finger ($\text{Middle}_{\text{ipsilateral-anterior}}$: $F(1,15) = 11.963$, $p = .004$, $\eta^2_p = .444$; $\text{Middle}_{\text{contralateral-anterior}}$: $F(1,15) = 7.448$, $p = .016$, $\eta^2_p = .332$; for index finger stimuli, all $F(1,15) < 2.012$, $p > .176$, $\eta^2_p < .118$ at all four electrode clusters; follow-up analyses here were based on separate *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for each possible combination of the different levels of the factors *hemisphere*, *anterior-posterior* and *site of stimulation*).

Similarly, a significant *hemisphere* by *observed tactile action feedback*-interaction ($F(1,15) = 7.281$, $p = .017$, $\eta^2_p = .327$) seemed to point to an increased N80 amplitude over the ipsilateral hemisphere ($F(1,15) = 9.573$, $p = .007$, $\eta^2_p = .390$; contralateral: $F(1,15) = .077$, $p = .785$, $\eta^2_p = .005$) when followed up with separate 4-way ANOVAs for the two hemispheres (see P100 analysis above) but post hoc analyses of a marginally significant *site of stimulation* by *observed tactile action feedback*-interaction ($F(1,15) = 4.239$, $p = .057$, $\eta^2_p = .220$) identified only the touch observation-related SEP modulations during middle finger stimulation as significant (Middle: $F(1,15) = 6.724$, $p = .020$, $\eta^2_p = .310$; Index: $F(1,15) = 1.133$, $p = .304$, $\eta^2_p = .070$; post hoc analyses here were based on separate *hemisphere* (2) by *anterior-posterior* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for the two different stimulated finger tips). Fig. 3.5.c contrasts the ERP waveforms evoked by tactile stimuli to the index and middle finger during the sight of the viewed index touch the object or merely the empty space next to it at a representative fronto-central electrode (Fc2c) and shows the topographic distribution of the significant ERP mean amplitude differences in the P50 and N80 latency range during middle finger stimulation.

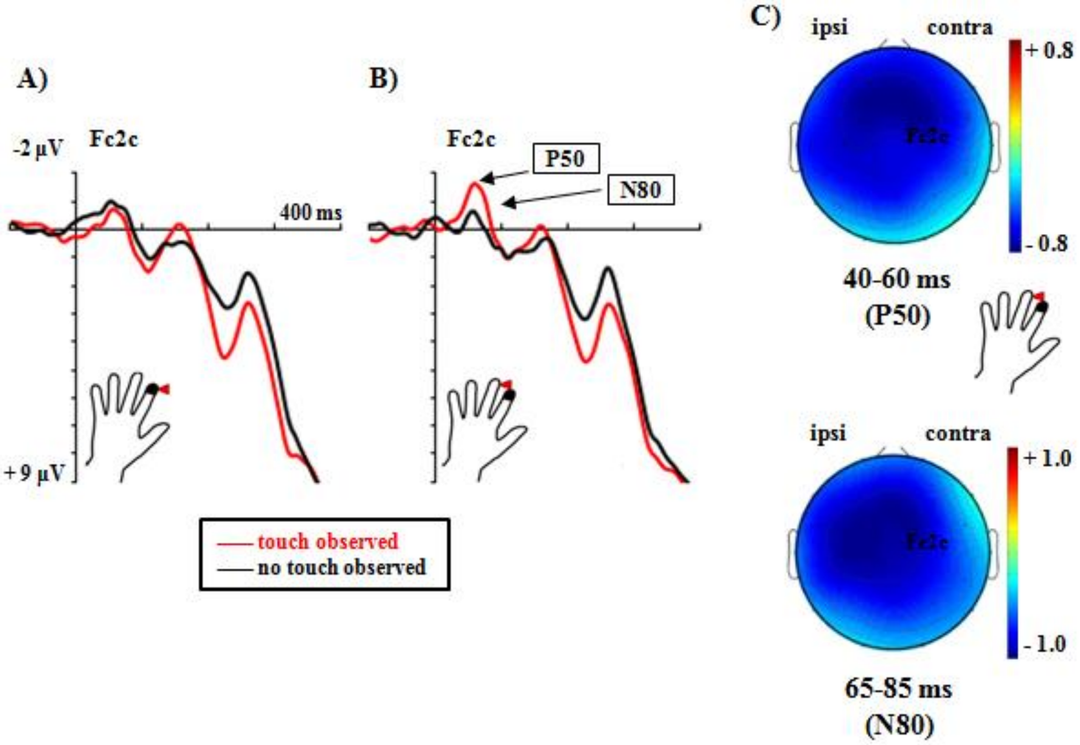


Fig. 3.5.c. Grand-averaged ERP waveforms in response to tactile stimuli to the anatomically congruent index finger **(A)** and the adjacent middle finger **(B)** during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line), at a representative fronto-central electrode over the hemisphere contralateral to the stimulated hand (Fc2c). The scalp maps in **(C)** show the topographic distribution of the significant touch observation-related ERP amplitude differences in the P50 and N80 latency range during tactile stimulation of the adjacent middle finger. Note that a negative difference indicates an increased negativity for both the P50 (whose polarity is reversed to negative at anterior electrodes) and the N80 amplitude during the sight of touch.

Only the late peaking somatosensory N140 component showed systematic SEP modulations for both stimulated finger locations in the form of a *hemisphere* by *observed tactile action feedback*-interaction (F(1,15) = 13.451, p = .002, η^2_p = .473; see P100 analysis above for a specification of the post hoc ANOVAs conducted to follow up this kind of 2-way interaction): Over the ipsilateral hemisphere only (F(1,15) = 8.681, p = .010, η^2_p = .367), the N140 amplitude was significantly more negative-going when the model's index finger was observed to touch the object rather than merely move through empty space. This ipsilateral touch observation-related effect was present at both anterior (F(1,15) = 7.060, p = .018, η^2_p = .320) and posterior electrode sites (F(1,15) = 7.299, p = .016, η^2_p = .327), as indicated when following-up a significant *hemisphere* by *anterior-posterior* by *site of stimulation* by *observed tactile action feedback*-interaction (F(1,15) = 10.086, p = .006, η^2_p = .402; see P50 analysis above for a specification of the post hoc ANOVAs conducted to follow up this kind of 4-way interaction). The N140 amplitude at contralateral electrode sites remained unmodulated by the sight of touch (all F(1,15) < 1.100, p > .311, η^2_p < .068). Fig. 3.5.d depicts the touch observation-related ERP modulations in the N140 latency range for both tactually stimulated fingers at a representative ipsilateral parietal electrode as well as the scalp topography of the difference in ERP mean amplitude for the two observational conditions.

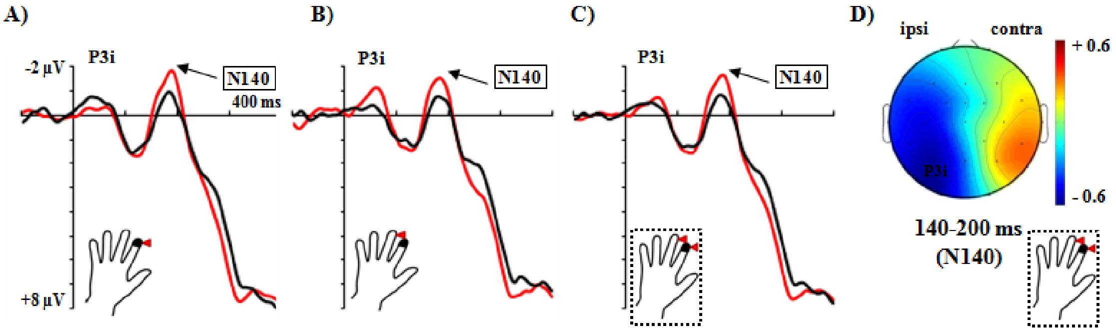


Fig. 3.5.d. Grand-averaged ERP waveforms in response to tactile stimuli to the anatomically congruent index finger **(A)**, the adjacent middle finger **(B)** and when collapsing across both stimulated fingers **(C)** during the observation of the model's index finger tip touch the object (red line) rather than merely the empty space next to it (black line), at a representative parietal electrode over the hemisphere ipsilateral to the stimulated hand (P3i). The scalp map in **(D)** shows the topographic distribution of the significant touch observation-related ERP amplitude differences (touch – not touch) in the N140 latency range when averaged across both tactually stimulated fingers. Note that a negative difference reflects an increased N140 amplitude during the sight of touch.

Finally, there were no significant differences in ERP mean amplitude as a function of which finger was concurrently tactually stimulated in any of the analysed time windows (for all main effects and interactions involving this factor, $F \leq 3.609$, $p \geq .077$, $\eta^2_p \leq .194$): A significant *anterior-posterior* by *site of stimulation*-interaction ($F(1,15) = 5.372$, $p = .035$, $\eta^2_p = .264$) pointed to a possible modulation in somatosensory processing in the N80 latency range but post hoc analyses did not confirm any significant differences in ERP mean amplitude elicited by index rather than middle finger stimulation at neither anterior ($F(1,15) = .299$, $p = .593$, $\eta^2_p = .020$) nor posterior electrode clusters ($F(1,15) = .609$, $p = .447$, $\eta^2_p = .039$; the respective follow-up analyses here were based on separate *hemisphere* (2) by *site of stimulation* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for the anterior and posterior, electrode cluster).

Empathy correlations

Possible links between the strength of touch observation-induced modulations in SEP amplitude and individual empathic skills were analysed for the anteriorly centred P50 and the more wide-spread N80 modulations during middle finger stimulation and for the ipsilateral N140 modulation found for both stimulated fingers. A table summarising the obtained trait empathy measures can be found in chapter 2.3.3 (Exp. 2.3) since the present sample of N=16 participated in both experiments in one EEG recording session.

The extent of the touch observation-related increase in P50 amplitude found anteriorly in the 40-60 ms post-stimulus onset latency range during middle finger stimulation did not show significant correlations with more than two isolated (anterior) electrodes for any of the empathy-related scales. For the more wide-spread N80 modulation found also during middle finger stimulation, the strength of the increase in N80 mean amplitude, however, was found to correlate significantly at several mostly ipsilateral-anterior electrode sites with the *cognitive empathy* subscale of the EQ (Fp1: $r_s(16) = .548$; Fp2: $r_s(16) = .608$; F3: $r_s(16) = .563$; F7: $r_s(16) = .521$; Fc1: $r_s(16) = .635$; C3: $r_s(16) = .499$; all $p \leq .05$; nearby Fc5 showed a marginally significant correlation: $r_s(16) = .494$, $p = .052$). In addition, three of these ipsilateral-anterior electrode sites also showed correlations with the IRI’s *personal distress* subscale (F3: $r_s(16) = -.570$; F7: $r_s(16) = -.601$; Fc1: $r_s(16) = -.592$; all $p \leq .05$; Fc5 again showed a marginally significant correlation: $r_s(16) = -.494$, $p = .052$). Crucially, high scores on the *cognitive empathy* subscale were associated with less pronounced N80 effects, while high scores on the *personal distress* subscale were associated with a more pronounced touch observation-induced N80 effect. The two empathy-related subscales as such correlated negatively with each other ($r_s(16) = -.565$, $p = .022$), suggesting a dissociation between these two components of empathic behaviour: Participants who described themselves as well able to cognitively adopt somebody else’s perspective did not tend to respond very emotionally to others’ distress and vice versa.

At the three mostly posterior and lateral electrode sites, the extent of the ipsilateral N140 enhancement during the sight of the model’s index finger touch the object during the tactile stimulation of either finger correlated, too, with the IRI’s *personal distress* subscale (Fc5: $r_s(16) = -.614$; Cp5: $r_s(16) = -.565$; P7: $r_s(16) = -.599$; all $p \leq .05$; nearby C3 showed a marginally significant correlation: $r_s(16) = -.484$, $p = .057$). The higher participants scored on this subscale, the more of an effect had the sight of touch on their ipsilateral N140 amplitude (see Fig. 3.5.e, panel C). Any additional correlations with other empathy-related subscales occurred only isolatedly at no more than two (frontal) electrodes and are thus not reported here.

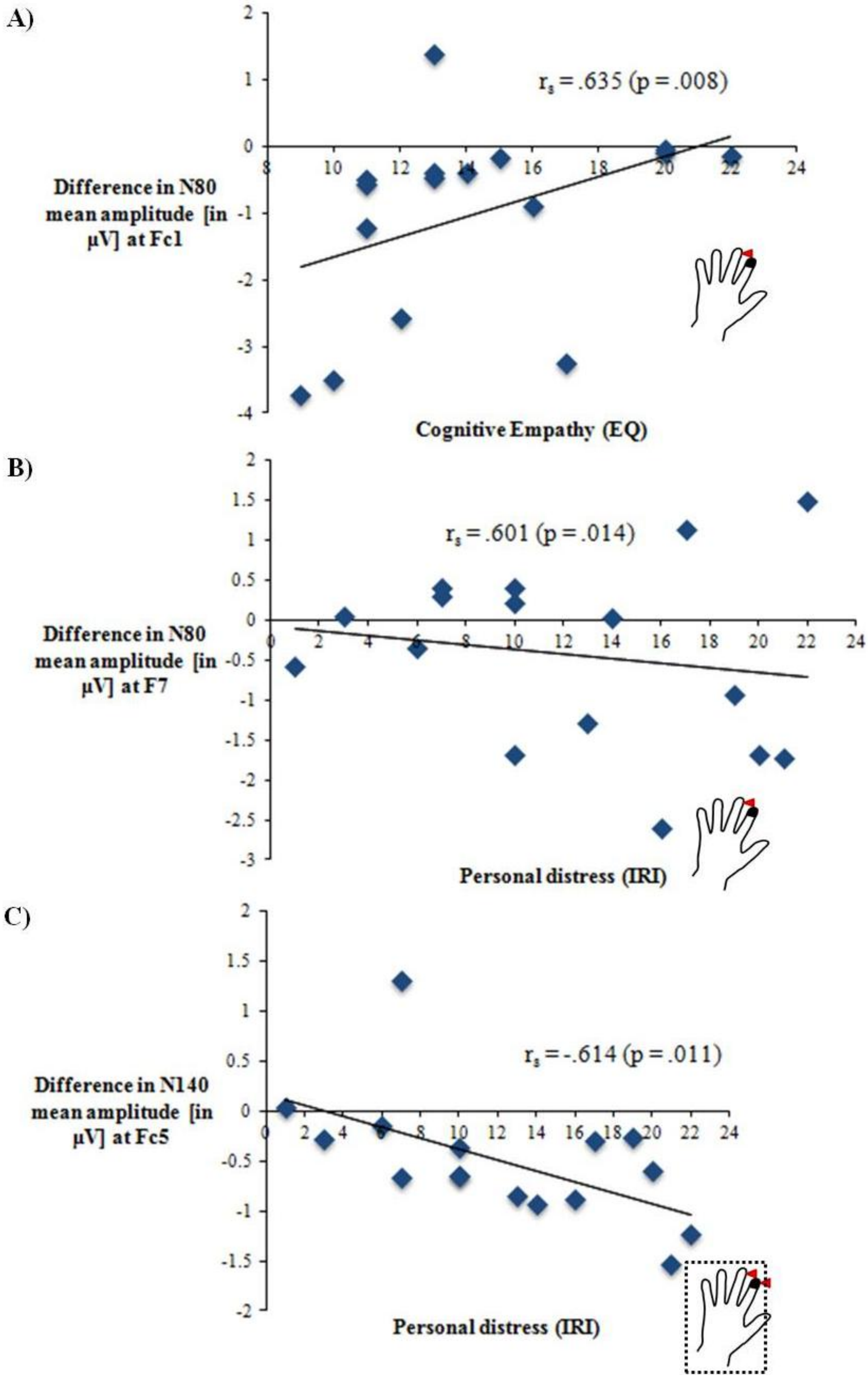


Fig. 3.5.e. (A + B) Difference in somatosensory N80 mean amplitude for the two types of observed tactile action feedback for tactile stimuli delivered to the middle finger as a function of individuals' self-reported *cognitive empathy* (EQ) and *personal distress* (IRI). **(C)** Difference in somatosensory N140 mean amplitude for the two types of observed tactile action feedback for tactile stimuli delivered to either finger as a function of individuals' self-reported *personal distress* (IRI).

3.5.4 Discussion

In Exp. 3.4, participants merely passively observed an index finger either touch an object or the empty space next to it after a very brief demonstration of the difference in tactile consequences associated with these movements at the beginning of the testing session. Somatosensory processing of tactile stimuli presented to participants' index and middle finger tips was, however, found to be almost entirely unmodulated by the observed tactile action feedback, suggesting that the somatosensory system did not resonate reliably enough with the tactile component in the visual display (finger touches object), possibly because it was too subtle to be sufficiently processed in the context of instructions to ignore the visual stimuli and to focus on the fixation cross only. Interestingly, enhancing participants' attention to the occurrence or absence of touch by having them report on each and every trial whether or not the model's index finger touched the object in the present study re-established some of the previously revealed SEP modulations (see Exp. 3.3), but also added some new findings.

Touch-observation related modulations in somatosensory processing: The anatomically congruent index finger

First of all, the sight of the model's index finger touch the object rather than merely the empty space next to it did modulate somatosensory processing during tactile stimulation of the anatomically congruent index finger tip, however, only for the late-latency N140 component whose ipsilateral (but not contralateral) amplitude was significantly enlarged during the sight of touch. In contrast to Exp. 3.3, the earlier N80 and P100 latency ranges were unaffected during index finger stimulation, suggesting yet again that the "observe and imitate"-protocol run at the beginning of Exp. 3.3 might have unduly biased participants' perception of the index movements in the context of experiencing touch on their own homologous finger tip. This is further corroborated by the finding that the N140 enhancement in the present study was not specific to somatosensory processing of index finger stimuli but was also found for middle finger stimuli. Ensuring that participants were briefly exposed to what it feels like to touch the object with *both* their index and middle finger tip prior to the experiment seemed to abolish the initially found specificity of the mirror touch response for the anatomically congruent finger (see Exp. 3.3). Instead, on which of the two adjacent finger tips the model actually felt the touch when making contact with the object no longer seemed to be represented in the triggered mirror touch response in this late latency window. The N140 component is thought to be generated (at least in parts) in bilateral SII (Tarkka et al., 1996; Valeriani et al., 2001a; see, however, Allison et al., 1992, Ku et al., 2007 and Tomberg, 1999, for another major source of the N140 in the bilateral frontal lobes, most likely activated by cortico-cortical connections with higher-order somatosensory areas in the posterior-parietal cortex), a higher-order somatosensory area whose somatotopic organisation generally tends to be less fine-grained than that in primary somatosensory areas (Hari et al., 1993; Maeda et al., 1999), especially when it comes to cortical finger representations (Hoechstetter et al., 2001; Ruben et al., 2001; Simoes et al., 2001). Visually induced mirror touch responses in such higher-order somatosensory areas might be associated with a similarly rough somatotopic, not clearly representing which on which finger a touch occurred, ultimately resulting in touch observation-related modulations in somatosensory processing irrespective of whether location of the observed and the felt touch match, at least when it comes to adjacent fingers of the same hand.

Touch-observation related modulations in somatosensory processing: The adjacent middle finger

Interestingly enough, making the touch-related visual stimuli more task-relevant re-established (and extended) the early-latency SEP modulations previously found in Exp. 3.3 during tactile stimulation of the adjacent rather than the anatomically congruent index finger: Similar to Exp. 3.3, the sight of an index finger touch an object rather than merely move through empty space was associated with a significant increase in P50 amplitude at anterior recording sites when tactile stimuli were presented to the adjacent middle finger tip but not to the index finger tip. The amplitude of the subsequent N80 component was found to be similarly enhanced during middle finger but not index finger stimulation but this amplitude change was much more wide-spread than the one for the P50. Both the P50 and the N80 components are thought to be generated in contralateral SI, in BA 1 and BA 3b, respectively (Allison et al., 1992; Hämäläinen et al., 1990). That processing in those primary somatosensory areas was significantly modulated by the sight of an index finger touch an object only during middle finger but not index finger stimulation might suggest, as previously discussed, that the concurrent somatosensory resonance response induced by the sight of finger movements (Avenanti et al., 2007; Avikainen et al., 2002; Gazzola & Keysers, 2009; Oouchida et al., 2004; Rossi et al., 2002) might be sufficiently somatotopically organised and fine-grained that it affects solely processing of stimuli delivered to the homologous index finger, obscuring the mirror touch response associated with the simultaneously observed touch for that finger. Somatosensory processing of stimuli to the adjacent finger might, on the other hand, be less affected by the sight of the neighbouring index finger moving as such, allowing the mirror touch response to stand out clearer (note that Exp. 2.3 suggest that the resonant response triggered by other’s touch sensations as such (rather than their movements) might actually not be contingent on a close anatomical match between where the touch is observed to occur (i.e. the index finger tip) and where participants’ are simultaneously stimulated themselves, at least for locations within one hand which might explain why mirror touch responses might be found during middle finger stimulation in the first place).

Interestingly, there were no significant SEP modulations as a function of the concurrently stimulated finger per se in the present study, in contrast to Exp. 3.2, 3.3 and 3.4 where somatosensory processing was found to differ contingent on whether the index or middle finger were stimulated, if inconsistently with respect to the affected latency range (N80, P100, N140) and the direction of the effect (increase or decrease in ERP amplitude during index finger stimulation as compared to middle finger stimulation). Assuming that those deviations did not merely index inherent differences in how tactile stimuli are processing at those two finger locations, it was speculated that they were associated with the fact that index finger stimulation was accompanied by the sight of a homologous finger moving (irrespective of whether or not it touches the object) while this was not the case during middle finger stimulation, corroborating the aforementioned notion that the automatic internal simulation of the proprioceptive features of observed movements (Avenanti et al., 2007; Avikainen et al., 2002; Gazzola & Keysers, 2009; Oouchida et al., 2004; Rossi et al., 2002) might occur in fine-grained and very finger-specific fashion. The absence of any significant effects in the present study does not necessarily contradict the above described explanation that the early mirror touch response was only detectable during middle finger stimulation but not during index finger stimulation because the internal simulation of the index finger movements interfered with the simulation of the observed tactile component – the difference might have been subtle but yet sufficient to obscure the touch observation-related mirror response. It is, however, conceivable that their absence is a direct result of the task instruction which increased the salience of the occurrence of touch, possibly making the movements per se less relevant. Interestingly, it has previously been found that the automatic motor response during action observation can be interrupted if participants are instructed to focus on a task-irrelevant action feature (Chong et al., 2009). In this context, it would be interesting to see whether a task instruction that shifts the attentional focus back to the actual movements rather than their tactile component (such as “Did the index finger move to the right or to the left?” rather than “Did the index finger touch the object?”) might re-instate SEP modulations as a function of the whether the tactile stimulation of a given finger is accompanied by the sight of the homologous finger moving or not – and also how this might affect the mirror touch response triggered by the tactile component of the movements, especially for the anatomically congruent finger.

Variations in touch observation-related modulations in somatosensory processing as a function of interindividual differences in trait empathy

With respect to the question as to whether the strength of the revealed touch observation-related ERP modulations depended on inter-individual differences in empathic dispositions, two empathy-related subscales were implicated in such correlations in the present study, namely the EQ's *cognitive empathy* subscale and the IRI's *personal distress* scale. For both the middle finger-specific increase in N80 amplitude and the unspecific increase in N140 amplitude triggered by the sight of the model's index finger touch the object rather than the empty space next to it, several ipsilateral-anterior and contralateral-frontoparietal electrodes, respectively, showed that said amplitude modulations were more pronounced in participants who scored high on the *personal distress* scale, a scale that quantifies the dispositional tendency to react with feelings of anxiety and discomfort to the observation of others' negative experiences (Davis, 1983). This subscale has recently been implicated in the strength of vicarious brain activity during the observation of pain in others (Saarela et al., 2007) but the present findings might indicated that interindividual differences in this aspect of trait empathy might also shape vicarious brain activity during the observation of non-painful touch in others. In addition, it was found that the middle finger-specific N80 enhancement during the sight of touch systematically co-varied at several mostly ipsilateral-anterior electrode sites with participants' scores on the EQ's *cognitive empathy* subscale, a subscale that taps a cognitive dimension of empathy (Lawrence et al., 2004). Interestingly, Schaefer et al. (2012) recently demonstrated that the strength of touch observation-induced activity in SI/BA 2 correlated significantly with participants' self-reported perspective-taking abilities (IRI) and thus also with a cognitive dimension of empathy, which seems of particular relevance here, given that the somatosensory N80 component is thought to be generated in contralateral SI (Allison et al., 1992). Importantly, it was, however, found in the present study that it was actually the participants who scored low on the *cognitive empathy* subscale who showed the more pronounced N80 effects during touch observation, an unexpected finding given that will be discussed in more detail in chapter 3.7. It should, however, also be noted that the empathy correlations revealed in both the N80 and N140 latency range were found only at a few (though topographically clustered) electrode sites and thus need to be interpreted with caution until replicated.

Conclusion

Increasing the salience of the tactile component of the observed index finger movements by making the occurrence of touch on the object task-relevant resulted in an ipsilateral increase in N140 amplitude when the model's index finger was seen to actually make contact with the object rather than merely move through empty space, for both the anatomically congruent index finger as well as the adjacent middle finger, suggesting that the mirror touch response in higher-order somatosensory areas might not clearly represent where exactly (i.e. on which finger) the observed touch occurs. Importantly, in the context of the increased attention to whether or not the observed index finger touches the object, the anteriorly-located middle finger-specific P50 enhancement found in Exp. 3.3 was replicated. In addition, also the subsequent N80 component showed a touch observation-related change in amplitude which, too, could only be found during tactile stimulation of the adjacent middle finger but not of the actually anatomically congruent index finger tip. Given that these middle finger-specific modulations were rather unexpected given that one might intuitively expect the most pronounced modulations to be found for the homologous finger, the subsequently reported Exp. 3.6 was conducted to test whether these surprising modulations during middle finger stimulation were specific to the “combination” of observing an index finger touch an object while the middle finger is stimulated (the index finger might be a particularly “special” finger given that it certainly more often used to touch and probe surface than any of the other fingers) or whether these modulations could also be found if the scenario was to be reversed: A middle finger is observed to touch an object while the index finger (i.e. the now “adjacent” finger) is tactually stimulated.

Experiment 3.6

Finger-specificity of touch observation-related modulations in somatosensory processing in the context of observing others' haptic touch sensations: Can strong SEP modulations for the adjacent rather than the anatomically congruent finger also be observed when the observed "touching" finger is not an index finger?

3.6.1 Introduction

In Exp. 3.2, the sight of an index finger touch an object rather than the empty space next to it was a solely associated with a decrease in N140 amplitude which was, however, specific to tactile middle finger stimulation and could not be found when the actually homologous index finger was stimulated. Albeit for much earlier components (P50 and P50-N80, respectively), similarly middle finger-specific touch observation-related modulations in somatosensory processing were found in the subsequent Exp. 3.3 and 3.5 whereas the processing of stimuli presented to the anatomically congruent index finger was yet again unaffected in these latency ranges. It was speculated that the fact that the sight of touch was inevitably associated with the sight of finger movements which in itself is likely to trigger somatosensory activity (Avenanti et al., 2007; Avikainen et al., 2002; Gazzola & Keysers, 2009; Oouchida et al., 2004; Rossi et al., 2002) in the course of an involuntary internal simulation of the proprioceptive features of the observed movements. Neuroimaging evidence suggests that the vicarious activations in somatosensory areas are somatotopically organised, representing which body part is seen to be in motion (Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004). While it is still unknown whether such a somatotopic organisation during movement observation might be fine-grained enough to even present different fingers of one hand, it is conceivable that, if it does occur in a sufficiently topographically organised fashion, somatosensory processing of index finger stimuli might be more affected than somatosensory processing of middle finger stimuli by the sight these movements (irrespective of the tactile component). Ultimately, this might have facilitated detection of mirror touch responses during middle finger stimulation but might have made it more difficult during index finger stimulation where a dissociation between tactile and proprioceptive features of the observed movements would have been necessary.

Regardless of what the precise mechanism behind the unexpectedly strong middle finger-specific mirror touch responses triggered by the sight of an index finger touch an object might actually be, it is also unclear whether these modulations for the adjacent finger are specific to a scenario in which an index finger is observed to move and touch or whether they might also be found if a different finger is observed while the adjacent one is stimulated. In comparison to the other fingers of the hand, the index finger is most certainly somewhat "special", being probably the one finger with which we, if we do not use the whole hand anyway, most often point and touch (e.g. when punching in numbers on a keypad, operating a touch screen or probing the texture of a surface) and with which we see other people point and touch (note that the "touching" in many studies on the effect of observing others' being touched is performed by an index finger; Banissy & Ward, 2007; Blakemore et al., 2005; Bolognini, Rossetti, Maravita, & Miniussi, 2011a; Cardini et al., 2011; Pihko et al., 2010; Serino et al., 2008b). The index finger has indeed been found to be more sensitive than the other fingers (Duncan & Boynton, 2007; Grant, Fernandez, Shilian, Yanni, & Hill, 2006; Vega–Bermudez & Johnson, 2001) in terms of tactile acuity and to have a larger cortical representation in SI (Duncan & Boynton, 2007). Modulations in somatosensory-related ERPs during the observation of a touching index finger might thus not necessarily affect somatosensory processing for both the observers' homologous and adjacent finger in the same way as the observation of e.g. a touching middle finger would.

The present study thus involved not only the observation of an index finger touch an object or merely the empty space next to it but also the observation of a middle finger perform the same movements while participants were tactually stimulated on either their index finger (as the homologous or non-homologous finger depending on the observational condition) or their middle finger (as the homologous or non-homologous finger also depending on the observational condition).

The findings in Exp. 3.5 in conjunction with those in Exp. 3.4 seemed to strongly indicate that the tactile component associated with the observed finger movements might be too subtle to result in clear mirror touch responses in the form of somatosensory-related ERP modulations if the visual stimuli are merely passively observed. Nevertheless, the present study once again utilised the colour change detection task, requiring participants to focus on the fixation cross rather than on the actual finger movements and whether or not they resulted in touch (see Exp. 3.5). There were indications in Exp. 3.4 that the passive observation of the model's index finger touch the object rather than the empty space next to it did affect the late-latency N140 but the statistical analysis were inconclusive with respect to both stimulated finger locations. By sticking to the same type of task used in Exp. 3.4, the present study might allow to clarify this in the context of a new (and slightly larger) sample of participants. In addition, utilising the same task again also allowed to verify the reliability of the assumed to be movement observation-related N80 and N140 effects found in Exp. 3.4, with the additional advantage that the present study included conditions in which the tactile stimulation of a given finger was accompanied by the sight of the homologous finger moving as well as conditions in which the tactile stimulation of a given finger was accompanied by the sight of the non-homologous finger moving (irrespective of whether touch occurred or not).

3.6.2 Methods

Participants. The twenty participants who were recruited to participate in this experiment were the same who also took part in Exp. 2.1. The order in which participants participated in the two studies was counterbalanced across participants, primarily in order to control for the increase in fatigue over the course of two experimental tasks which required only infrequent responses on part of the participants.

Stimuli. To ensure all hand images were as comparable as possible with respect to the relative and absolute positions of the hand and the object as well with respect to illumination and contrast, two entirely new sets of colour images were created: The first set comprised three new images depicting a left hand resting on a table top with the index finger in three different positions: In a neutral position with the index slightly elevated from the table top ($\text{index}_{\text{neutral}}$) or with the index finger lowered down, either touching the top left corner of the object ($\text{index}_{\text{touch}}$) or hovering in the empty space next to the object ($\text{index}_{\text{notouch}}$). The second set showed a left hand with the middle finger in the same three positions, i.e. in a neutral position ($\text{middle}_{\text{neutral}}$) and lowered down, either touching the object in the same location as the index finger ($\text{middle}_{\text{touch}}$) or merely hovering in the empty space next to the object ($\text{middle}_{\text{notouch}}$). As in the first set of images, all other fingers of that left hand were slightly curled back and resting comfortably on the table top (see Fig. 3.6.a).

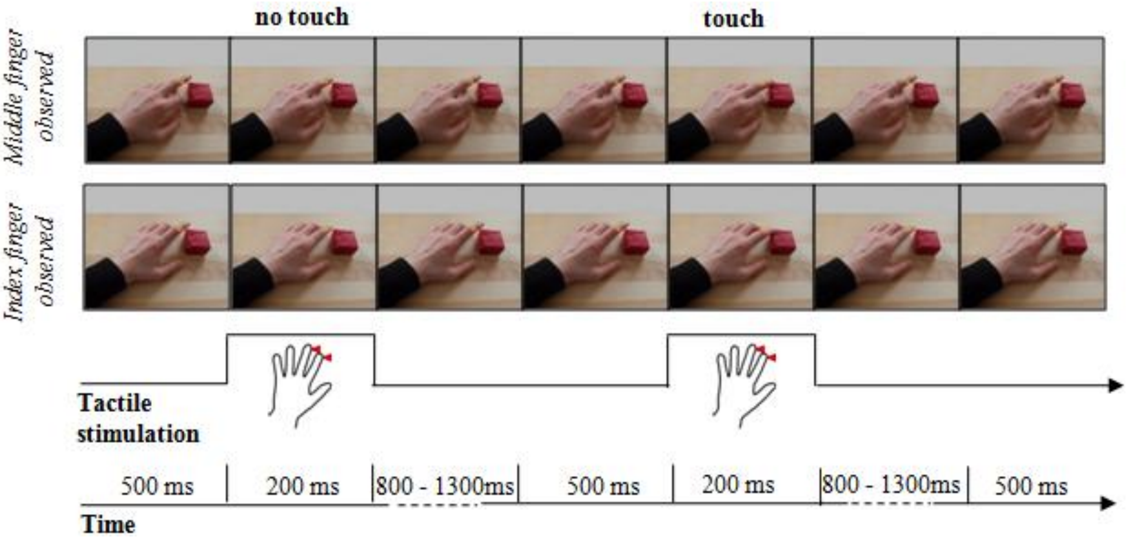


Fig. 3.6.a. Schematic representation of the typical sequence of visual and tactile events in touch and no touch trials, respectively. Whether participants observed an index finger or a middle finger touch either the object or merely the empty space next to it was manipulated block-wise.

The tactile stimuli were the same as in previous experiments. Two finger locations were tactually stimulated: The left index finger and the left middle finger.

Procedure. The experimental set-up and procedure were the same as in Exp. 3.4 with the following modifications: Rather than observing exclusively an index finger either touch the object or merely the empty space next to it, participants observed the same two movements also performed by the middle finger of the same hand. Which finger was concurrently observed was manipulated block-wise: Participants viewed the either touch-related or touch-unrelated movements of a given finger for eight consecutive blocks. Half of the participants were presented with the sight of index finger movements first, half of the participants were presented with the sight of middle finger movements first. In four blocks each, tactile stimuli were simultaneously delivered to either the anatomically congruent or the adjacent finger. For half the participants, the congruent finger was stimulated first, for the other half, the adjacent finger was stimulated first. With four consecutive blocks for each of the four combinations of observed and concurrently tactually stimulated finger, participants performed 16 experimental blocks in total. Each block consisted of 62 trials, 25 trials each on which the observed finger was seen to touch the object or merely the empty space next to it, respectively, and 12 catch trials (approx. 19 % of all trials) on which a colour change of the fixation cross occurred and a verbal response was required.

Prior to the eight consecutive blocks during which a given finger was observed to either contact the object or not, participants were presented with a short demo of the to-be-observed movements of that finger (3 trials for each observational condition, presented in random order), followed by the instruction to casually try out the observed movements for themselves with their corresponding finger on the object from the hand images placed in front of them. No explanation was given as to why participants were to do this.

Recording and data. The procedures for recording, pre-processing and segmenting the obtained EEG data as well as the criteria for artifact rejection were exactly the same as for Exp.s 3.3, 3.4 and 3.5.

Statistical analysis. ERP mean amplitudes were computed for each combination of observed tactile action feedback and concurrently stimulated finger location for four latency windows centred around the amplitude peaks of the following four SEP components: P50 (40-60 ms post-stimulus onset), N80 (65-85 ms post-stimulus onset), P100 (100-120 ms post-stimulus onset) and N140 (145-175 ms post-stimulus onset). The approximate peak latencies of each component were identified visually at posterior electrode sites over the hemisphere contralateral to the tactually stimulated left hand and averaged across all eight experimental conditions. The mean ERP amplitudes for each latency window were then subjected to

2x2x2x2x2x5 repeated measures ANOVAs with the within-subject factors *hemisphere* (ipsilateral vs. contralateral), *anterior-posterior* (anterior vs. posterior), *observed finger* (index finger vs. middle finger), *stimulated finger* (index finger vs. middle finger), *observed tactile action feedback* (touch vs. no touch) and *electrode site* to investigate whether the unexpected pattern of SEP modulations during middle finger rather than index finger stimulation and thus the adjacent rather than the anatomically congruent finger (Exp. 3.2, 3.3 and 3.5) would occur in a similar fashion when somebody else's middle finger is observed to either touch an object or not.

3.6.3 Results

Behavioural performance

Participants rarely missed any of the infrequent colour changes of the fixation cross (mean detection rate 99.8%) and produced only very false alarms (< 1%), suggesting that they paid close attention to the visual display despite its repetitive nature.

Table 3.6.a shows the response times for all eight conditions. While response times for detecting a brief colour change did not differ as a function of the concurrently observed or tactually stimulated finger (both $F(1,19) \leq 1.314$, $p \geq .266$, $\eta^2_p \leq .065$), participants were yet again (see also Exp.s 2.1, 2.2 and 3.1) somewhat slower in reporting a random colour change of the fixation cross if this colour change was accompanied by the sight of a finger touch the object (M = 538.41 ms; STD = 65.95) rather than merely move through empty space (M = 526.36, STD = 66.99; $F(1,19) = 22.540$, $p < .001$, $\eta^2_p = .543$), irrespective of which finger was viewed ($F(1,19) = .633$, $p = .436$, $\eta^2_p = .032$). With a mean difference of 12.05 ms (STD = 11.35 ms), this deviation in response latency was, however, very small.

Table 3.6.a. Reponses times for detecting infrequent colour changes of the fixation cross as a function of the observed-to-move finger, the concurrently tactually stimulated finger tip and the observed tactile action feedback.

	Index observed				**Middle observed**			
	Index stimulated		**Middle stimulated**		**Index stimulated**		**Middle stimulated**	
	touch	***no touch***	***touch***	***no touch***	***touch***	***no touch***	***touch***	***no touch***
M	535.33	528.46	540.98	526.49	536.28	520.46	541.05	530.02
SD	78.75	73.39	73.17	76.81	60.26	61.52	66.43	71.56

Electrophysiological data

The observation of somebody else experience a tactile sensation as result of actively making contact with an object seems to modulate early stages of concurrent somatosensory processing in the observer, as found in e.g. Exp.s 3.1, 3.3 and 3.5. However, the previous data sets in this thesis provided inconsistent results as to how finger-specific any such modulations actually are and also as to how early they really occur (see, in particular, the P50 effect for middle in Exp. 3.3). Some data sets (Exp. 3.2, 3.3 and 3.5), in fact, seemed to suggest that modulations in somatosensory processing of concurrent tactile stimuli were more reliable (or at least appeared larger) when it was actually the adjacent middle finger rather than the anatomically congruent index finger tip that was tactually stimulated during the observation of somebody else's index finger move and touch an object. In order to elude whether this unexpected "finger-specific" effect was specific for the observation of an index finger with concurrent tactile stimulation to the index and middle fingers of the corresponding hand, the present study added an additional observation condition in which somebody else's middle finger was observed to either touch the object or the empty space next to it while again the index and middle finger of the corresponding hand was tactually stimulated. Figures 3.6.b and 3.6.c show the resulting ERP waveforms during tactile stimulation of the index and middle finger, respectively, while a moving index finger was observed, just as in Exp.s 3.2-3.5. Figures 3.6.d and 3.6.e, on the other hand, depict the ERP waveforms during tactile stimulation of the middle and index finger, respectively, when, crucially, a middle finger was observed to touch or merely approach an object. Fig. 3.6.f contrasts the resulting ERP waveforms during the observation of touch and no touch, respectively, on the object, for all four experimental conditions at two representative centro-parietal electrodes.

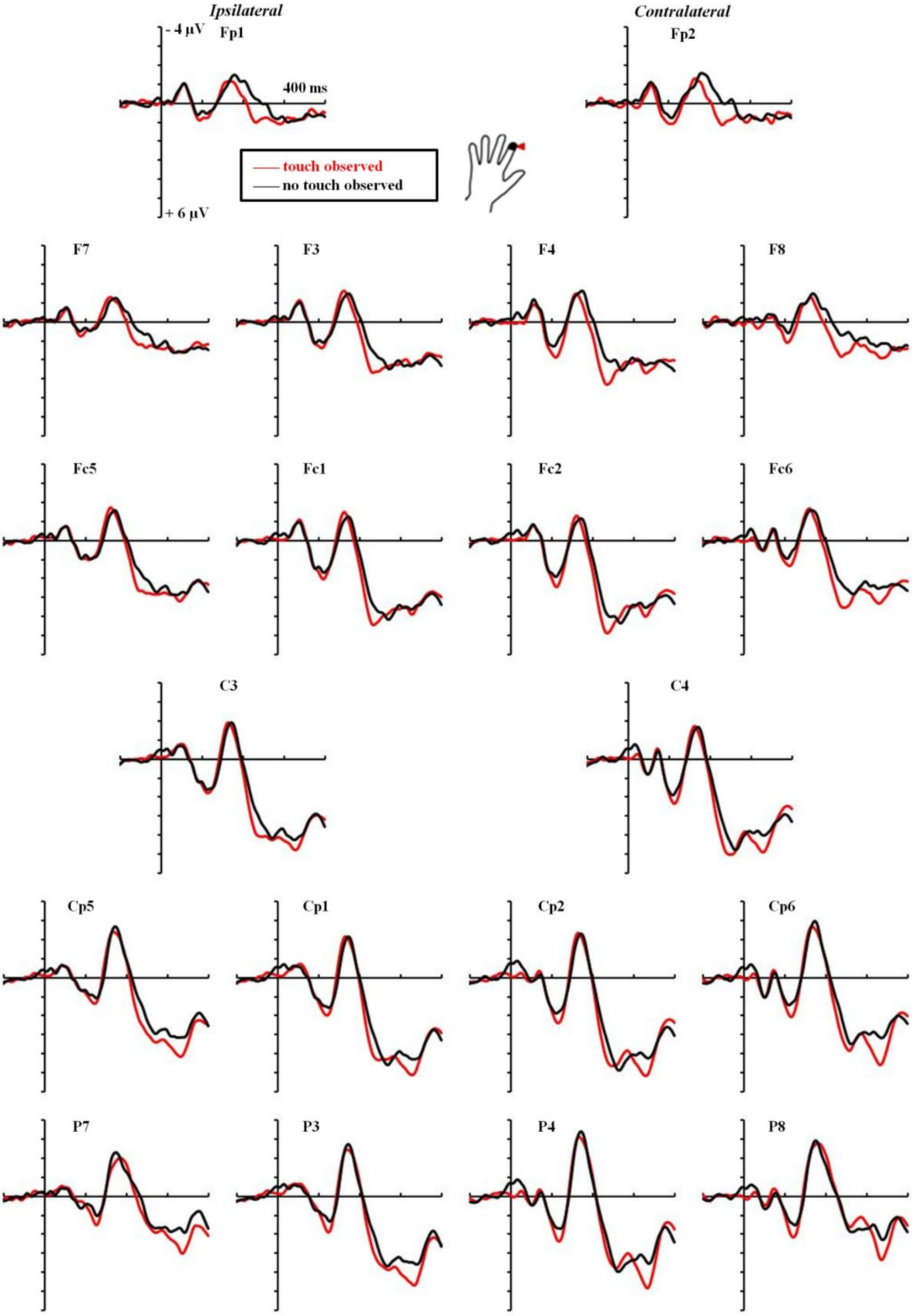


Fig. 3.6.b. Grand-averaged ERP waveforms in response to **tactile stimuli to the index finger** during the **observation of the model's corresponding index finger** touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

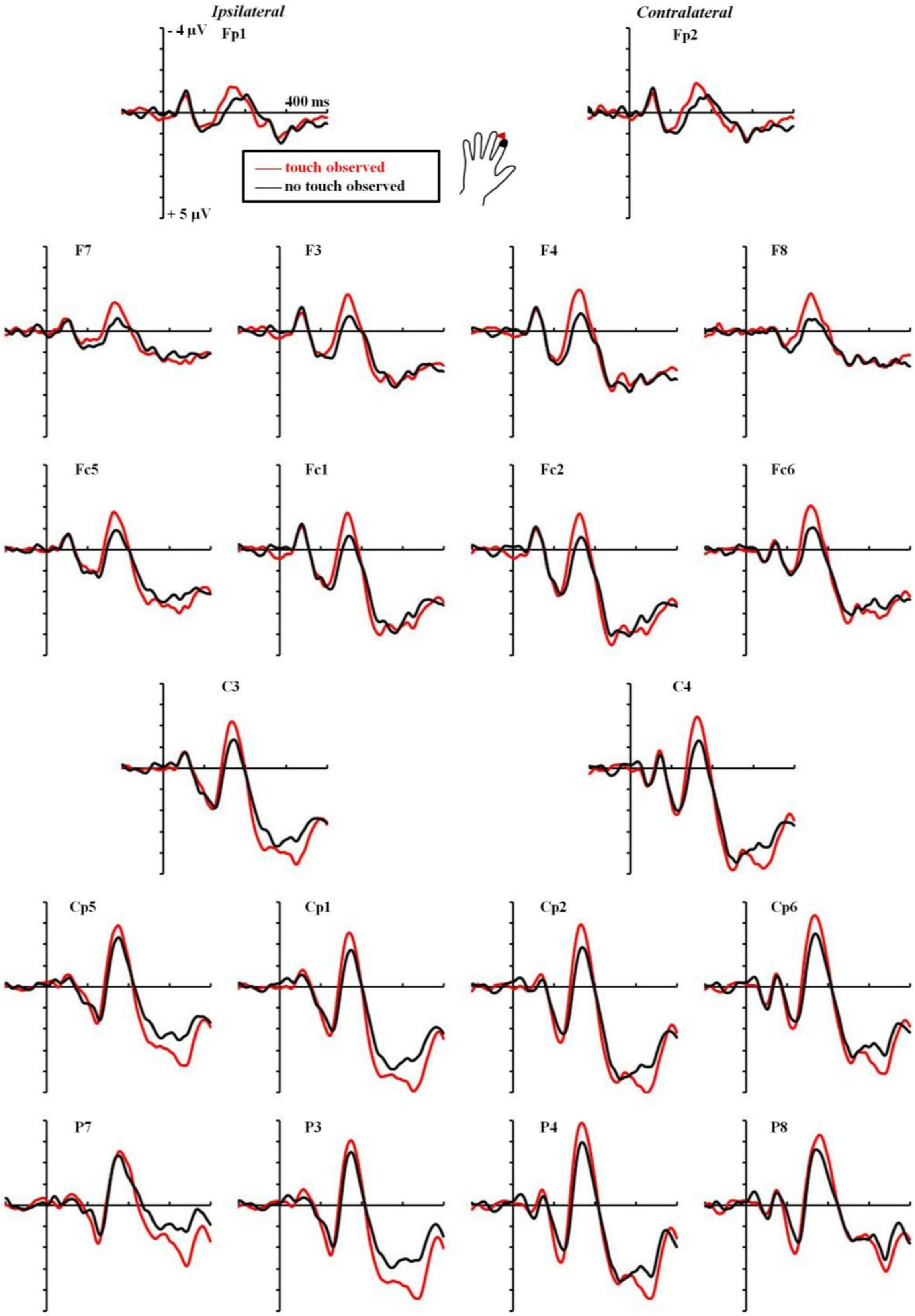


Fig. 3.6.c. Grand-averaged ERP waveforms in response to **tactile stimuli to the middle finger** during the **observation of the model's index finger** touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

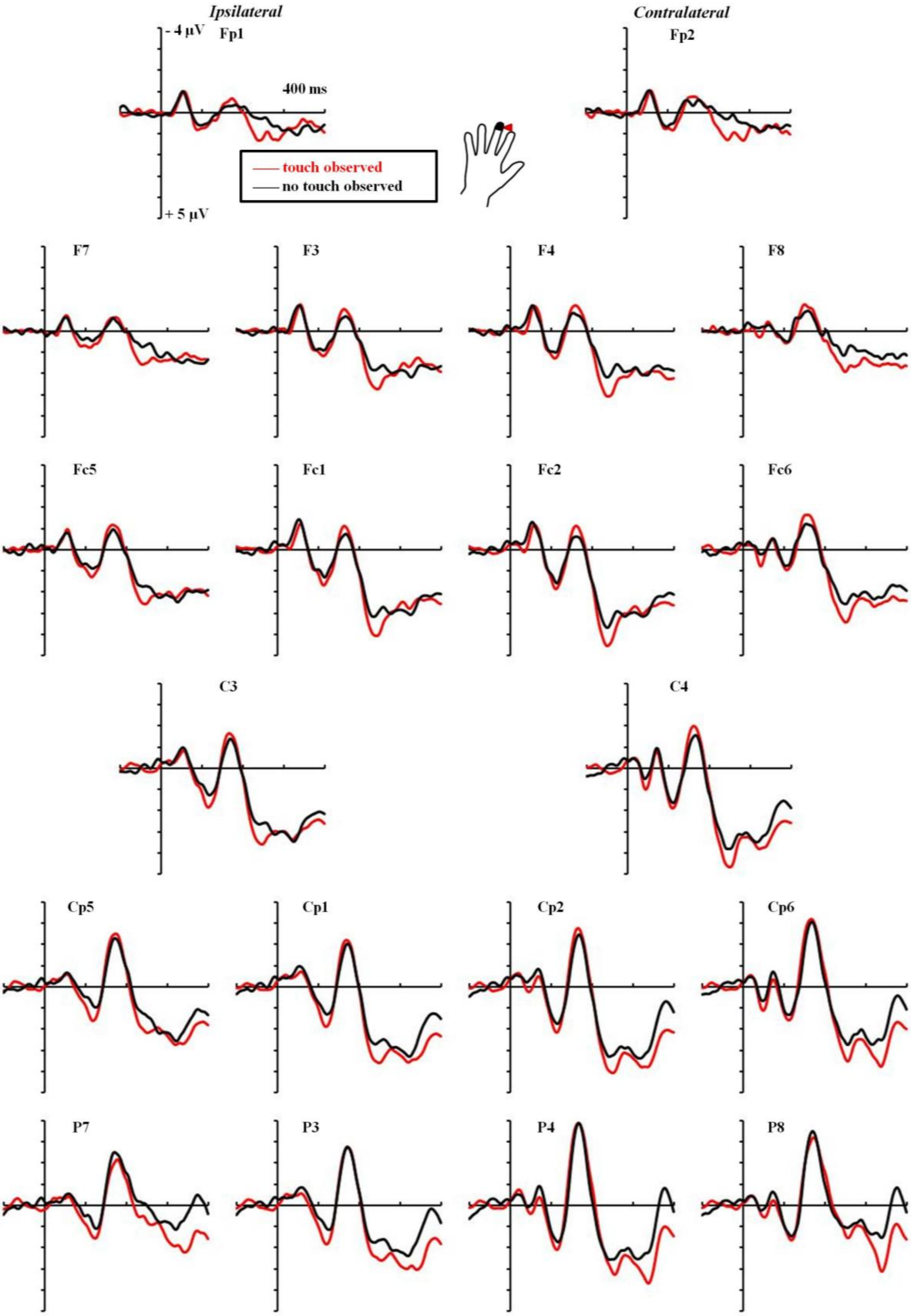


Fig. 3.6.d. Grand-averaged ERP waveforms in response to **tactile stimuli to the middle finger** during the **observation of the model's corresponding middle finger** touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

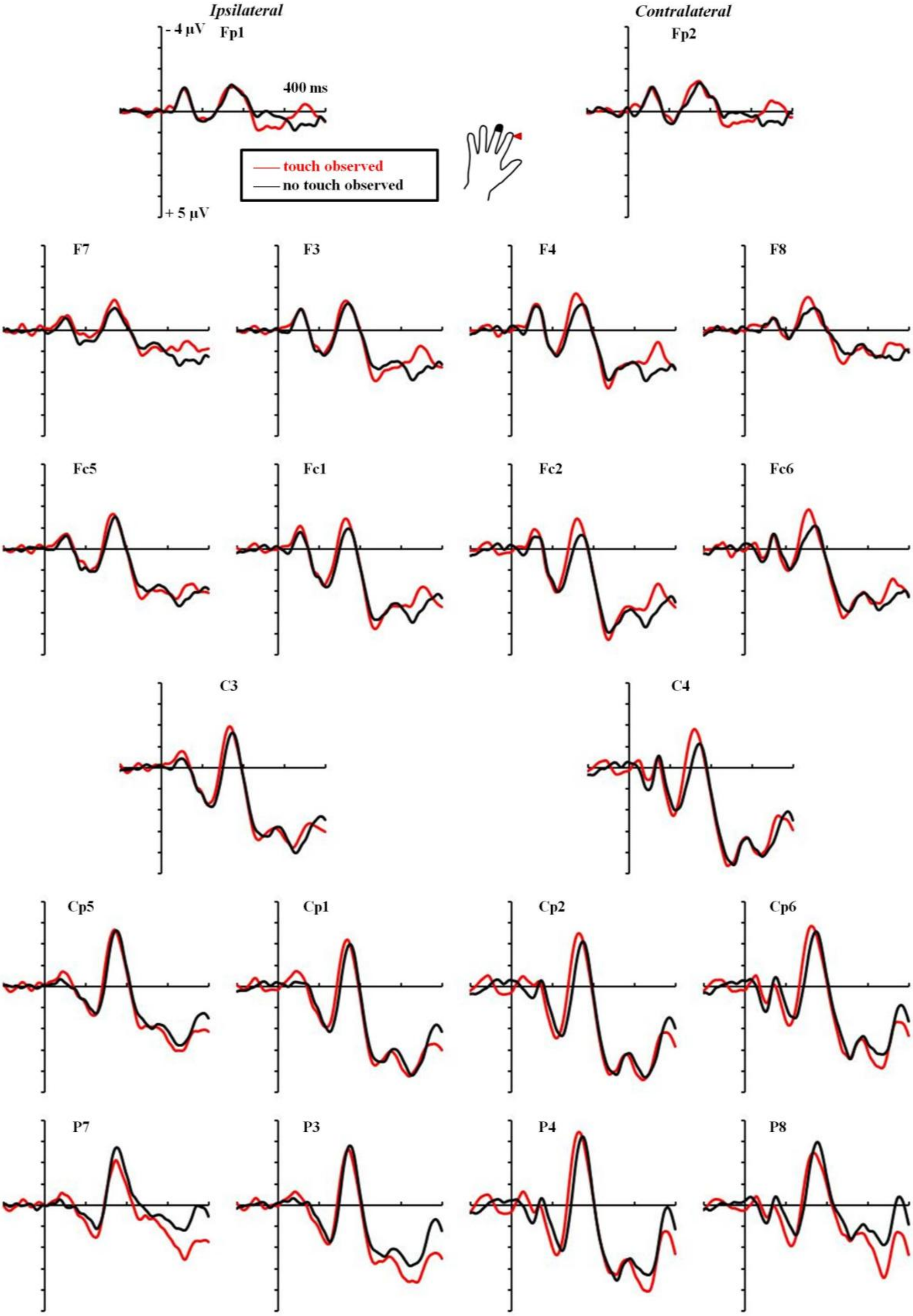


Fig. 3.6.e. Grand-averaged ERP waveforms in response to **tactile stimuli to the index finger** during the **observation of the model's middle finger** touch the object (red line) rather than merely the empty space next to it (black line). Shown are all electrode sites included in the statistical analysis.

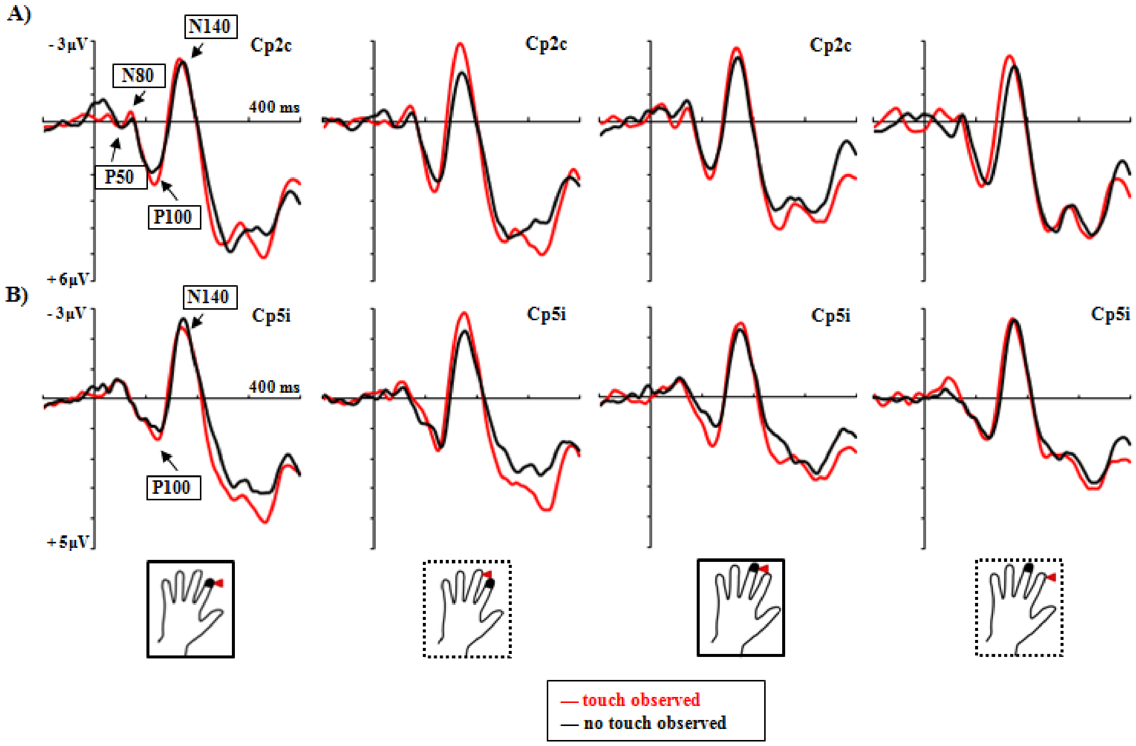


Fig. 3.6.f. Grand-averaged ERP waveforms during the sight of touch or no touch on the object for all four combinations of tactually stimulated finger and concurrently observed finger, at two representative electrodes over both hemispheres (**A)** Cp2c and **B)** Cp5i). The hand icons point out the tactually stimulated finger location in a given condition with a red triangle and highlight the simultaneously observed-to-touch finger tip in black. A solid black frame indicates that the stimulated and observed-to-touch finger corresponded while a dotted frame indicates that stimulated and observed finger were adjacent.

The statistical analyses on the mean SEP amplitudes in the specified latency ranges did not reveal any systematic touch observation-related modulations for the early-latency somatosensory P50 and N80 components (for both main effects of the factor *observed tactile action feedback*, $F(1,19) \leq .310$, $p \geq .584$, $\eta^2_p \leq .016$; for all interactions involving this factor, $F(1,19) \leq 4.056$, $p \geq .058$, $\eta^2_p \leq .176$).

For the subsequent somatosensory P100 component, a significant *anterior-posterior* by *observed tactile action feedback*-interaction ($F(1,19) = 6.588$, $p = .019$, $\eta^2_p = .257$) pointed to a significant touch observation-induced P100 modulation over posterior ($F(1,19) = 7.561$, $p = .013$, $\eta^2_p = .285$) but not anterior electrode sites ($F(1,19) = .573$, $p = .458$, $\eta^2_p = .029$; the follow-up analyses here were based on two separate *hemisphere* (2) by *observed finger* (2) by *stimulated finger* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for the anterior and posterior electrode cluster). This effect was, however, further modulated by a significant 5-way interaction between *hemisphere*, *anterior-posterior*, *observed finger*, *stimulated finger* and *observed tactile action feedback* ($F(1,19) = 7.291$, $p = .014$, $\eta^2_p = .277$. Based on the visual inspection of the ERP waveforms elicited in the four conditions, it seemed as if the enlarged P100 amplitude at posterior electrode sites during the sight of touch occurred primarily in the congruent conditions in which the observed and the felt touch occurred at the same finger (see Figures 3.6.b and 3.6.d), primarily ipsilaterally for stimuli to the index finger tip and primarily contralateral-posteriorly for stimuli to the middle finger tip. Simple effects analyses based on *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs conducted separately for all possible combinations of the levels of the four remaining factors, however, confirmed a reliable touch observation-related increase in P100 mean amplitude only at posterior electrodes over the ipsilateral hemisphere in response to tactile stimuli to the middle finger tip while a middle finger was observed to touch the object ($F(1,19) = 7.615$, $p = .012$, $\eta^2_p = .286$; see Fig. 3.6.g for the topographic distribution of this effect). The modulations seen in the 100-120 ms post-stimulus latency range when the observed and stimulated finger was the index finger were not large or reliable enough to be significant at any of the electrode clusters (all $F(1,19) \leq 2.411$, $p \geq .137$, $\eta^2_p \leq .113$).

Unlike the somatosensory P100 component, the subsequent N140 was found to be modulated whenever the felt and observed touch occurred on different fingers: In the associated 145-175 ms post-stimulus latency range, a significant main effect of the *observed tactile action feedback* was found ($F(1,19) = 13.012$, $p = .002$, $\eta^2_p = .406$) but following-up an also significant *observed finger* by *stimulated finger* by *observed tactile action feedback*-interaction ($F(1,19) = 5.394$, $p = .031$, $\eta^2_p = .221$) with separate *hemisphere* (2) by *anterior-posterior* (2) by *observed tactile action feedback* (2) by *electrode site* (5)-ANOVAs for all four different combinations of observed and concurrently tactually stimulated finger indicated that this effect was driven by the two conditions in which observed and stimulated finger were different: If tactile stimuli were presented to the middle finger while an index finger was seen to touch the object, the N140 mean amplitude was in a wide-spread fashion significantly larger ($F(1,19) = 16.148$, $p = .001$, $\eta^2_p = .459$) for the sight of touch than for the sight of no touch. Similarly, if tactile stimuli were presented the index finger while a middle finger was seen to touch the object, the N140 mean amplitude was also enhanced. The latter modulations were, however, only marginally significant ($F(1,19) = 4.196$, $p = .055$, $\eta^2_p = .181$), less wide-spread (see Fig. 3.6.g below) and also smaller in effect size than the one observed when touch was felt on the middle finger but seen on the index finger.

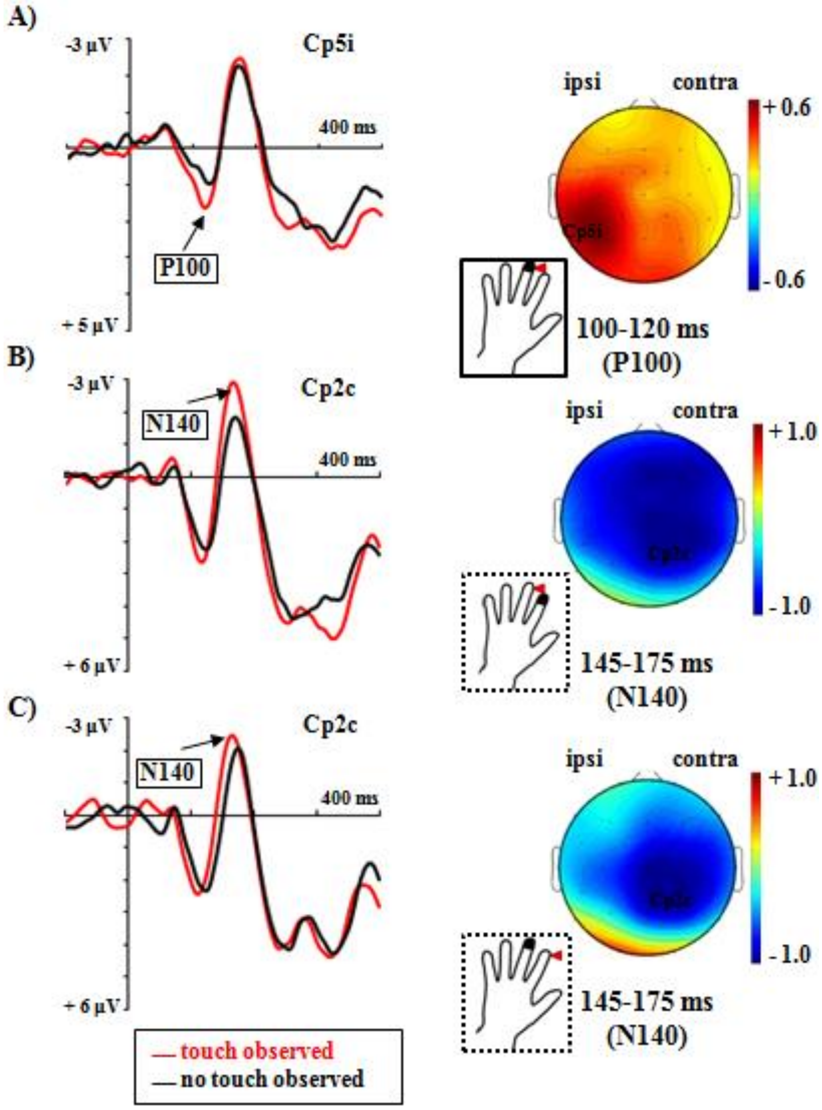


Fig. 3.6.g. A) Grand-averaged ERP waveforms in response to tactile middle finger stimulation while it was also a middle finger that was observed to either touch an object (red line) or merely the empty space next to it (black line), at representative ipsilateral centro-parietal electrode (Cp5i), along with the topographic distribution of the significant difference in SEP mean amplitude in the P100 latency range in this condition. Note that a positive difference reflects an increase in P100 amplitude during the sight of touch. **B)** and **C)** Grand-averaged ERP waveforms in response to tactile stimuli to the middle finger **(B)** or the index finger **(C)**, respectively, when it was the adjacent finger that was observed to either touch (red line) or merely approach the object (black line), at representative contralateral centro-parietal electrode (Cp2c), along with the topographic distribution of the difference in SEP mean amplitude in the N140 latency range in these two conditions. Note that a negative difference reflects an enlarged N140 amplitude during the sight of touch. Note also that the touch observation-related increase in N140 amplitude in **(C)** was only marginally significant.

While there were no wide-spread SEP modulations in the form of a main effect of the observed finger or the simulated finger as such for any of the analysed components (all $F(1,19) \leq 1.887$, $p \geq .186$, $\eta^2_p \leq .090$), the somatosensory N80 and N140 did show localised effects of either one or both factors at certain electrode clusters. For the N80 component, following-up a significant *anterior-posterior* by *observed finger*-interaction (F(1,19) = 4.698, p = .043, η^2_p = .198) indicated for anterior electrodes only a significantly more negative-going N80 amplitude during the observation of a middle rather than an index finger (F(1,19) = 6.782, p = .017, η^2_p = .263; follow-up analyses to investigate the effect of the observed finger as a function of the anterior-posterior electrode location were based on two 5-way ANOVAs (*hemisphere* (2) by *observed finger* (2) by *stimulated finger* (2) by *observed tactile action feedback* (2) by *electrode site* (5)) conducted separately for the anterior and posterior electrode cluster). Fig. 3.6.h shows the revealed modulation in SEP amplitude in the 65-85 ms post-stimulus onset time window at two representative frontal electrodes. Note that at anterior electrode sites, there was no peak in the N80 latency range (the relevant part of the waveform is therefore highlighted in red) and that the difference in SEP amplitude as a function of whether an index or a middle finger was currently observed was extremely small.

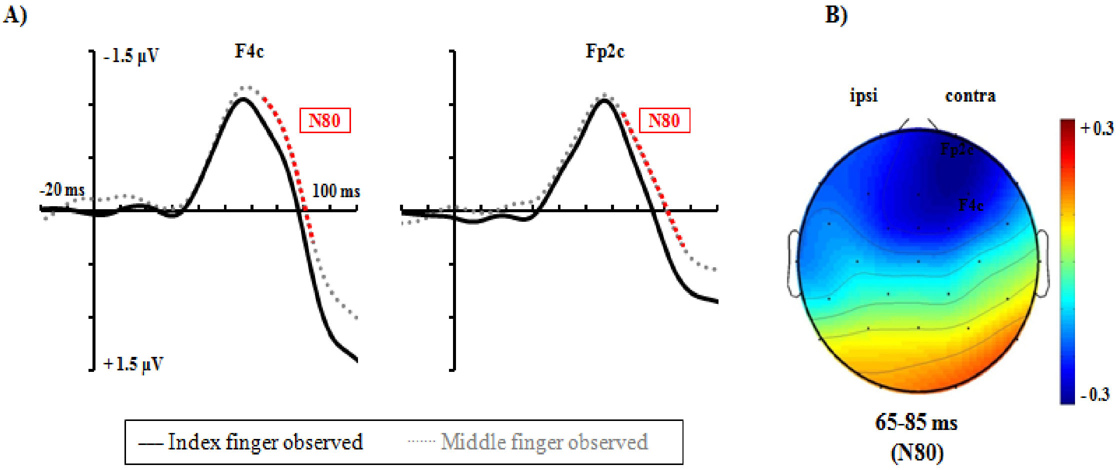


Fig. 3.6.h. **(A)** Grand-averaged ERP waveforms in response to tactile stimulation during the observation of either index or middle finger movements, irrespective of whether participants' index or middle finger was concurrently tactually stimulated, at two representative frontal electrodes (Fp2c and F4c). Note the small scale regarding the associated changes in µV and also reduced time window from 20 ms pre-stimulus to 100 ms post-stimulus. **(B)** Topographic distribution of the difference in mean ERP amplitude during observation of middle finger as compared to index finger movements. Note also here the small scale regarding the difference in µV. A negative difference indicates an increased negativity in the N80 latency range during middle finger stimulation.

In addition, a significant *hemisphere* by *anterior-posterior* by *stimulated finger*-interaction (F(1,19) = 10.818, p = .004, η^2_p = .363) revealed in follow-up analyses based on *stimulated finger* (2) by *observed finger* (2) by *observed tactile action feedback* (2) by *electrode site* (2)-ANOVAs conducted separately for the four electrode clusters a significantly enlarged N80 amplitude during tactile stimulation of the middle finger as compared to the index finger in the contralateral-posterior electrode cluster (F(1,19) = 6.751, p = .018, η^2_p = .262). For the N140 component, there was also a significant *hemisphere* by *anterior-posterior* by *stimulated finger*-interaction (F(1,19) = 4.855, p = .040, η^2_p = .204) for which follow-up analyses showed a significantly more negative-going N140 amplitude at ipsilateral-anterior electrode sites for index finger stimuli as compared to middle finger stimuli (F(1,19) = 6.628, p = .019, η^2_p = .259). Fig. 3.6.i visualises the respective ERP modulations as a function of the concurrently stimulated finger.

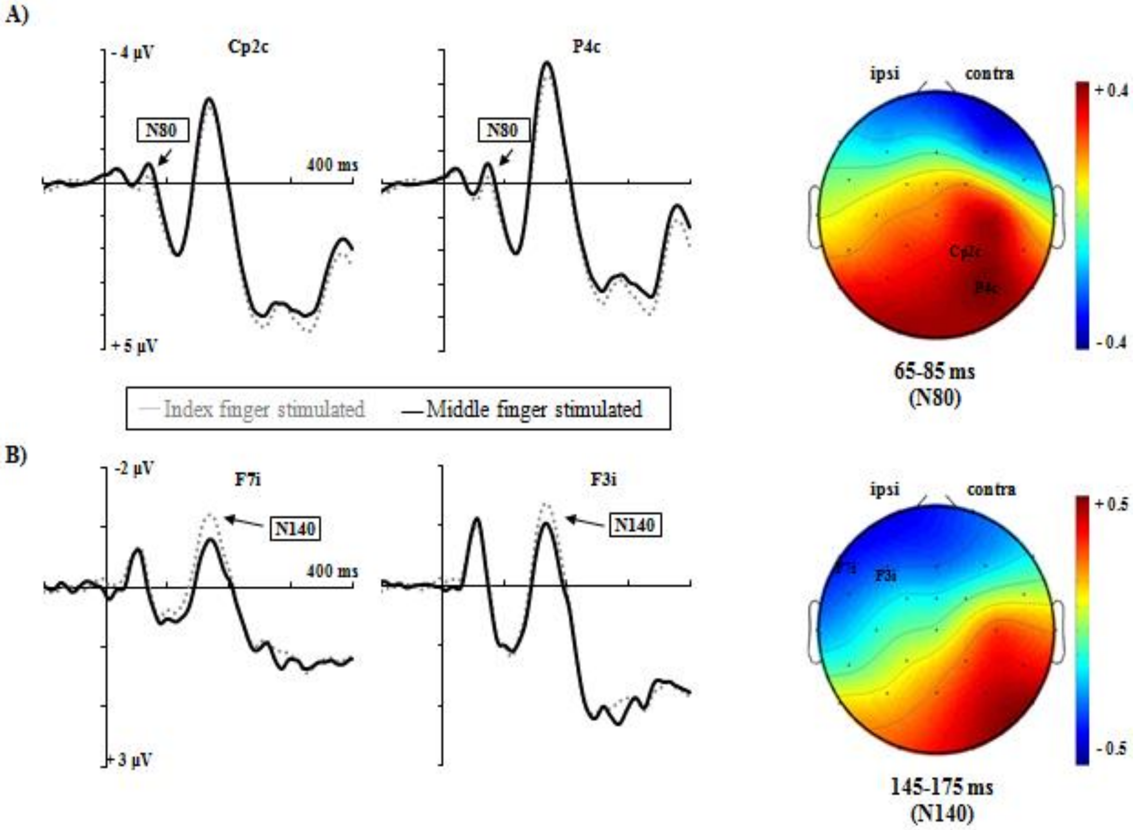


Fig. 3.6.i. (A) Grand-averaged ERP waveforms in response to tactile stimulation of either the index or middle finger movements, irrespective of what kind of finger movements or what kind of action feedback participants concurrently observed, at two representative posterior electrodes, along with the scalp distribution of the corresponding difference in ERP mean amplitude in the 65-85 ms post-stimulus time window (N80). Note that a positive difference indicates a reduced N80 amplitude during index finger stimulation. **(B)** Grand-averaged ERP waveforms in response to tactile stimulation of either the index or middle finger, irrespective of what kind of finger movements or what kind of action feedback participants concurrently observed, at two representative frontal electrodes, along with the scalp distribution of the corresponding difference in ERP mean amplitude in the 145-175-ms post-stimulus time window (N140). Note that a negative difference indicates an enhanced N140 amplitude during index finger stimulation.

Empathy correlations

To sum up, concurrent somatosensory processing was systematically modulated in the 100-120 ms post-stimulus latency range (P100) when observed and felt touch occurred on the same (middle) finger and in the 145-175 ms post-stimulus latency range when observed and felt touch occurred on adjacent fingers. The strength of the touch observation-related P100 effect over ipsilateral-posterior electrodes during the observation and stimulation of the middle finger was found to correlate with the IRI's *personal distress* subscale at three electrode sites (Cp1: $r_s(20) = .516$, Cp5: $r_s(20) = .538$, P3: $r_s(20) = .513$; all $p \leq .05$). The more participants reported a tendency to react distressed to others' misfortune, the more pronounced was their touch observation-related difference in P100 mean amplitude at these electrode sites (see Fig. 3.6.j).

For the N140 modulations revealed for the two conditions in which observed and felt touch occurred on adjacent fingers, no empathy-related correlations at all were found with respect to the clearly significant and wide-spread N140 effect for the sight of a touching index finger during middle finger stimulation (all $p > .05$). The strength of the less reliable and more contralaterally lateralised N140 effect for the sight of a touching middle finger during index finger stimulation, on the other hand, did correlate at several posterior electrode sites with the EQ's *social skills* subscale as well as with the IRI's *fantasy scale* but since the effect as such failed to reach significance, these correlations were disregarded.

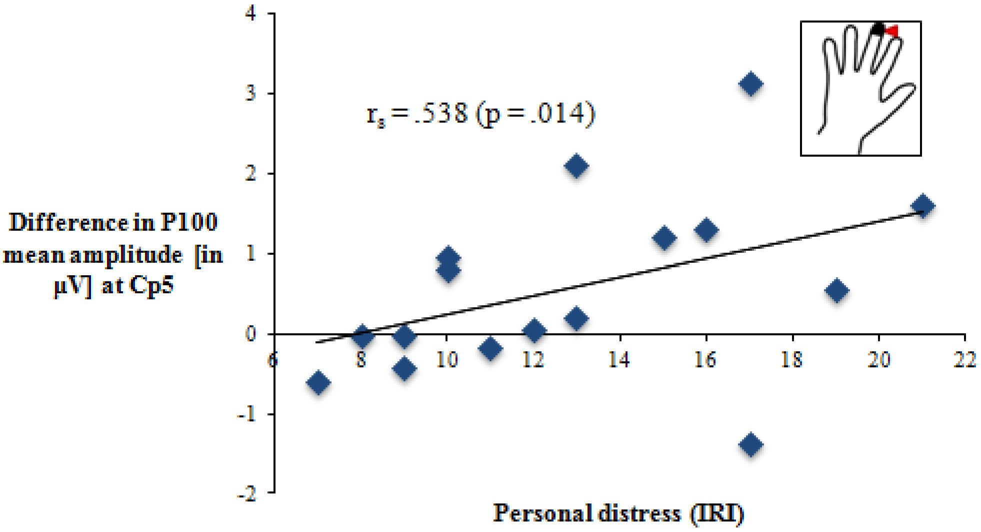


Fig. 3.6.j. Mean touch observation-related P100 amplitude difference at Cp5 during the observation and stimulation of the middle finger as a function of self-reported level of *personal distress* (IRI) in response to witnessing others in distress.

3.6.4 Discussion

The pattern of results found in the present study was rather complex, given that the experimental manipulations involved not only the observed tactile feedback (touch vs. no touch) and the concurrently stimulated finger location (index finger vs. middle finger) but also the concurrently observed-to-move-and-touch finger (index finger vs. middle finger).

Modulations in somatosensory processing as a function of the observed tactile action feedback

The statistical main analysis indicated that early-stage somatosensory processing was unaffected by the concurrent sight of touch: Neither the P50 nor the N80 mean amplitude was significantly altered as a function of whether the observed finger (irrespective of whether it was an index or a middle finger) was seen to touch the object or not. This replicated previous findings from Exp. 3.1, 3.2 and 3.4 in this thesis where these early latency ranges also did not show any mirror touch-related EPR modulations (not even for the "adjacent" finger) when participants merely passively observed the touch-related stimuli and thus corroborates the notion that SI-related mirror touch responses might depend on a sufficient amount of attention being paid to the occurrence of touch (either by making the tactile component relevant to participants' task (Exp. 3.5) or by making them sufficiently aware of it by having them imitate the observed movements more extensively prior to the experiment (Exp. 3.2). Note that the early P50 (P45) modulation during the sight of a hand being passively touched with a cotton bud (Bufalari et al., 2007) was also found in the context of an explicit instruction to focus on what the touched person might be feeling while participants in the present study were actually instructed to ignore the presented visual stimuli.

The mid- and late-latency P100 and N140 components were both found to be modulated by the sight of touch, however, in a specific way: In the P100 latency range associated with higher-order somatosensory processing in SII (Allison et al., 1992; Hämäläinen et al., 1990; see, however, Tomberg et al., 2005, for posterior-parietal area 7b as another possible source of the P100), the sight of touch resulted in a significant ipsilateral-posteriorly located increase in P100 mean amplitude, however, only when participants' middle finger was stimulated and only when it was also a middle finger that was observed to tap on the object, indicating that the vicarious somatosensory activity did code on which finger the observed touch occurred. When the index finger was both observed and tactually stimulated, the P100 amplitude appeared similarly enlarged (albeit with a more contralaterally-centred scalp topography) but this case, the modulation was not reliable enough to be significant. Note that the P100 was implicated in a putative mirror touch response during the sight of a touching index finger in Exp. 3.3 where this mid-latency modulation was assumed to be facilitated by an increased awareness of the tactile component of the observed index finger movements after a brief imitation protocol at the beginning of the experiment. That touching an object with the middle finger tip might have been perceived as more unusual than doing so with the index finger tip might have had a similar effect here, enhancing the salience of the tactile component during the sight of those middle finger movements. It is, however, unclear why the P100 amplitude was found to be enhanced rather than reduced (see Exp. 3.3 and also Exp. 3.1) during the sight of touch.

For the subsequent N140 component, it was yet again the non-homologous finger for which SEP modulations were found: The mean amplitude of this late-latency component was found to be significantly increased whenever the felt and observed touch occurred on different fingers, particularly reliably so when an index finger was observed to touch the object while participants' adjacent middle finger was tactually stimulated (when a middle finger was observed to tap on the object while the index finger was stimulated, the increase in N140 was only marginally significant since it was less wide-spread). In conjunction with the very similar appearing (non-significant) trend for a N140 enhancement during observation of a touching index finger and tactile stimulation to the middle finger found in Exp. 3.4, this again points to the possibility that the concurrent internal simulation of the proprioceptive features of the observed finger movements might make it easier to detect mirror touch responses for the adjacent rather than the homologous finger.

Modulations in somatosensory processing as a function of the observed and/or concurrently stimulated finger

In Exp. 3.4, it was found that the amplitude of the somatosensory N80 component was reduced in a wide-spread fashion during index as compared to middle finger stimulation while the subsequent N140 amplitude showed a reversed modulation pattern, with an increased amplitude during index rather than middle finger stimulation (albeit only at ipsilateral anterior electrode sites). Assuming that these modulations as a function of which finger was stimulated did not merely reflect inherent differences between two fingers (such as e.g. the fact that the index finger is generally more sensitive than the middle finger (Vega–Bermudez & Johnson, 2001), has a larger cortical representation in SI (Duncan & Boynton, 2007) and is more likely to be used to touch and probe surfaces if only one digit is to be involved), it was speculated that these modulations in both early and late somatosensory processing might be associated with the internal simulation of the proprioceptive features of the observed index movements as such (Avenanti et al., 2007; Avikainen et al., 2002; Gazzola & Keysers, 2009; Oouchida et al., 2004; Rossi et al., 2002) which might have affected the homologous index finger much more than the adjacent middle finger. In the present study, both the N80 and the N140 component were yet again found to be sensitive to which finger was concurrently stimulated but also to which finger was concurrently observed, however, not in the specific fashion that might have been expected:

Interestingly enough, the N80 amplitude was again found to be reduced during index as compared to middle finger stimulation, albeit only at contralateral-posterior electrode sites and thus in a less wide-spread fashion than found in Exp. 3.4. Importantly, this reduction in N80 amplitude was not modulated by which finger was concurrently observed to move (irrespective of whether it touches the object or not), i.e. there was no indication that the N80 effect was sensitive to whether or not the concurrently observed finger was a homologous or non-homologous finger, a discrimination, one might, however, expect when assuming that the difference in SEP amplitude between index and middle finger found in Exp. 3.4 is associated with the observation of a homologous finger moving during index but not during middle stimulation (during middle finger stimulation, it is “a” finger moving). At the same time, anterior electrode only showed a significantly increased N80 amplitude (very small effect, though) during the observation of middle finger as compared to index finger movements, irrespective of which finger was concurrently tactually stimulated, possibly indicating that the vicarious somatosensory activity during the internal simulation of the observed movements might have been sensitive to the fact that actually performing middle finger movements in the observed way feels proprioceptively a bit unusual and possibly restricted (isolated middle finger movements while all adjacent fingers rest firmly on the table top), most certainly in comparison to performing the exact same movements with the index finger. Interestingly, vicarious activity in somatosensory areas has previously been found to be particularly strong during the sight of biomechanically impossibly movements (Avenanti et al., 2007; Costantini et al., 2005), coding the abnormal noxious somatic sensations that would be associated with actually trying to execute the seen movements.

For the later-peaking N140, it was found that this component was significantly more negative-going during index as compared to middle finger stimulation at a subset of ipsilateral-anterior electrode, thus replicating the index finger-specific N140 enhancement revealed in Exp. 3.4, including its topographic distribution. Again, this deviation in somatosensory processing of tactile stimuli presented to the index rather than the middle finger was not further modulated as a function of whether it was an index or a middle finger that was concurrently observed in motion. That somatosensory processing of index finger stimuli thus differed at both the N80 and N140 latency ranges from that of middle finger stimuli regardless of the concurrently observed finger casts some doubts on the initially proposed possibility that the altered SEP amplitudes during index as compared to middle finger stimulation might reflect a high degree of finger specificity during the internal simulation of the proprioceptive component of observed finger movements, thus affecting primarily somatosensory processing of tactile stimuli presented to the observed-to-move finger but not the adjacent one. Instead, it appears to be the case that somatosensory processing of tactile stimuli presented to the index differs from that of tactile stimuli presented to the middle finger for some other, yet unclear reason. While the index and middle finger do generally differ with respect to e.g. their tactile sensitivity (Vega–Bermudez & Johnson, 2001) and also the size of their cortical representations in SI (Duncan & Boynton, 2007), there are currently no studies that suggest that SEPs evoked by the (separate) tactile stimulation of these two particular digits differ in amplitude. In fact, Franzén and Offenloch (1969) directly compared SEPs in response to index and middle finger stimulation and did not find any significant differences. Importantly, in Exp. 2.3 of the present thesis, somatosensory processing of tactile stimuli (in the context of observing a static hand being touched) was also not altered as a function of whether the index or the middle finger tip was stimulated, pointing to the possibility that the observed index finger-specific SEP modulations revealed in the present study might nevertheless have occurred specifically in the context of observing finger movements, regardless of which finger. For some reason, somatosensory processing of tactile stimuli to the index finger might be particularly sensitive to the sight of finger movements (even if it is not an index finger that is seen to move), maybe due to the index finger being the most dextrous and flexible finger that is also most often involved in pointing movements and in touching and probing surfaces. More research will be needed to shed more light on the effects of observing finger movements on somatosensory processing for the different fingers of one hand and the index finger in particular. In a first step, it seems advisable to establish a baseline for somatosensory processing of index finger stimuli by including a movement-free observational condition such as e.g. viewing a static finger. In addition, somatosensory processing of index finger stimuli should not only be compared to stimuli to an immediately adjacent finger (middle finger) but also to the stimulation of more distant fingers, such as the ring or little finger to obtain a more complete picture of possible variations in somatosensory processing at different fingers in the context of observing movements.

Variations in touch observation-related modulations in somatosensory processing as a function of interindividual differences in trait empathy

For three centroparietal and parietal electrodes over the ipsilateral hemisphere, it was found that the strength of the touch observation-related P100 modulation during concurrent middle finger stimulation and observation co-varied significantly with participants' scores on the IRI's *personal distress* scale. The more participants tended to report to respond with feelings of discomfort and distress to others' negative experiences, the more pronounced was the increase in P100 mean amplitude. This relationship was in line with findings in Exp. 3.5 which also implicated (albeit at different latency ranges) this affective component of empathy in the context of observing the (non-painful) tactile consequences of others' actions. Chapter 3.7 will attempt to summarise and evaluate all the empathy-related correlations found in the experiments of this chapter in more detail, discussing them in the light of findings from other domains that also point to shared neural representations as the neural basis of empathy (Gallese, 2003; 2007; 2004; Keysers & Gazzola, 2006).

Conclusion

All in all, the findings of the present study suggested that (passively) observing others' action-related touch sensations modulated later-stage somatosensory processing (N140), primarily, however, for tactile stimuli presented to the adjacent rather than the anatomically congruent finger. For the anatomically congruent finger, the involuntary internal simulation of the proprioceptive component of the observed movements in the observer's own somatosensory system might make it more difficult to dissociate the touch observation-related modulations in somatosensory processing from the movement observation-related ones, especially when the observed touch sensation in itself is very subtle (i.e. a brief tap with the finger tip rather than e.g. a full-hand grasp or a multi-digit object manipulation). Interestingly enough, somatosensory processing was also found to be modulated at an earlier latency range (P100) but this effect was specific to concurrent middle finger stimulation and observation, possibly because observing a middle finger touch an object in the depicted way may have appeared somewhat unusual, resulting in an enhanced salience of this observational condition.

Apart from the touch observation-related SEP modulations, it was again found that index finger stimuli were processed somewhat differently from middle finger stimuli (N80, N140), even if the SEP amplitude differences were very small and localised. These modulations were, however, not contingent on which finger was concurrently observed to move, indicating that these SEP difference might not after all be brought by a highly finger-specific internal simulation of the observed finger movements. More research will be needed to shed more light on why and how tactile stimuli were found to be processed differently in several of the experiments in this chapter, depending on whether they were presented to participants' index or middle finger.

Summary and discussion of chapter 3

Summary and discussion of Exp.s 3.1 – 3.6

Observing others' actions does not only vicariously activate a wide-spread fronto-parietal network of motor areas (Buccino et al., 2001; Chong et al., 2008a; Hari et al., 1998; Kilner et al., 2009; Mukamel et al., 2010; Rizzolatti et al., 1996b; Shmuelof & Zohary, 2007) but also the observer's somatosensory cortex, due to the involuntary internal simulation of the proprioceptive features of the seen movements (Avikainen et al., 2002; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004; Raos et al., 2004; 2007; Rossi et al., 2002; Voisin et al., 2011b). What has so far not been considered very explicitly is the fact that the observed actions are often object-directed and thus also involve a tactile component from e.g. grasping and manipulating an object which is, however, of particular significance given the previous findings of vicarious somatosensory activity during the sight of (passive) touch (Blakemore et al., 2005; Bufalari et al., 2007; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012; 2009; Wood et al., 2010; see also Exp. 2.1 – 2.4). Chapter 3 of this thesis presented a series of six ERP studies that were among the first to explicitly address the question as to whether observing others' *action-related* tactile sensations, too, induces a distinct somatosensory resonance response that, importantly, stands out from any movement observation-related vicarious somatosensory activity. To this purpose, participants observed a model perform either finger movements that resulted in a tactile sensation (from e.g. briefly tapping on a table top or on a object) or kinaesthetically similar finger movements that were not associated with a tactile sensation while somatosensory-related ERPs were recorded as an index of somatosensory activity. To explore how clearly somatosensory mirror touch responses might represent the precise finger with which the observed "touching" was performed, SEPs were not only obtained in response to tactile stimuli to participants' homologous finger tip but also to e.g. participants adjacent finger tip in most studies (3.2 - 3.6).

Modulations in somatosensory processing in the context of observing others' action-related touch sensations

The findings of the aforementioned six ERP studies did indeed suggest that observing others' action-embedded tactile sensations (at least under certain conditions) modulates ongoing somatosensory processing, indicating that the sight of active touch vicariously activates the observer's somatosensory system above and beyond movement observation-related somatosensory activations (see also Turella et al., 2012). The revealed touch observation-related

SEP modulations were often somewhat small but given that the observed touch events were rather subtle and presented in the context of finger movements which in themselves most likely triggered somatosensory activity, this was not unconceivable. It might in fact also explain why the revealed SEP modulations were so sensitive to slight changes in the experimental procedures such as how extensively participants were exposed to what it actually feels like to perform the observed movements prior to the experiment or whether the concurrently stimulated finger locations was manipulated block-wise (Exp. 3.3 – 3.6) or on a trial-by-trial basis (Exp. 3.2). Especially for early-latency SEP modulations (P50/N80), it seemed to be a precondition that participants were sufficiently aware of the touch-related difference between the two types of observed movements, as a result of either having ensured that participants repeatedly imitated the relevant movements, including the touching of the e.g. object, before the experiment (Exp. 3.3) or making the touch/no touch-dimension of the visual stimuli task-relevant (Exp. 3.5). Also slightly later occurring SEP modulations in the P100 latency range were only found when participants had initially briefly imitated the later-to-be-observed movements (Exp. 3.3) or when the salience of the touch-related movements was increased by somewhat unusual appearing movement features such as isolated middle finger movements (3.6). Future studies may thus want to investigate changes in somatosensory activity in the context of more explicitly touch-related visual stimuli such as a hand either perform a full-hand grasp of an object in (as compared to merely mimic a grasp next to the object (see e.g. Turella et al. (2012)'s stimulus material) or hand manipulating an object with all five fingers (as compared to performing the same finger movements without an object (see e.g. Avikainen et al. (2002)'s stimulus material).

A rather interesting finding that emerged across all five studies in which not only the anatomically congruent but also the adjacent finger was tactually stimulated was that touch observation-related SEP modulation, especially during early-stage somatosensory processing (P50/N80), tended to be found primarily for the finger adjacent to one actually seen to move and touch. This might be associated with the concurrent internal stimulation of the proprioceptive features of the observed movements which, too, triggers vicarious activity in the somatosensory cortex (Avikainen et al., 2002; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004; Raos et al., 2004; 2007; Rossi et al., 2002; Voisin et al., 2011b). While it has yet to be investigated how clearly somatotopically organised such movement observation-related vicarious somatosensory activity actually is when it comes to different fingers of one hand, it is conceivable that it might indeed be quite finger-specific, given the fine-grained and highly effector-specific fashion in which vicarious *motor* activity represents the moving digit during finger movement observation (Avenanti et al., 2007; Romani et al., 2005; Urgesi et al., 2006) and the close reciprocal connections between motor and somatosensory areas during action execution but possibly also during action observation (cf. Gazzola & Keysers, 2009). If movement observation-related somatosensory activity were to be quite finger-specific, it seems plausible that the mirror touch response associated with the simultaneously observed touch for that finger might be obscured by that movement observation-associated activity. Somatosensory processing of tactile stimuli to the adjacent finger, on the other hand, might be less affected by the sight of the neighbouring finger move, allowing the mirror touch response to stand our clearer. Note that this speculation is based on the assumption that vicarious somatosensory in response to the sight of touch might – in contrast to movement observation-related activity – does not very clearly represent on which exact finger that tactile sensation was seen to occur (see Exp. 2.3 in chapter 2), explaining why modulations in somatosensory processing of tactile stimuli presented to e.g. the middle finger might be found during observation of e.g. an index finger touch an object in the first place.

In fact, the repeatedly encountered SEP amplitude differences at both early- (N80) and later-stage (P100/N140) somatosensory processing for index as compared to middle finger stimulation, irrespective of observed tactile feedback (see Exp.s 3.2, 3.3 and 3.4), were initially thought to be related to the aforementioned open question of how finger-specific movement observation-related somatosensory activity might be. Given that participants in Exp.s 3.2, 3.3 and 3.4 observed exclusively index finger movements, it was speculated that SEP modulations as a function of the concurrently stimulated finger (index vs. middle finger) might indeed reflect that movement observation-related vicarious somatosensory activity is highly finger-specific and thus affects somatosensory of tactile stimuli to the index finger (as the finger also observed to move) as compared to tactile stimuli to the adjacent middle finger (as the adjacent, unobserved finger). However, this explanation had to be queried when the results of Exp. 3.4 revealed that the SEP differences during index as compared to middle finger stimulation were actually not contingent on whether an anatomically congruent or an adjacent finger was observed in motion. At the same time, it seemed as if the SEP differences between index and middle finger stimulation nevertheless occurred in the specific context of observing finger movements, especially since there were no indications in Exp. 2.3 that index finger stimuli were processed differently from middle finger stimuli when participants observed a static hand. How finger-specific vicarious somatosensory activity during movement observation is will thus have to be eluded in future studies, with special consideration of the fact that the index finger might somewhat differ from the other fingers of the hand.

Variations in touch observation-related modulations in somatosensory processing as a function of interindividual differences in trait empathy

As for possible links between the strength of touch observation-related SEP modulations and participants' empathic dispositions in the context of observing others' action-related touch sensations, it was again primarily empathy measures that tap the emotional side of empathy (the EQ's *emotional reactivity* subscale and the IRI's *personal distress* scale, respectively) that were found to be predictive of how strongly (later-stage) somatosensory processing (P100/N140) was modulated by the sight of others' active touch experiences (see, however, Exp. 3.3 and 3.5 for exceptions). This pattern thus resembled the also mainly emotional empathy-related relations between the strength of touch observation-related SEP changes and individuals' empathic traits revealed in Exp.s 2.1 – 2.3 in the context of observing others' being passively touched on their hand. As already pointed out in chapter 2.5, this focus on emotion-related empathy dimensions was somewhat unexpected, given that variations in the extent to which vicarious somatosensory activity is triggered the sight of others' movements, touch or pain are most commonly found to relate to interindividual differences in cognitive dimensions of empathy (e.g. Avenanti et al., 2009; Cheng et al., 2008; Costantini et al., 2008; Gazzola et al., 2006; Schaefer et al., 2012). The findings of the ERP studies in the present chapter as well as those in chapter 2 do, however, suggest that vicarious somatosensory activity might be linked to emotional aspects of empathy, too. This relationship might previously not have been detected due e.g. differences in the temporal resolution of the employed neuroscientific methods (fMRI, TMS-induced MEPs, oscillations vs. ERPs) and/or the used experimental paradigms and specific empathy measures.

Another interesting finding that, too, resembled a trend revealed in Exp.s 2.1-2.4 in chapter 2, was that touch observation-related SEP modulations during early-stage somatosensory processing (N80) were linked to individual levels of (albeit cognitive) trait empathy in a negative fashion, i.e. high-empathy participants tended to show smaller rather than larger SEP amplitude differences (Exp. 3.5). While it can only be speculated how such a counterintuitive relationship is mediated (see chapter 2.5), their presence certainly highlights the importance of using complementary neuroscientific methods and the advantages of the high temporal resolution of EEG which allows to study vicarious brain activity in time windows of only a few milliseconds and thus to detect also very rapid and/or short-lived effects and their modulations.

Conclusions

All in all, the six ERP studies presented in this chapter demonstrated that also observing others' action-related touch sensations can modulate somatosensory processing in the observer, provided that participants were sufficiently aware of the difference in tactile consequence associated with the observed finger movements which was rather subtle in the stimulus material used here. That mirror touch responses tended to be found for the finger adjacent to the one observed to move and touch might demonstrate how easily movement observation-related vicarious somatosensory activity can obscure a much subtler touch observation-related resonance response in the somatosensory system. At the same time, it highlights the need for more research into the somatosensory side of movement simulation –an aspect which has until recently been neglected in favour of the motor side of action simulation – to establish, for instance, how effector-specific vicarious movement observation-related somatosensory activity is.

Chapter 4

Behavioural effects of observing others' (action-related but also passively experienced) touch sensations on tactile processing in the observer

Chapters 2 and 3 of thesis reported a series of ERP studies that investigated possible electrophysiological correlates of mirror touch, both in the context of witnessing others' being passively touched on their body and of observing them actively touch e.g. an object. Touch observation-related ERP modulations (see chapter 2 and 3 as well as Bufalari et al., 2007) corroborate the notion of shared neural representations for felt and observed touched as initially suggested by neuroimaging findings (Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Schaefer et al., 2012; 2009) at a neural level (see also Pihko et al, 2010, and Wood et al., 2010). What has, however, barely been investigated to date is what measurable *behavioural* effects observing somebody else experience touch (be it from being passively touched or from actively performing a movement that results in contact with a surface) might have on the observer's ongoing sensory perception of tactile information from their own body.

The general conclusion based on findings of the very few studies that have addressed the question of behavioural effects of mirror touch so far is that observing somebody else's body being touched seems to enhance tactile perception in the observer. Serino et al. (2008b) tactually stimulated healthy participants on their facial cheeks (either unilaterally or bilaterally) while presenting them with videos depicting either their own or somebody else's face being either touched or merely approached by one or two fingers. Using a *tactile confrontation task*[22], Serino et al. (2008b) could show that participants were significantly more accurate in judging bilaterally delivered touch stimuli in their face correctly as bilateral (that is without erroneously not detecting the weaker stimulus) when observing a human face being touched rather than being merely approached. While this effect was larger when viewing their own face, it was also present when viewing another person's face. The observation of touch thus seemed to increase tactile acuity for self-experienced tactile sensations (see also (Serino et al., 2009).

In an entirely different approach, Schaefer et al. (2005b) found that watching a video depicting a right hand being touched with a stick on the index finger improved participants'

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[22] Serino et al. (2008b) aimed to simulate an extinction phenomenon often found in brain-damaged patients who fail to report the contralesional stimulus when being stimulated tactually on both sides of their body. Thus, they systematically delivered a weaker tactile stimulus on one cheek and a stronger one on the other cheek assuming that the strong stimulus would occasionally extinguish the weaker one in trials with double stimulation on both cheeks. Accordingly, the authors were primarily interested in bilateral stimulation trials (and also did not find any modulations by vision for the unilateral stimulation trials)

tactile sensitivity, as indexed by a decrease in sensory threshold measured by applying von Frey filaments[23] to the fingertip. No such modulation in sensory thresholds was found when subjects watched a video in which the approaching stick did not touch the depicted right hand but merely moved through the empty space beneath it. This apparent threshold modulation induced by the repetitive observation of touch on the video hand also seemed to last for several minutes as the threshold specification conducted after the video presentation required several different steps and was thus relatively time-consuming.

It should, however, be noted that the enhancement effect reported by Schaefer et al. (2005b) was measured in a blocked design in response to the repetitive observation of touch on the video hand (as opposed to non-touch) for 15 consecutive minutes while counting the movements of the stick which appears to be a rather intense exposure to such touch-related visual information. Serino et al. (2008b) and Serino et al. (2009), on the other, elegantly demonstrated that the sight of others' touch sensations is capable to induce, on a trial-by-trial basis, rapid modulations in tactile processing. It is, however, unclear whether any such visuotactile modulations could also be found for non-face body stimuli. Faces constitute a quite special category of corporeal stimuli and might, for instance, have induced particularly strong mirror touch responses in the somatosensory system, possibly exaggerating the behavioural effect of the sight of touch (see chapter 2.1.). In addition, it is unclear whether concurrent tactile processing is also altered when quantified with more basic tactile tasks than the one used by Serino et al. (2008b) where tactile acuity was measured in the context of the competition between two concurrent tactile stimuli that differed in their intensity. Moreover, it has also not been investigated yet whether also the sight of others' *haptic* touch sensations (see chapter 3) is associated in measurable changes in tactile processing at a behavioural level. The main part of the present chapter (chapter 4.1) thus reports a series of behavioural experiments which aimed to test by means of several different tactile tasks whether observing the tactile consequences of others' actions modulates tactile processing in the observer (Exp. 4.1.1-4.1.5.). Exp. 4.1.1 employed a speeded tactile intensity discrimination task while participants in Exp. 4.1.2 and 4.1.3 were asked to directly compare the intensities of two successively presented tactile stimuli. In Exp. 4.1.4, participants were presented with tactile stimuli of varying intensities and had to rate the perceived intensity of each stimulus on a rating scale. In Exp. 4.1.5, participants performed a detection task on near-threshold tactile stimuli. During all four experimental tasks, participants observed finger movements that either included a tactile component or not. Chapter 4.2, on the other hand, briefly reports a behavioural study in which it was tested whether the

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[23] Von Frey hairs are made from e.g. nylon filaments of varying lengths and diameters and are widely used in research and clinical settings to probe tactile sensitivity by pressing the filaments against a given skin area.

sight of *passive* touch on somebody else's body would induce the same modulation found in Exp. 4.1.3 in response to observing somebody else's active touch sensation in the context of a direct intensity comparison task.

4.1 Behavioural effects of observing others' haptic touch sensations

Behavioural effects of observing others' action-related touch sensations on tactile processing in the observer

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Experiment 4.1.1. (Tactile intensity discrimination task)

4.1.1.1 Introduction

As described above, observing (passive) touch on somebody else's body has previously been found to enhance tactile acuity for concurrently presented tactile stimuli (Serino et al., 2008b). The present study aimed to investigate whether the sight of touch might improve task performance also in the context of a straightforward tactile intensity discrimination task and when participants did not observe other-related passive touch sensations but active finger movements that were associated with a tactile sensation from touching a surface. On each trial, participants had to indicate whether a tactile stimulus presented to their index finger tip was either weak or strong while they observed a model's index finger either tap on the table top or lift up into empty space. It was hypothesised that, if the sight of touch was to be found to affect tactile processing with this particular type of task, observing touch might facilitate the discrimination of the two tactile stimulus intensities, resulting in decreased response times and/or increased discrimination accuracy as compared to observing a similar finger movement that does not result in a tactile sensation for the model. Importantly, the viewing others' movements has previously been found to affect tactile information processing in itself at least at a neural level (Avikainen et al., 2002; Rossi et al., 2002; Voisin et al., 2011b). Including an additional observational condition in which the observed finger did not move but briefly changed its colour thus allowed to also explore whether the mere sight of movements (irrespective of whether they are associated with a tactile sensation or not) affects performance in this basic tactile intensity discrimination task.

4.1.1.2 Methods

Participants. 21 neurologically healthy volunteers (10 males, 11 females) aged between 18 and 36 years took part in the experiment. Two of the obtained data sets had to be excluded from (parts of) the analysis: One female participant was not able to discriminate the two presented stimulus intensities at all and performed on chance level (50 %) throughout. For another male participant, a malfunction of the microphone resulted in a large number of missing response times which is why his data set had to be excluded from the reaction time (but not the accuracy data) analysis.

Thus, a total of 19 volunteers (9 males, 10 females) remained in the sample with an average age of 23.32 years (SD = 4.96 years). All but one were right-handed and all had normal or corrected-to-normal vision by self-report. Participants were naive as to the purpose of the experiment and gave informed consent to participate after a detailed explanation of the involved procedures. Participants received either course credit or were paid £ 7/h for their participation in the study. The procedures were approved by the local ethics committee at City University London and conducted in accordance with Declaration of Helsinki.

Stimuli. The task-irrelevant visual stimuli were the same as in Exp. 3.1 in chapter 3, depicting a right hand from an egocentric perspective resting on a table top, with the index finger in either a neural position (neutral), in a lowered position in which the finger tip touches the table (tap) or in an elevated position (lift) in which no contact with a surface occurs. An additional image showed the index finger in its neutral position but tinted in blue (control). This latter movement-free observational condition was included in case the mere observation of movements in itself was to affect tactile processing. Fig. 4.1.1.a shows how presenting the stimulus images in rapid succession in a chronological sequence created the impression that the index finger either briefly tapped the table top or was lifted up into empty space before resuming its neutral position. Alternatively, the index finger merely changed its colour but did not move.

During the passive observation of these visual stimuli, participants had to perform a speeded tactile discrimination task. Tactile stimuli were presented using a purpose-built 12-volt solenoid which drove a metal rod with a blunt conical tip against the participants' skin for 200 ms whenever a current was passed through it. This solenoid and the metal rod were embedded in a small wooden block for stability and participants were asked to position their right index finger right on top of the opening for the stimulator in a relaxed fashion, i.e. without pressing down on the stimulator. Tactile stimuli were delivered at two different intensities by varying how far the metal rod protruded from its wooden casing. To mask any sounds made by the tactile stimulator, continuous white noise (65 dB SPL) was played through headphones.

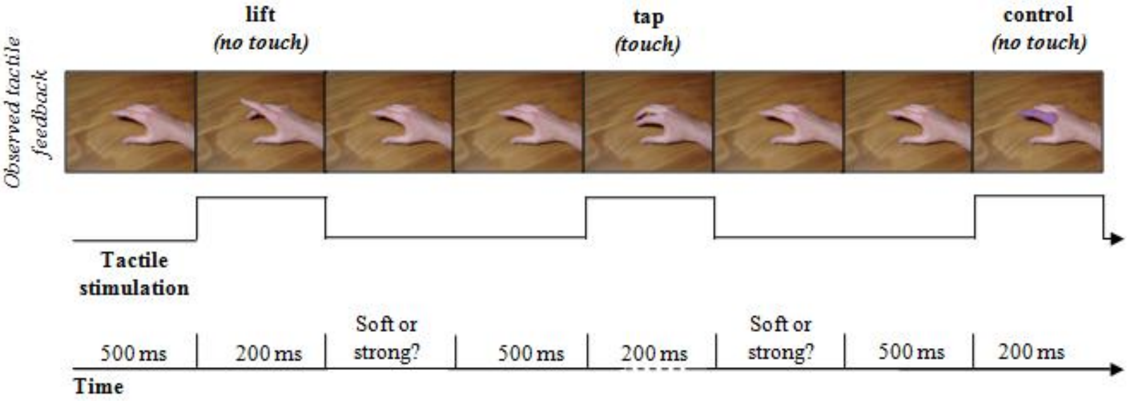

Fig. 4.1.1.a. Schematic representation of the typical sequence of visual and tactile events in tap, lift and control trials, respectively.

The visual stimuli were presented on a computer screen located approximately 75 cm in front of the participants and the presentation of the both the visual and the tactile stimuli was controlled by E-Prime (Psychology Software Tools Inc., version 1.1).

Procedure. Participants sat in a dimly lit lab room resting their right arm on a table in front of the them with the right index finger tip positioned on the tactile stimulator. Both arms and hands as well as the tactile stimulator were covered by a piece of cloth to make sure participants could not see the tactually stimulated body part since visual access to one's own body during tactile stimulation has been found to modulate tactile processing (Kennett et al., 2001; Press et al. 2004).

The task at hand was a speeded tactile discrimination task: On each trial, participants were presented with a tactile stimulus and had to report verbally as quickly as possible whether the intensity of the presented stimulus was either "soft" or "strong", without thinking about their decision for too long. The two target intensities were chosen as relatively similar to each other to ensure that the task was sufficiently difficult since previous research had indicated that effects of concurrent (body-related) visual information on tactile processing can most readily be observed in challenging tasks were such a "boost" is most beneficial (Longo, Cardozo, & Haggard, 2008; Press et al., 2004). While performing this tactile discrimination task, participants were instructed to continuously fixate on the fixation cross superimposed over the hand stimuli but to ignore the finger movements and the colour change, respectively, completely. A free-standing microphone positioned in front of the participants recorded the response times for the vocal responses.

Each trial began with a presentation of the hand in a neutral position for 500 ms, followed by 200 ms presentation of the hand with the index finger in either a lifted (lift) or lowered position (tap) or remaining in the neutral position but tinted in blue (control). The onset of this critical stimulus image was concurrent with the presentation of a tactile stimulus of one of two intensities to the participants’ right index finger tip for an equally long duration. Subsequently, the hand was again shown in its neutral position until a vocal response occurred and was manually coded by the experimenter. As soon as the participants’ response was coded as “soft”, “strong” or “invalid” (when participants e.g. stuttered or coughed), a new trial began.

Overall, there were 5 experimental blocks with 120 trials. Each experimental block contained 20 trials for each combination of tactile stimulus intensity (soft vs. strong) and observed tactile feedback (lift vs. tap vs. control), presented in random order. At the end of each block, participants were presented with a summary of their task performance (mean reaction time, mean accuracy, number of mistakes).

Before the actual experiment started, participants were presented with a short demo of the two involved tactile stimulus intensities in the absence of the visual hand stimuli. While fixating on an orange fixation cross superimposed on a black background, 10 tactile stimuli of each intensity were delivered to their finger tips in random order, followed by on-screen feedback indicating the just presented stimulus intensity. Participants then performed an initial practice block of 15 trials for each intensity presented in random order in which they were to discriminate the two stimulus intensities while fixating on a fixation cross on a black screen only. This simplified practice block was then followed by a practice block that was equivalent to an experimental block (i.e. participants now fixated on a fixation cross superimposed on the hand images described above), except for a reduced trial number (15 trials for each combination of stimulus intensity and observed tactile feedback, i.e. 90 trials in total). This procedure was to ensure that participants were sufficiently accurate in the discrimination of the two rather similar tactile stimulus intensities.

Throughout the experiment, the experimenter used a camera to monitor whether participants were fixating on the screen as instructed. During the initial practice blocks, some participants tended to avert their gaze from the visual stimuli or close their eyes altogether whenever they struggled with discriminating the tactile stimuli, often without noticing it. After making them aware of this and reminding them to fixate on the fixation cross throughout, all participants were well able to follow this instruction

4.1.1.3 Results

The average accuracy in discriminating the two tactile stimulus intensities was 70.21 % across all experimental conditions (SD = 7.03 %) which indicated that the task was rather difficult for most participants.

To test whether the type of observed tactile feedback modulated the accuracy with which participants discriminated the tactile stimuli presented to their finger tip, a 3 x 2 repeated measures ANOVA was conducted on the percentage of trials on which the stimulus intensity was correctly identified with the factors *type of tactile feedback* (tap vs. lift vs. neutral) and *stimulus intensity* (weak vs. soft). Greenhouse-Geisser corrected p-values are reported where violations of the sphericity assumption were indicated. Significant main or interaction effect involving the factor *type of tactile feedback* were followed up with paired t-tests (two-tailed) and an appropriately Bonferroni-adjusted α–level.

There was a significant main effect of the observed tactile feedback on the percentage of correctly discriminated stimulus intensities (F(2, 38) = 3.353, p = .046, η^2_p = .150). In comparison to observing a motionless finger briefly change its colour ($M_{control}$ = 71.5 %; $SD_{control}$ = 8.3 %), observing somebody else's finger move seemed to slightly impair the intensity discrimination of concurrently delivered tactile stimuli on the observer's body, even more so if the observed movement resulted in a tactile sensation (tap) ((M_{tap} = 68.9 %, SD_{tap} = 6.5 %) vs. (M_{lift} = 70.2 %, SD_{lift} = 7.6 %)), as visualised in Fig. 4.1.1.b. Statistically, this trend could, however, not be confirmed by follow-up analyses based on paired t-tests: There was no significant difference in discrimination accuracy between the observation of a lifting movement and the control condition (t(19) = -1.097, p = .286, r = .244) or between the observation of a lifting movement and tapping movement (t(19) = -1.784, p = .090, r = .379), respectively. The descriptively most prominent difference in discrimination accuracy (see Fig. 4.1.1.b) between observing a tapping movement and observing a mere colour change of the finger (t(19) = -2.431; p = .025, r = .487) did not survive Bonferroni-correction (Bonferroni-corrected α = .017) but might at least be considered a non-significant trend.

There was no significant main effect of stimulus intensity (F(1,19) = 3.276, p = .086, η^2_p = .147) on discrimination accuracy and also no significant interaction between observed tactile feedback and stimulus intensity (F(2,380) = 2.308, p = .113, η^2_p = .108).

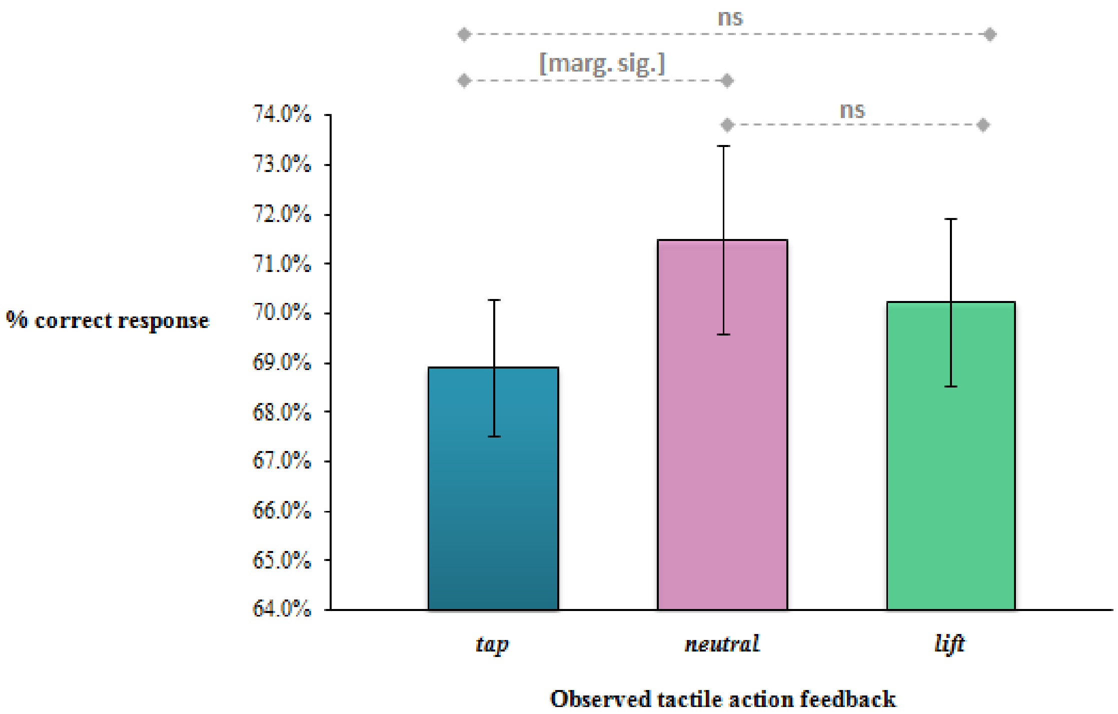

Fig. 4.1.1.b. Mean proportion of correctly discriminated tactile stimuli as a function of the concurrently observed tactile action feedback. The vertical bars indicate the standard errors of the respective means proportions.

Another 3 x 2 repeated measures ANOVA with the factors *type of tactile feedback* (tap vs. lift vs. neutral) and *stimulus intensity* (weak vs. soft) was conducted on the time it took participants to discriminate the stimuli. Only response times for correctly discriminated trials were included in the RT analysis. In addition, all trials with response times of less than 200 ms or more than 1500 ms were removed, with the former most likely reflecting response-unrelated artifacts (e.g. coughing or movement of the participant) and the latter possibly indicating a lack of attention during a given trial. Slow responses of up to 1500 ms were not removed due to the difficultness of the task and to retain as many trials with correct responses as possible. On average, 1 % of the trials were removed (SD = 1.8%). Again, Greenhouse-Geisser were applied if indicated.

Overall, there was a significant main effect of tactile stimulus intensity, (F(1,18) = 13.129; p = .002, η^2_p = .422) with participants identifying a strong stimulus correctly as strong on average 25.9 ms (SD = 31.1 ms) quicker than identifying a weak stimulus as weak. In addition, there was also a significant main effect of the observed tactile feedback (F(2,36) = 8.420; p = .001, η^2_p = .319). Follow-up analyses based on a Bonferroni-adjusted α–level of .017 revealed that the reaction time for identifying the intensity of a concurrently presented tactile stimulus was significantly impaired by observing the index finger performing a tap (M_{tap} = 782.9 ms; SD_{tap} = 137.0 ms) in comparison to it remaining still and only briefly change its colour ($M_{control}$ = 765.9 ms $SD_{control}$ = 131.7 ms; t(18) = 4.091; p = .001, r = .694). Merely observing a touch-unrelated finger movement (M_{lift} = 772.6 ms; SD_{lift} = 130.2 ms) seemingly also impaired reaction time (if to a lesser extent) when contrasted to the movement-free control condition but this difference was not significant (t(18) = 2.047; p = .056; r = .435). Also the direct comparison between the observation of a touch-related (tap) and a touch-unrelated (lift) finger movement was not significant (t(18) = 2.090; p = .051, r = .442).

Crucially, there was, however, also a significant interaction between the observed tactile feedback and the stimulus intensity (F(2,36) = 5.668, p = .007, η^2_p = .239). To follow-up this interaction, pairwise t-tests with a Bonferroni-adjusted α–level of .0083 were carried out to determine the simple effects of the observed tactile feedback at each intensity level separately. This revealed that only for strong stimuli, observing a touch-related tapping movement significantly impaired reaction times both in comparison to observing a touch-unrelated lifting movement (t(18) = 4.009; p = .001, r = .687; M_{tap} = 778.19 ms; SD_{tap} = 135.93 ms; M_{lift} = 748.99 ms; SD_{lift} = 129.08 ms) and to observing a movement-free control condition (t(18) = 3.480, p = .003, r = .634; $M_{control}$ = 755.44 ms; $SD_{control}$ = 135.86 ms)[24]. Reaction times during the observation of lifting movements or a movement-free control condition, on the other hand, did not differ significantly (t(18) = -.948, p = .356, r = .218).

For weak stimuli, no such pattern was found. Instead, the only significant difference in reaction time was found when contrasting the observation of lifting movements with the movement-free control condition (t(18) = 3.528, p = .002, r = .639): Participants were significantly slower in correctly identifying a weak stimulus when the presentation of this weak stimulus was accompanied by the sight of a (touch-unrelated) lifting movement rather than a motionless finger (M_{lift} = 796.28 ms, SD_{lift} = 133.40 ms; $M_{control}$ =776.41 ms, $SD_{control}$ = 130.46 ms). Interestingly, the observation of a tapping movement did not have such an effect in comparison to the control condition (t(18) = 1.315, p = .205, r = .296; M_{tap} = 787.60, SD_{tap} = 142.86) when the to-be-identified stimulus was weak, despite the presence of a finger movement. Fig. 4.1.1.c depicts the mean response latencies during the observation of tapping and lifting index finger movements as well as during the sight of a brief colour change of the static index finger separately for both strong and weak tactile stimuli.

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[24] Neither of these differences correlated in strength with the overall task accuracy of the participants (p ≥ .269).

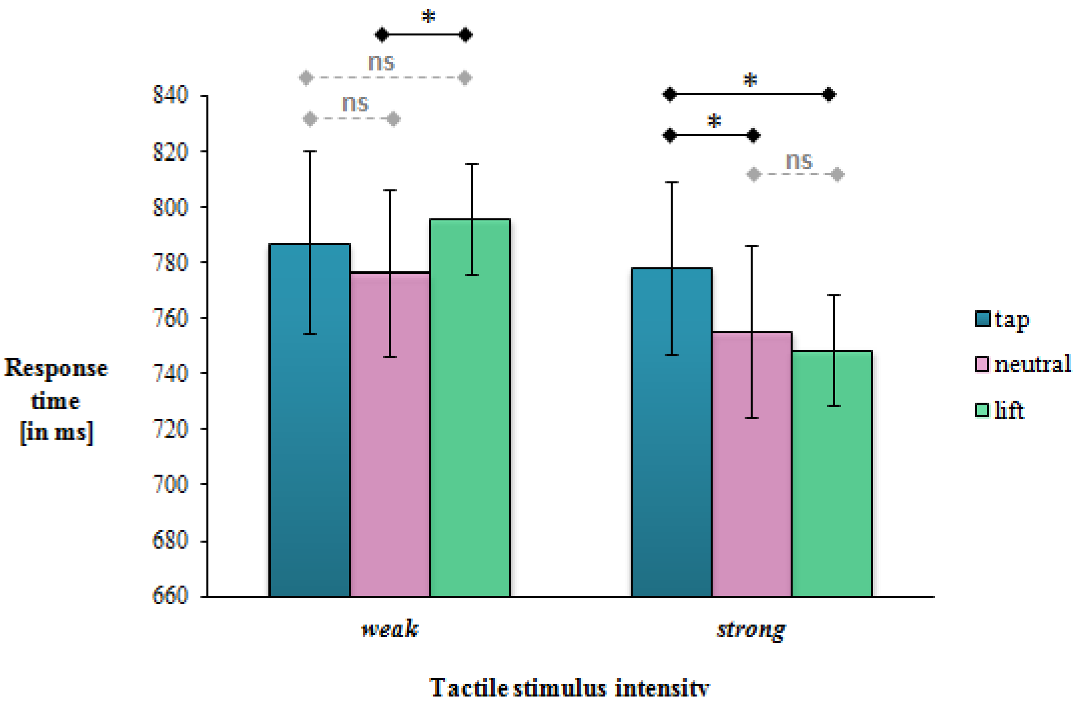

Fig. 4.1.1.c. Mean reaction time in tactile discrimination task in ms as a function of observed tactile feedback and tactile stimulus intensity. The vertical bars indicate the standard errors of the respective means.

4.1.1.4 Discussion

In the present study, participants performed a speeded intensity discrimination task in which they had to identify on each trial whether a presented tactile stimulus was weak or strong while simultaneously observing task-irrelevant visual stimuli that depicted a model's index finger either tap on a table top, lift up into empty space or briefly change its colour. Crucially, the sight of a touch-related finger movement (tap) affected task performance in a complex and somewhat unexpected fashion: First of all, observing the model's index finger perform a tapping movement on the table top seemed to, overall, interfere with the tactile discrimination task rather than facilitating it, resulting in longer response times and also a reduced discrimination accuracy (albeit the latter was only a non-significant trend) as compared to observing the index finger merely change its colour but not move. Observing an index finger movement that did not result in a tactile sensation from making contact with a solid surface, on the other hand, did not induce such a detrimental effect on task performance as compared to motionless colour change of the corresponding finger. While this might suggest that the observation of an additional tactile component during the sight of tapping as compared to lifting movements might be responsible for the significant drop in task performance in contrast to the static control condition, it is nevertheless important to note that a direct comparison between tapping and lifting movements did not reveal a significant difference in task performance, indicating that it might after all be difficult to clearly dissociate the effect of the observed tactile component from the effect of the observed movement component in which the tactile event was embedded.

A detrimental effect of observing a somebody else's active touch sensation was in any case somewhat unexpected given the beneficial effect of observing (albeit passive) touch on tactile processing found by Serino et al. (2008b) and Schaefer et al. (2005b) with two different paradigms. The revealed systematic interaction between the observed visual stimuli and the tactile stimulus intensity might, however, help to shed more light on the possible mechanisms that brought about an increase in response times in the present experiment: Interestingly enough, considering the effects of observing the three different observation conditions separately for the two stimulus intensities indicated that the overall negative effect of observing tapping movements was actually driven by the response time modulations during the presentation of high-intensity tactile stimuli: For those strong tactile stimuli, the sight of tapping movements resulted in a significant increase in the time it took participants to correctly identify those stimuli as strong, not only in comparison with the movement-free control condition but also in comparison with lifting movements. This could suggest that specifically the observation of an action-related touch sensation might have systematically decreased the perceived intensity of the presented tactile stimuli, making it more difficult to distinguish the strong stimuli from the effectively weak stimuli. The finding that response times for strong stimuli were unaffected by the sight of lifting movements indicated that it might indeed have been the observed tactile feedback that characterised the tapping movements that interfered with the intensity discrimination and also ruled out that the suggested decrease in perceived stimulus intensity was an unspecific movement observation-related sensory suppression-like effect usually observed during the actual execution of movements (e.g. Juravle, Deubel, Tan, & Spence, 2010; Williams et al., 1998; see Voisin et al. (2011b) in particular for the first account of somatosensory suppression during the mere observation of actions).

Importantly, no detrimental effect of observing a tapping movement as compared to the motionless control condition or the sight of lifting movements was found for weak stimuli[25]. Sticking to the speculative explanation of a decrease perceived tactile stimulus intensity during

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[25] During the presentation of weak tactile stimuli, it was in fact the sight of lifting movements that interfered with a fast discrimination of the presented stimulus intensity: Participants were significantly slower in identifying a weak tactile stimulus as weak when they concurrently observed an index finger lifting movement as compared to mere colour change of the corresponding finger. The sight of tapping movement did not have such an effect on response latencies. This finding points to a certain peculiarity of the lifting movements (in contrast to the tapping movements) which will be addressed when discussing an also lift observation-related unexpected effect in Exp. 4.1.2.

the sight of an action-related tactile sensation proposed above, such a reduction in perceived intensity did not inhibit a “soft”-response since this was the prevalent response anyway. The finding that the sight of tapping movements affected primarily the accurate identification of strong stimuli but not of weak stimuli seems to argue against an unspecific interference effect of observing touch (e.g. participants being distracted by the sight of touch when also feeling touch on their body) since one would expect such an interference effect to be equally present for both stimulus intensities. It should, however, also be taken into consideration that participants were overall slower in correctly identifying weak stimuli as “weak” than in correctly identifying strong stimuli as “strong”, irrespective of the observational condition, presumably due to the more ambiguous nature of the weak stimuli. As far as the possible effects of observing a action-related touch sensation on discrimination times is concerned, it is possible that those might only be measurable in fast and thus sufficiently spontaneous responses and the average response latency for weak stimuli in the present task was simply too slow to allow such touch observation-related modulations to come out.

As for the aforedescribed increase in response latencies for the correct identification of strong stimuli in the context of observing a movement-related touch sensation described above, it should also be considered that it might not reflect an actual change in perceived stimulus intensity after all but some sort of response bias (participants being e.g. aware that the sight of touch might bias their judgment and effortfully trying to compensate for response biases). Alternatively, some sort of distracting incompatibility effect might also have been at work, such as a perceived incongruency between observing a finger moving *downwards* while tactile stimuli are presented from below with a metal rod that is driven *upwards* against participants’ skin. In both cases, it seems, however, difficult to explain why any such response bias or incompatibility effect would affect response latencies during the observation of tapping movements as compared to the neutral condition or the sight of lifting movements only for strong stimuli but not for weak stimuli.

Given that the discrimination task was rather difficult for most participants (the mean accuracy across all experimental conditions was only approximately 70%), it should in any case be taken into account that the response time analysis was based on a relatively small number of experimental trials with correct responses and its results should thus be interpreted with caution. It would be interesting to test whether a similar pattern of intensity-contingent touch observation-related response time modulations would also be found if the task was to be made easier by selecting two stimulus intensities that are easier to distinguish.

Whilst being only a speculative explanation for the drop in task performance during the sight of tapping movements when strong stimuli were presented in the present study, the possibility that observing others’ action-related touch sensations might under certain circumstances modulate and in fact actually decrease the perceived intensity of concurrent tactile stimuli was further explored in the subsequent Exp. 4.1.2 in which a direct intensity comparison task allowed to assess the perceived intensity of presented tactile stimuli in the context of observing tapping and lifting movements more directly and in a response bias-free fashion. Since the main focus of the present thesis was on the effects of observing others' action-related touch sensations on tactile processing rather than the effects of observing others' movements per se on tactile processing, no static control condition was included in Exp. 4.1.2. and tapping movements that comprised a tactile component and lifting movements that did not contain such a tactile component were compared directly.

Experiment 4.1.2. (Tactile intensity direct comparison task)

4.1.2.1 Introduction

In Experiment 4.1.1, it was found that observing somebody else tap on a table top with the index finger significantly impaired how quickly participants were capable of correctly discriminating a strong tactile stimulus concurrently presented to their own index finger from a weak one, as compared to observing the very same index finger being lifted up into empty space or remain still and briefly change its colour. It was speculated that the sight of somebody else's action-related tactile sensations might have been associated with a decrease in the perceived intensity of the tactile stimuli delivered to participants' own finger, making it more difficult to distinguish strong stimuli from weak ones. The present experiment aimed to follow up this suspected intensity-decreasing effect of seeing tapping movements by having participants directly compare, on each trial, the perceived intensities of two tactile stimuli successively presented to their index finger and to indicate which one appeared more intense to them in a 2-alternative forced-choice (2AFC) paired comparison procedure similar to the one used by Odgaard, Arieh and Marks (2003) and Odgaard, Arieh and Marks (2004) for cross-modal enhancement effects on perceived brightness and perceived loudness, respectively. Crucially, each tactile stimulus was accompanied either by the sight of a touch-related tapping movement or a touch-free lifting movement. With such a paired-stimulus design controlling better for a response bias than a single-stimulus design (cf. Odgaard et al., 2003), this task aimed to shed more light on whether concurrent stimuli are indeed perceived as less intense in the context of observing somebody else tap on a table rather than lift the finger up into empty space and if so, if this effect reflects an interaction between observed and felt touch during early-stage sensory processing in the context of shared neural representations for observed and felt touch (e.g. Blakemore et al., 2005; Bufalari et al., 2007; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010) rather than a response bias during later-stage decisional processing. If the observation of a finger tapping-related touch sensation indeed diminishes the perceived intensity of concurrent stimuli to the observer's corresponding finger, participants should select tactile stimuli accompanied by seeing the index finger touch the table top significantly less often as more intense than stimuli paired with seeing the index finger merely lift up into empty space.

4.1.2.2 Methods

Participants. 20 neurologically healthy volunteers, aged between 18 and 31 years (mean age: 22.0 years; SD = 3.6) participated in the experiment. All participants were female, right-handed and had normal or corrected-to-normal vision by self-report. All participants were naive as for the purpose of the study and received either £ 7/h or course credits for their participation. The procedures were approved by the local ethics committee at City University London and conducted in accordance with Declaration of Helsinki

Stimuli. The task-irrelevant visual stimuli were the same hand images as the ones used in Exp. 4.1.1 (and Exp. 3.1) except that there was no motion-free control condition in this experiment and the image depicting the index finger in blue was therefore not included here. Again, participants saw the index finger of a right hand in three different positions: Extended in midair in a neutral position ("neutral"), lifted up into empty space ("lift") or lowered down onto the table top ("tap"). By rapidly replacing the neutral position (see Fig. for presentation times) with either the "lift" or the "tap" position and vice versa, the impression of movement was created. Crucially, one of the movements ("tap") was associated with a tactile sensation while the other one ("lift") was not.

In synchrony with the visual stimuli, tactile stimuli were presented for 200 ms to participants' right index finger tip using the same purpose-built tactile stimulator as in Exp. 4.1.1. Participants positioned their right index finger on top of a small wooden block in which the tactile stimulator was embedded. Tactile stimuli were delivered at three different intensities by varying how far the metal rod protruded from its wooden casing. To mask any sounds made by the tactile stimulator whenever it was triggered, white noise (65 dB SPL) was played through headphones throughout the experiment.

The presentation of both the visual and the tactile stimuli was controlled by E-Prime (Psychology Software Tools Inc., version 1.1).

Procedure. Participants were seated at distance of approximately 75 cm from the computer monitor where the task-irrelevant visual stimuli were to be presented during the tactile comparison task. Their right arm rested on a table in front of them, such that their hand was in a similar position to the observed hand, i.e. with the inside of the forearm and the palms facing down. The tip of their right index finger rested comfortably on the wooden block containing the tactile stimulator. The index and middle finger of their left hand were placed on a keyboard to operate the response keys. A wooden panel ensured that participants could not see their hands (see chapter 4.1.2). A camera placed under the panel allowed the experimenter to continuously check for finger twitching indicating that participants (wittingly or unwittingly) imitated the finger movements they observed. Participants were instructed to fixate on the fixation cross but to ignore the observed hand and its finger movements.

The task at hand was a 2-AFC direct comparison task: On each trial, participants were presented with two consecutive tactile stimuli and had to indicate whether the first or the second one felt more intense by pressing either “1” or “2” on the keyboard while ignoring the simultaneously observed finger movements. Fig. 4.1.2.a shows a schematic representation of the visual and tactile events in a typical trial.

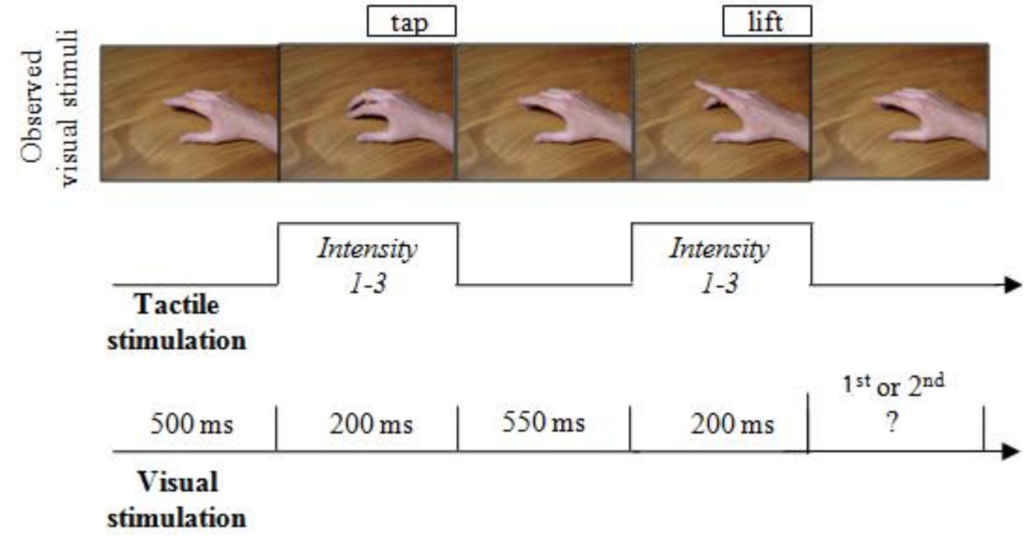

Fig. 4.1.2.a. Schematic representation of the sequence of (visual and tactile) events in a typical critical trial. In *critical trials*, the intensity of the two consecutive tactile stimuli was identical, one tactile stimulus being accompanied by the observed index finger perform a tap on the table top (tap) and the other one being accompanied by the observed index finger perform a lifting movement into empty space (lift). In *control trials*, both tactile stimuli were equally intense and accompanied by the same hand images (e.g. tap - tap). Only in *catch trials*, the tactile stimuli indeed differed in intensity, again paired with the same hand image repeated twice.

Each trial started with a presentation of a hand image with the index finger in its neutral position for 500 ms. Subsequently, the first tactile stimulus was presented for 200 ms, accompanied by the presentation of a hand image with the finger either in the “lift” or in the “tap” position for the same duration. This was followed by showing the index finger first back in its neutral position for 550ms and then again either lifted into empty space or lowered down touching the table top for 200 ms. The onset and duration of the second tactile stimulus was again aligned with this critical hand image, resulting in an inter-stimulus interval between the onset of the first tactile stimulus and the onset of the second one of 750 ms. Finally, the hand was yet again presented back in its neutral position, signalling the end of the trial. Spontaneously and without too much reflection, participants were then to indicate which one of the two tactile stimuli had felt more intense, the first one or the second one. There was no time limit for responses and the next trial was started once participants had indicated their choice by pressing either "1" or "2" on the keyboard.

Crucially, there were three different types of trials in each block: Critical trials, control trials and catch trials, presented in random order. On the *critical trials*, the intensity of the two consecutive tactile stimuli was the same but one tactile stimulus was accompanied by seeing the index finger tap on the table top (resulting in a tactile sensation) while the other one was accompanied by seeing the index finger being lifted (resulting in no tactile sensation). In each experimental block, 30 such critical trials (10 for each of the three intensity levels) were presented in random order. In 50% of these critical trials, the first tactile stimulus was paired with a lift image while the second stimulus was accompanied by a tap image *(lift - tap*), in the remaining 50% of the trials, this order was reversed (*tap - lift*). If the sight of a tap was indeed associated with a decrease in perceived intensity of concurrent tactile stimuli, the proportion of trials in which the tactile stimulus paired with the observation of a tapping movement was selected as more intense should significantly smaller than the proportion of trials in which participants chose the tactile stimulus accompanied by the sight of a lifting movement as more intense.

Another 30 trials of each block (10 per intensity level) were *control trials* in which both the intensity of the two tactile stimuli and the accompanying hand images were the same, i.e. both tactile stimuli were paired with either seeing the index finger tap on the table or lift into empty space, respectively *(tap - tap* or *lift - lift*). Participants were assumed to perform at chance level (50%) on these trials, i.e. guessing randomly and selecting the first tactile stimulus as more intense about as often as selecting the second tactile stimulus as more intense.

Finally, 16 trials of each block were *catch trials* in which the two successive tactile stimuli did indeed differ in intensity. To avoid interference by simultaneously presenting conflicting touch-related visual information, both tactile stimuli on each trial were paired with the same hand images (i.e. *tap – tap* or *lift – lift*). These catch trials were randomly interspersed with the critical and control trials to allow an online measure of task performance. The performance feedback given to the participants at the end of each block was exclusively based on the performance on these catch trials.

All in all, there were 76 trials in each experimental block, presented in random order, and each participant performed 4 blocks with short breaks in between to counteract tiredness.

Prior to the experiment, participants were presented with a short visual presentation of the index finger movements they would be observing later on (7 trials in each observational condition in random order) and instructed to simultaneously imitate the movements, i.e. to perform the same lifting and tapping movements as seen on the screen. This was to ensure that participants were aware of the difference in tactile consequences associated with the two different finger movements, though no such explanation was provided to them. Subsequently, participants performed a practice block (equivalent to an experimental block with the same number of trials) to familiarise them with the direct comparison task and to establish a reasonably sufficient accuracy on the catch trials (at least 70%).

Data analysis. For the critical trials, the percentage of trials on which participants chose the tactile stimulus as more intense that was accompanied by observing the index finger tap on the table top was calculated along with the (complementary) percentage of trials on which participants chose the tactile stimulus as more intense that was accompanied by observing the index finger lift up into empty space as more intense (averaged across trials on which the first or the second tactile stimulus, respectively, was paired with the touch image). For the control trials, the percentages of trials on which the first vs. the second stimulus was chosen as more intense was computed, separately for control trials on which both tactile stimuli were paired with a tap image and control trials on which both were paired with a lift image. One-sample t-tests were conducted to establish whether revealed deviations from the chance level of .5 were significant.

4.1.2.3 Results

On the catch trials on which the intensity of the presented tactile stimuli did differ while the visual information was kept constant, participants correctly identified the more intense tactile stimulus on 75.4 % (SD = 8.67 %) of the trials, indicating that the task was difficult but that the chosen stimulus intensities were reasonably distinguishable in direct comparison. Despite most of the stimuli appearing very similar, participants nevertheless managed to maintain their focus on the task.

On critical trials, when participants were presented with two tactile stimuli of the same intensity but either the first one or the second one was accompanied by observing the model's index finger tap the table top while the other one was accompanied by observing the model's index finger lift up into empty space, participants showed a tendency to judge tactile stimuli associated with viewing a lifting rather than a tapping movement as more intense: On 56.02 %

of the critical trials (SD = 9.47 %), participants chose the tactile stimulus that was paired with the observation of a touch-free lifting movement as the more intense one which was a significant moderate deviation from chance level (one-sample t-test; t(19) = -2.853; p = .010; d = .636)[26]. The observation of a tapping movement, on the other hand, thus seemed to make a concurrent tactile stimulus appear less intense.

On control trials where both tactile stimuli were accompanied by the observation of tapping movements, participants performed on chance level without any tendency to select either the first (M = 50.64 %, SD = 11.13%) or the second tactile stimulus (M = 49.36 %, SD = 11.13%) as more intense (one-sample t-test; t(19) = .255; p = .801; d = .058). On control trials where both tactile stimuli were accompanied by the observation of lifting movements, participants showed, however, a significant response bias: Rather than selecting either the first or the second tactile stimulus as the more intense one at random given that both the tactile stimulus intensity and the observed movements were exactly the same, participants tended to opt for the second stimulus on significantly more than 50 % of these control trials as one would expect by chance (M = 55.36 %, SD = 8.08 %; t(19) = 2.965; p = .008; d = .663).

Fig. 4.1.2.b shows the deviations from chance level for the critical trials as well as for the two different types of control trials.

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[26] Kolmogorov-Smirnov tests indicated that the assumption of normal distribution was violated for this variable (D(20) = .220, p = .012). Re-running this as well as all the subsequent comparisons in this chapter with one-sample Wilcoxon signed rank tests as the non-parametric alternative to one-sample t-tests, however, rendered the exactly the same pattern of test results. In order to maintain consistency with the statistical analyses in chapters 4.1.3 and 4.2.1, the parametric test results are reported here.

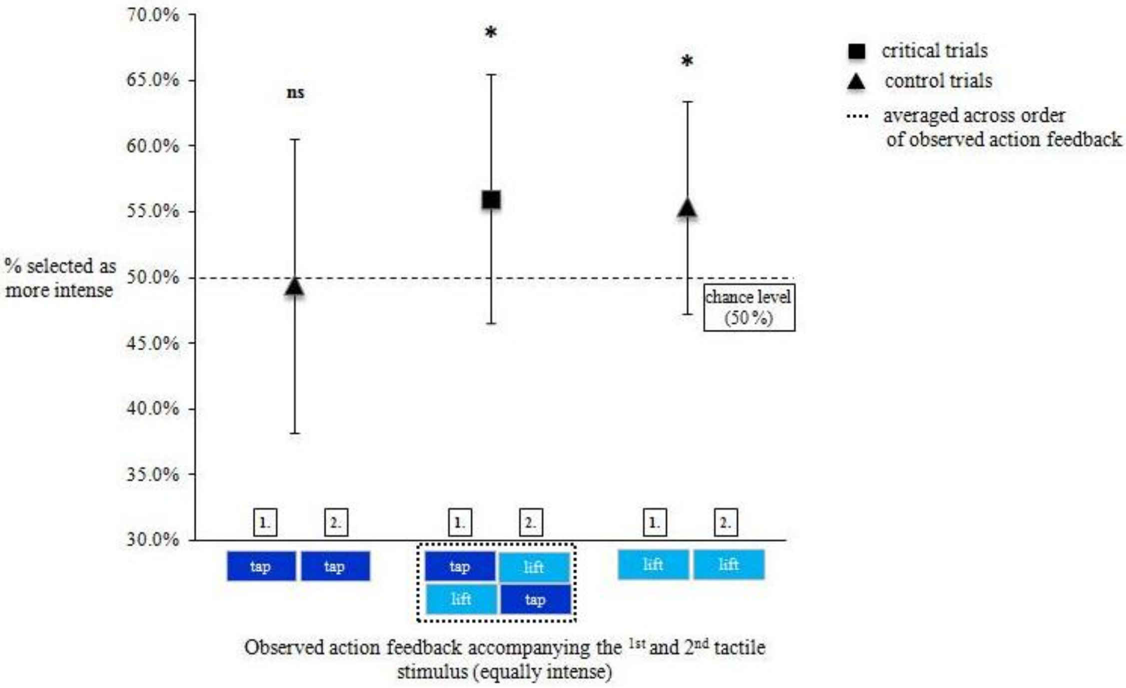

Fig. 4.1.2.b. Proportion of the critical trials on which the tactile stimulus paired with the observation of a lifting rather than a tapping movement was selected as more intense as well as the proportions of both types of control trials on which the second rather than the first tactile stimulus was chosen as more intense while the observed finger movements were the same. Asterisks indicate significant deviations from chance level = 50 %.

4.1.2.4 Discussion

When presented with two successive tactile stimuli of the same physical intensity in a 2AFC direct comparison task, participants in the present study tended to select the stimulus accompanied by the sight of a lifting movement significantly more often as the more intense one than the stimulus accompanied by the sight of a tapping movement. By implication, this meant that the observation of a tapping movement seemed to make a concurrent tactile stimulus appear less intense, corroborating the favoured explanation in Exp. 4.1.1 that sight of a tap impaired participants in discriminating a strong tactile stimulus from a weak one because it was associated with an decrease in perceived tactile stimulus intensity, making strong stimuli perceptually more similar to weak ones. That observing somebody else move their finger in a fashion that resulted in a tactile sensation from contact with a surface modulated the perceived intensity of a tactile stimulus concurrently delivered to participants' corresponding finger as compared to observing a similar movement that did not have such tactile consequence suggest that processing the felt and the observed action-related touch might have interacted during early-stage tactile processing, indicating that shared neural representations for experienced and merely observed touch (e.g. Blakemore et al., 2005; Bufalari et al., 2007; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010) are not only activated by the sight of others' passive tactile sensations but also by the sight of others' action-related tactile experiences (Turella et al., 2012). What was, however, somewhat unexpected was the finding that the aforedescribed visuo-tactile interaction seemed to result in a decrease rather than an increase in perceived tactile stimulus intensity. While intensity-related modulations in tactile processing in the context of observing touch have so far not been directly tested, previous findings seemed to indicate that the sight of (passive) touch "boosts" tactile perception (Schaefer et al., 2005b; Serino et al., 2008b). However, rather than engaging in speculations on why and how observing active touch might have brought about the observed *decrease* in perceived tactile intensity at this stage, it should be noted that some unexpected findings specific to the sight of lifting movements both in the present study and also in Exp. 4.1.1 shed some doubt on the reliability of the supposedly touch observation-related effects revealed in these two studies, considering that observing lifting movements in particular appeared to induce its very own modulations despite being merely intended as a condition that controls for the presence of movement, indicating that lifting movements differ from observing tapping movements in more ways than merely the presence or absence of a tactile component after all. First of all, participants in the present study showed a significant response bias in the control trials in which two effectively equally intense tactile stimuli were accompanied by the sight of a lifting movement. Rather than randomly choosing one of the two stimuli as the more intense one on each trial, given that both the tactile and the visual stimuli were the same, participants opted in a proportion of trials significantly above chance level for the second tactile stimulus as the more intense one. No such response bias was present in the control trials in which both tactile stimuli were paired with the sight of tapping movements. Here, participants performed – as expected – at chance level. While it is unclear why the sight of lifting movements left participants prone to a response bias whereas the sight of tapping movements did not, this dissociation clearly indicates that contrasting tapping and lifting movements in the quest to investigate the effects of observing action-related touch sensations might be confounded with other differences between the two movement types. Also in Exp. 4.1.1, there was some indication that observing lifting rather than tapping movements is somewhat peculiar: For weak stimuli only, it was found that participants were significantly slower in identifying a weak stimulus as "weak" when they concurrently observed a lifting movement rather than a mere colour change of the finger. Observing a tapping movement did not have such an effect. Apart from the fact that a tapping movement includes a tactile sensation from making contact with the table top, it is most importantly the movement direction (up vs. down) that distinguishes tapping and lifting movements. If similar result patterns as those found here and in Exp. 4.1.1. would also occur when presenting the very same lowering and lifting movements with the observed hand not resting on a table top but being held up in empty space so that also the tapping movement would not include a tactile sensation, this would be a clear indication that also the movement direction and not only the presence or absence of a tactile component plays a role in modulating ongoing tactile processing (or in inducing a response bias) when it comes to judging the intensity of concurrently delivered tactile stimuli. It should, however, also be noted that, at least when the observed hand is positioned with the palm facing downwards, lifting a finger up even further from an anyway elevated position might appear more unusual than lowering the finger down from a midair neutral position, yet again irrespective of whether the movement was ultimately associated with a tactile sensation or not. It would therefore be interesting to also test what the outcome of the present study (and Exp. 4.1.2, for that matter) would be if the observed hand was to be shown e.g. with the palm facing upwards: In this position, it would be the lowering of the index finger that is somewhat awkward as compared to lifting it.

All in all, the findings of the present study were somewhat difficult to interpret with respect to the effects of observing touch-related finger movements on tactile processing since observing lifting movements, chosen as an observational control condition in which movement but no tactile event was observed, were associated with an unexpected response bias in the control trials which possibly indicated (along with lift-specific findings in Exp. 4.1.1) that lifting movements might not have been an ideal comparison condition. For this reason, a new sample of participants was asked to perform the very same 2AFC direct intensity comparison task reported here in a new experiment (Exp. 4.1.3) with the tactile stimuli being accompanied by the sight of finger movements that were better controlled with regards to movement direction and how restricted actually performing those movements feels: Again, a model's hand was shown resting on a table top, with the index finger raised in slightly elevated position. Importantly, in both the "touch" and the "no touch"-condition, the index finger was subsequently observed to perform a lowering movement and to then resume in its neutral starting position. In the "touch"-condition, the index finger briefly made contact with a small object place positioned close to the hand when moving downwards while in the "no touch"-condition, the finger merely moved through the empty space next to the object.

Another methodological modification was the use of a smaller tactile stimulator that could be attached directly to participants' finger tip. In both Exp. 4.1.1 and the present study, participants positioned their finger in a relax fashion on top of a wooden block in which the tactile stimulator was embedded. While there were no indications in the results that participants systematically varied the pressure with which they pressed down on the stimulator as a function of the observed finger movements[27], this arrangement was most certainly not ideal.

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[27] The most likely behaviour for participants would be to (unwittingly and subtly) imitate the observed tapping and lifting movements, increasing the pressure on the stimulator during the sight of tapping movements and decreasing it during the sight of lifting movements. The former might have resulted in

Experiment 4.1.3. (Tactile intensity direct comparison task)

4.1.3.1 Introduction

Exp. 4.1.2 found that when having to indicate which one of two successively presented tactile stimuli feels more intense, participants tended to choose the tactile stimulus paired with the sight of a lifting movement rather than a tapping movement. While this response pattern seemed to suggest that, by implication, observing a tapping movement made concurrent tactile stimuli appear less intense, some doubt emerged as to whether touch-unrelated differences between the two types of movements (such as e.g. the movement direction) might have been responsible for the outcome of this comparison. The present study therefore aimed to re-investigate the effect of observing an action-related tactile sensation on paired comparisons of tactile stimulus intensities in the context of two finger movements with the same movement direction and the presence/absence of a tactile sensation during the movement as the only defining difference.

4.1.3.2 Methods

Participants. 20 neurologically normal volunteers, aged between 19 and 38 years (mean age: 24.2 years; SD = 4.7) participated in the experiment (5 males and 15 females). The majority of participants were right-handed, with only two participants being ambidextrous by self-report. All had normal or corrected-to-normal vision. Participants were naive as for the purpose of the study and received either £ 7/h or credits for their participation. The procedures were approved by the local ethics committee.

Stimuli. The task-irrelevant visual stimuli used in the present study were the same as in Exp. 3.2 to 3.5, depicting a left hand as seen from a egocentric first person perspective resting on a table next to a neutral object. The hand was shown in three different postures (see e.g. Fig. 3.2.a in chapter 3): In a neutral position with the index finger slightly elevated from the table top and "hovering" above the object (neutral) and in a lowered position in which the tip of the index finger either touched the corner of the neutral object (touch) or merely the empty space right next to it (no touch).

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tactile stimuli appearing more intense (due to an increased contact with the stimulator) while the latter might have resulted in tactile appearing less intense (due to a decreased contact between the skin and the stimulator). The actual results in the present study suggested, however, the reversed pattern, i.e. tactile stimuli were judged as less intense when accompanied by the sight of tap and more intense when paired with the sight of a lift.

Importantly, tactile stimuli in the present study were presented by means of a tactile stimulator attached directly to participants' finger tip with medical tape to ensure that participants could not (wittingly or unwittingly) increase or decrease the contact between the stimulator and their skin during the experiment. The stimulator was a small purpose-built 12-volt solenoid which drove a plastic rod with a blunt conical tip against the participants' skin whenever a current was passed through it (the same type of stimulator also used in all ERP studies in chapter 2 and 3 of this thesis). A particularity of the used tactile stimulator was that it did not allow to directly manipulate tactile stimulus intensity. Therefore, it was actually the duration of a selected tactile stimulus (a single tap) that was varied in a way that resulted in differences in duration subtle enough to be subjectively perceived as slight differences in tactile intensity rather than stimulus duration. The selected stimulus presentation times were 1, 2 and 3 ms, with 1 ms resulting in a rather soft tactile stimulus, 2 ms resulting in a slightly stronger stimulus and 3 ms resulting in an even stronger tactile stimulus, due to subtle differences in how far the plastic rod could protrude from its casing during these very brief activations of the solenoid.

Procedure. The experimental procedure was the same as in Exp. 4.1.2, with the following modifications: Again, participants were asked to rest their left arm on a table in front of the them such that their hand was in a similar position to the observed hand, i.e. with the inside of the forearm and the palms facing down. The tactually stimulated left index finger was to be kept still in a slightly elevated position, not touching the table top, to ensure that the attached tactile stimulator was not in contact with table top. Since the intensity of the delivered tactile stimuli was manipulated by very subtle changes in stimulus duration (see above), the presentation times in each trial were slightly different from the ones in Exp. 4.1.2: Again, each trial started with a presentation of a hand image with the index finger in a neutral position for 500 ms. Subsequently, the first tactile stimulus was presented for 1-3 ms, accompanied by the presentation of a hand image with the finger lowered either touching the neutral object or the empty space next to it for 200 ms[28]. After showing the index finger back in its neutral position for 550 ms, the second tactile stimulus was presented for 1-3 ms, once more aligned with the onset of a hand image again showing the index either in contact with the surface of the object or not for 200 ms. The presented tactile stimuli were thus much shorter than those in Exp. 4.1.2. while the inter-stimulus interval between the onset of the first tactile stimulus and the onset of

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[28] The actual duration of the presented critical hand images (touch or no touch) was 200 ms in total, made up of 1-3 ms during the presentation of the tactile stimulus and, depending on the duration of the preceding tactile stimulus, another 197-199 ms after the offset of this tactile stimulus. Presenting the index finger either in touch with the object or merely hovering in the empty space next to it for 200 ms followed by an image of the finger in a neutral position created the impression of a quick but realistic-appearing movement.

the second one was the again 750 ms (since the overall presentation times for the visual stimuli were the same as in Exp. 4.1.2). Signalling the end of the trial, the index finger was then depicted back in its neutral position and participants were to indicate which one of the two tactile stimuli had felt more intense, the first or the second one by pressing either “1” or “2” on the keyboard.

The three different types of trials (critical trials, control trials and catch trials) randomly presented in each of four experimental blocks in the present study were the same as in Exp. 4.1.2. Prior to the experiment, participants were also again presented with a short presentation of the involved actions (7 trials in each observational condition) and instructed to imitate the observed movements, i.e. to touch the small box from the images placed on a small piece of cardboard in front of them with their left index finger tip whenever they saw it being touched on the screen. This was to ensure that participants were aware of the difference in tactile consequences associated with the two different observed finger movements, even though no such explanation was provided to them. This was followed by a short practice block (equivalent to an experimental block except for a reduced number of trials) to familiarise participants with the direct comparison task and to establish a reasonably sufficient accuracy on the catch trials (at least 70%).

Data analysis. For the critical trials, the percentage of trials on which participants chose the tactile stimulus as more intense that was accompanied by observing the index finger touch the object was calculated (averaged across trials on which the first or the second tactile stimulus, respectively, was paired with the touch image). For the control trials, the percentage of trials on which the first stimulus was chosen as more intense was computed, separately for control trials on which both tactile stimuli were paired with a touch image and control trials on which both were paired with a no-touch image. One-sample t-tests were conducted to establish whether revealed deviations from the chance level of .5 were significant.

4.1.3.3 Results

On average, participants correctly identified the more intense stimulus in 82.1 % of the catch trials (SD = 8.3 %), confirming that the chosen tactile stimulus intensities were reasonably distinguishable in direct comparison when the associated visual information was kept constant.

On control trials, when both the first and the identical second tactile stimulus were accompanied by the same visual information (either the index finger touching the object or the index finger merely touching the empty space next to it), participants performed at chance level: With 49.9 % on average (SD = 7.3 %) when both stimuli were paired with observing the index finger touch the object, the percentage of trials on which they chose the first tactile stimulus as more intense did not significantly differ from the chance level of 50 % (one-sample t-test; t(19) = -.061; p = .952; d = .014). Similarly, when both stimuli were paired with viewing the finger merely move through empty space, the percentage of trials on which the first stimulus was selected as more intense (M = 50.8 %; SD = 6.5 %) did also not differ from the chance level (t(19)= .516; p = .612; d = .123).

However, when participants were presented with two identical tactile stimuli while one was paired with observing the index finger touch the object and the other one with observing the same finger only touch the empty space next it (critical trials), participants tended to judge the stimulus associated with viewing the touch movement as more intense on 54.5 % of the trials (SD = 4.9 %). This deviation from chance appeared small but nevertheless highly significant (t(19) = 4.067; p = .001; d = .918). Fig. 4.1.3.a shows the mean proportions of critical trials on which stimulus accompanied by the sight of touch was chosen as more intense along with the proportion of control trials (separately for both control conditions) on which the first stimulus was selected as more intense.

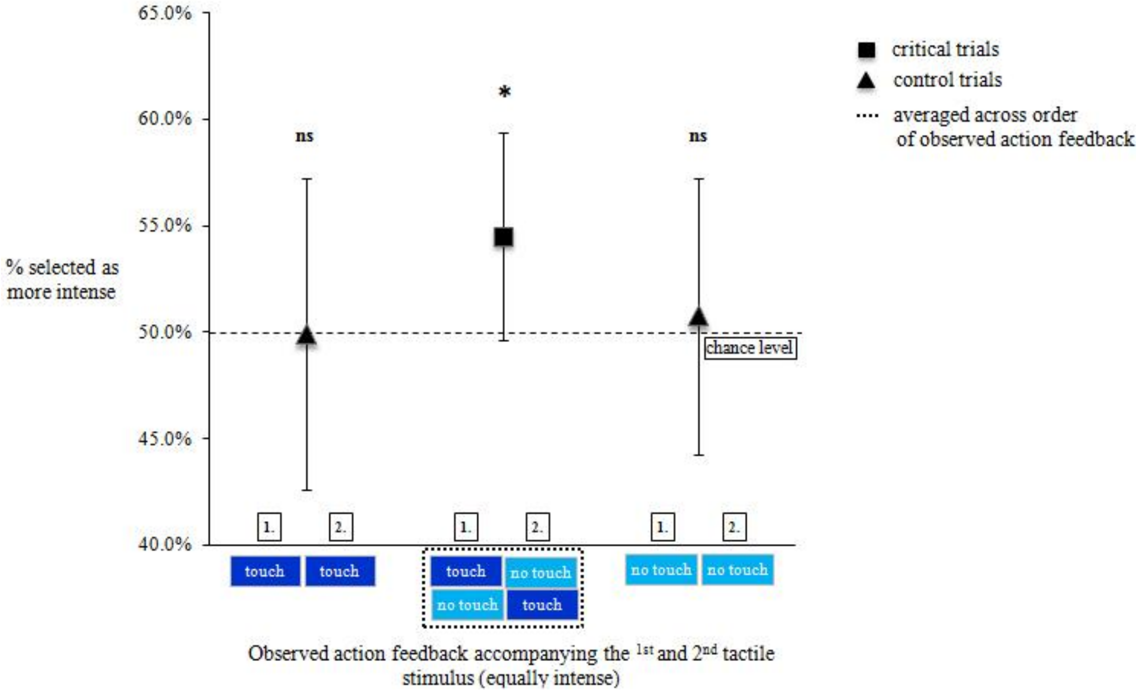

Fig. 4.1.3.a. Proportion of the critical trials on which the tactile stimulus paired with the sight of the observed index finger touch the object rather than the empty space next to it was selected as more intense as well as the proportions of both types of control trials on which the first rather than the second tactile stimulus was chosen as more intense while the observed finger movements were the same. Asterisks indicate significant deviations from chance level = 50 %.

4.1.3.4 Discussion

As in Exp. 4.1.2, participants in the present study were asked to indicate on each trial which one of two consecutively presented tactile stimuli felt more intense. Importantly, the two stimuli were effectively of the same intensity in the critical trials but their onset was accompanied by the sight of somebody else's index finger either touch an object (touch) or merely the empty space next to it (no touch). Interestingly enough, participants tended to systematically select the tactile stimulus paired with the sight of touch as more intense – in marked contrast to Exp. 4.1.2 where the sight of an action-related touch sensation (a tap on the table top) resulted in participants choosing a concurrently delivered tactile stimulus less often as more intense when contrasted with a stimulus that was paired with the sight of a finger movement that did not involve a tactile component (a lift into empty space). Importantly, the intensity-enhancing effect of observing somebody else actively touch an object revealed here appears more reliable, given that the new stimulus material ensured that the two contrasted finger movements did indeed differ only with respect to whether or not they included a tactile component or not, while the tapping and lifting movements observed in Exp. 4.1.2 might not have been sufficiently comparable. What had raised particular concerns about the appropriateness of lifting movements as comparison condition that includes movement but no tactile component in Exp. 4.1.2 was the finding that participants showed an unspecific response bias (that is a significant tendency to select the second tactile stimulus more often as more intense than the first one when a random response pattern was expected) in those control trials in which both tactile stimuli were accompanied by the sight of a lifting movement while no such effect was present in the control trials in which both tactile stimuli were accompanied by the sight of a tapping movement, hinting at the possibility that the lifting movements were perceived differently from the tapping movements and not necessarily so due the presence or absence of a tactile component. In the present study, on the other hand, participants performed – as expected – at chance level in both types of control trials (i.e. *touch – touch* and *no touch – no touch* control trials), corroborating the notion that ensuring that both types of observed movements were more comparable also with respect to e.g. the movement direction allowed to obtain more reliable results in this 2AFC direct comparison task. While it cannot be ruled out entirely, it appears, on the other hand, unlikely that the fact that the presented tactile stimuli in the present study were much shorter than those presented in Exp. 4.1.2 and that participants observed a left rather than a right hand here were responsible for the reversal of the touch observation-related effect on the perceived intensity of the presented tactile stimuli.

The present study might thus, to my knowledge, be the first one that directly demonstrates that the sight of somebody else's (active) touch sensation can modulate the perceived intensity of tactile stimuli to the observer's own body, most likely via the activation of shared neural representation for experienced and merely observed touch (e.g. Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012; 2009). The finding that observing a (action-related) tactile sensation effectively increases the perceived intensity of concurrent tactile stimuli might also explain why seeing a face being touched (rather than being merely approached) reduced the extinction of a weak tactile stimulus in Serino et al. (2008b)'s tactile confrontation task: The perceived intensity of the weak stimulus was enhanced, rendering it less likely to be extinguished by a concurrent strong stimulus.

It is, however, important to note that while paired-comparisons of two stimulus intensities presented within the same trial are generally considered to be less susceptible to a response biases, it can nevertheless not entirely be ruled out that participants' tendency to select the tactile stimuli accompanied by the sight of touch as more intense did not reflect a genuine perceptual enhancement during early-stage sensory processing after all but a response bias during later-stage decisional processing (cf. Odgaard et al., 2003). Participants might simply have tended to judge a stimulus as more intense when they concurrently observed a tap on an object because such a stimulus-response association appeared more logical or compatible to them. Seeing a finger touch an object rather than moving the empty space next to it might also have had an unspecific alerting effect, resulting in participants selecting the tactile stimulus associated with this more salient visual input as the more intense one. Based on the data collected in the present study, neither of these alternative explanations can be entirely dismissed. The results of the tactile detection task reported in chapter 4.1.5 corroborate, however, the interpretation that witnessing somebody else's active touch sensations results indeed in a genuine enhancement in tactile sensitivity in the observer: Statistical analyses of the relevant signal detection theory statistics indicated that the sight of touch (as compared to the sight of no touch) induced a systematic increase in perceptual sensitivity (as indexed by d') while the response bias criterion c remained unchanged.[29]

Before reporting the aforementioned tactile detection task in full detail, another experiment will be described that more directly addressed whether the sight of somebody else touch an object rather than the empty space to next modulates the perceived intensity of concurrent tactile stimuli on the observer's body: Exp. 4.1.4 tested whether a similar touch observation-related enhancement in perceived tactile intensity found in the present study can also be measured when participants are simply asked to judge the subjective intensity of a

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[29] Even so, it should be borne in mind that the mechanisms that underlie a possible response bias of some sort in the context of selecting one of two successively presented supra-thresholds as more intense in the context of a either touch-related or touch-unrelated visual information might differ from those that bring about a possible response bias in a tactile detection task with near-threshold tactile stimuli. The absence of a response bias in Exp. 4.1.5 thus does not necessarily mean that there was also no response bias in the present study.

variety of different tactile stimuli on a rating scale. While such single-stimulus judgements are generally more prone to responses biases (cf. Odgaard et al., 2003), they nevertheless provide an interesting insight into the range of psychophysical tasks in which touch observation-related modulations of tactile perception might be measurable.

Experiment 4.1.4. (Isolated tactile intensity judgment task)

4.1.4.1 Introduction

The present study should be considered a complementary approach to Exp. 4.1.3. in investigating the question of whether observing others' action-related touch sensations enhances the perceived intensity of concurrent tactile stimuli on the observer's body. The experimental procedure was an adaption of Gillmeister and Eimer (2007)'s method used to investigate tactile enhancement of perceived loudness. On each trial, participants were to judge the intensity of an isolated tactile stimulus presented to their left index finger tip by means of an eight-point rating scale. Crucially, the onset of each tactile stimulus was accompanied by task-irrelevant visual stimuli depicting a hand touch either an object or merely the empty space next to it with the index finger. The critical question was whether this type of isolated intensity judgements would also be found to be affected by touch-related visual information, showing systematically higher intensity ratings during the sight of touch as compared to the sight of no touch.

4.1.4.2 Methods

Participants. 22 female participants were recruited for this experiment. The data sets of two of the participants had to be excluded from the analysis: For one participant, the overall pattern of responses suggested that she was not following instructions, judging all presented tactile stimuli as of medium intensity and thus not showing the typical increase in perceived intensity with increasing stimulus intensity. The other participant persistently ignored the instruction to look at the screen and to fixate on the visual stimuli. Thus, 20 participants remained in the sample, ranging in age from 18 to 23 years (M = 19.7 years, SD = 1.6). All but three were right-handed and had normal or corrected-to-normal vision by self-report. All participants were first-year undergraduate psychology students and received course credit in exchange for their participation.

Stimuli. Task-irrelevant visual stimuli were the same colour images as in Exp. 4.1.3., depicting a left hand resting on a table top with the index finger either elevated in a neutral position, lowered and touching a red box or lowered but not touching the box. An orange fixation dot was superimposed slightly below the extended index finger on all images.

In contrast to Exp. 4.1.3, suprathreshold tactile stimuli here were presented by playing a 100 Hz sine wave sound file for a duration of 20 ms through a bone conductor attached to the left index finger (see details in chapter 4.1.5), resulting in a short vibration of the bone conductor against the skin, perceivable as a brief tactile pulse. The sound file was presented at six different volumes (E-Prime controlled; -1500, -1200, -900, -600, -300, 0), resulting in suprathreshold stimuli to the finger tip that ranged in intensity from low to medium to high. Preliminary piloting confirmed that the selected sound volumes yielded a linear increase in judged tactile intensity as a function of the actual intensity on the eight-point intensity judgement scale used in this experiment.

To ensure that participants could not hear the brief buzz of the bone conductor whenever it vibrated, white noise was played through headphones throughout the experiment. A camera positioned right next to the computer screen allowed the experimenter to monitor participants' eye gaze direction to make sure they followed instructions and continuously fixated on the visual stimuli.

Procedure. Participants rested their left arm on a table in front of them, with the palm facing downwards. Their left index finger with the tactile stimulator rested comfortably on a foam cushion to ensure that the bone conductor did come into contact with the table top and participants could relax the stimulated finger. Participants were informed that the visual stimuli present on a computer screen at a distance of approximately 75 cm in front of them were task-irrelevant but that they were nevertheless to fixate on the fixation cross throughout. Each trial began with the presentation of the image showing the index finger in a neutral position for 500 ms (neutral), followed by the image depicting the index finger in a lowered position either touching the box on its left top corner (touch) or merely hovering in the empty space next to the object (no touch) for 200 ms. In synchrony with the onset of this critical visual stimulus, a 20 ms tactile stimulus was presented at one of the six suprathreshold intensities. Subsequently, the visual display showed the hand back in its neutral position and participants were instructed to rate the perceived intensity of the presented tactile stimulus on a scale from 1 to 8. While this task was un-speeded, participants were nevertheless instructed to respond spontaneously and to not think about their rating for too long. Once participants' verbal response was recorded by the experimenter, the next trial started after a random delay of 0-300 ms. Fig. 4.1.4.a shows a schematic representation of the sequence of visual and tactile events in a trial.

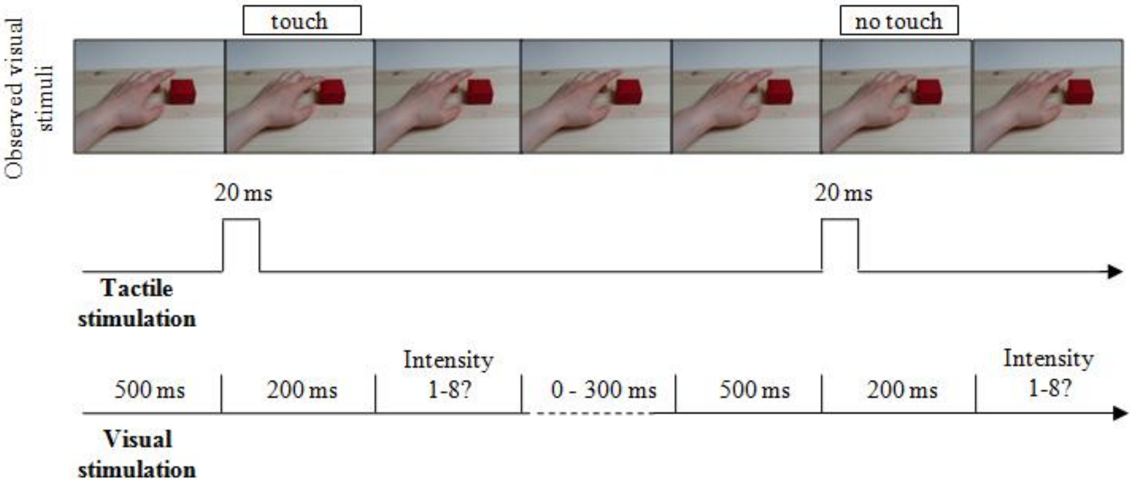


Fig. 4.1.4.a. Schematic representation of the sequence of visual and tactile events in a trial. The critical stimulus image accompanying the onset of the tactile stimulus is depicts the model's index finger either touch the object (touch) or merely the empty space next to it (no touch).

Each of the six tactile stimulus intensities was presented 8 times per block, accompanied by the sight of the index finger touch the object or merely the empty space next to it, respectively, on four trials each. Each block thus contained 48 trials in total, presented in random order. Participants completed six experimental blocks, being reminded at the beginning of each block to make use of the full range of the 8-point scale and to respond spontaneously. At the end of each block, participants were provided with accuracy feedback based on the following criteria: For intensity levels (1) and (2), intensity ratings up to 3 or 4, respectively, were considered a correct response. For intensity level (3), correct responses were 2, 3, 4 and 5, for intensity level (4), correct responses were 3, 4, 5 and 6. For intensity level (5), correct ratings were 4, 5, 6 and 7 and for intensity level (6), correct ratings were 5, 6, 7 and 8. This simplified feedback allowed the experimenter to monitor task performance without drawing participants' attention to the fact that there were actually more increments on the rating scale than there were tactile intensity levels.

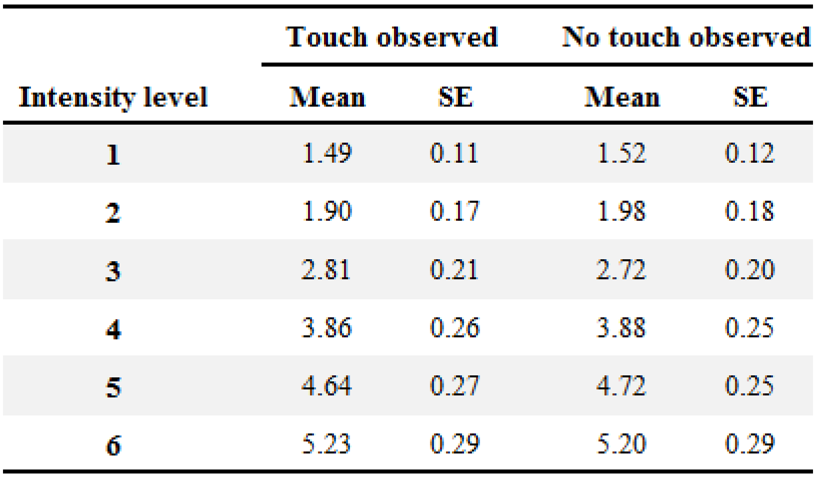
Before the start of the experiment, the visual as well as a selection of the tactile stimuli were demonstrated to the participants. First, participants viewed a short demo of the hand images they would later be observing (7 trials in each observational condition in random order), simultaneously imitating the seen index finger movements by either tapping on a small object positioned in front of them or merely lowering their index finger next to it. This was to ensure that participants were aware of the different tactile consequences associated with the otherwise very similar appearing index finger movements, though no such explanation was given to the participants.

Next, participants were told that they would be presented with a random selection of the diverse tactile stimulus intensities they would be feeling during the subsequent intensity judgment task. Effectively, it was only the intensities (1), (4) and (6) that were presented three times each in random order, followed by a verbal label on the screen identifying the respective stimulus as either a “low”, ”medium” or “high” intensity stimulus. This was followed by a short practice block (equivalent to an experimental block but with only half the number of trials) to familiarise participants with the task at hand. At the end of the practice block as well as at the end of each experimental block, participants were provided with some task performance feedback to allow the experimenter to monitor whether participants were following the task instructions and to keep participants motivated during an ambiguous task.

4.1.4.3 Results

Table 4.1.4.a shows the mean tactile intensity judgments at the six levels of presented tactile stimulus intensity for when participants concurrently observed the model’s index finger either make contact with the object or merely move through empty space.

Table 4.1.4.a. Mean tactile intensity ratings and standard errors for each level of tactile stimulus intensity as a function of the concurrently observed tactile feedback.



	Touch observed		No touch observed	
Intensity level	**Mean**	**SE**	**Mean**	**SE**
1	1.49	0.11	1.52	0.12
2	1.90	0.17	1.98	0.18
3	2.81	0.21	2.72	0.20
4	3.86	0.26	3.88	0.25
5	4.64	0.27	4.72	0.25
6	5.23	0.29	5.20	0.29

Since the distribution of the intensity judgements tended to be positively skewed especially for the lower intensity levels, the rating scores of each participant for each condition were log-transformed to allow parametric analysis. A repeated measures ANOVA compared these log-transformed intensity judgments for two within-subject factors *intensity* (1-6) and *observed tactile feedback* (touch vs. no touch). As expected, there was a main effect of intensity ($F(5,95) = 130.271$, $p < .001$, $\eta^2_p = .873$), confirming that participants distinguished between the different tactile stimulus intensities and rated them differently (for all pairwise comparisons between the different intensity levels, $p < .001$). However, there was no effect at all of the observed tactile feedback on the ratings of perceived tactile intensity ($F(1,19) = .173$, $p = .682$, $\eta^2_p = .009$), not even in an interaction with the presented stimulus intensity ($F(5,95) = .720$, $p = .610$, $\eta^2_p = .037$). As can also be seen in Fig. 4.1.4.b, the (log-transformed) mean intensity ratings did not tend to differ at all as a function of the touch-related visual information, irrespective of the presented intensity levels.

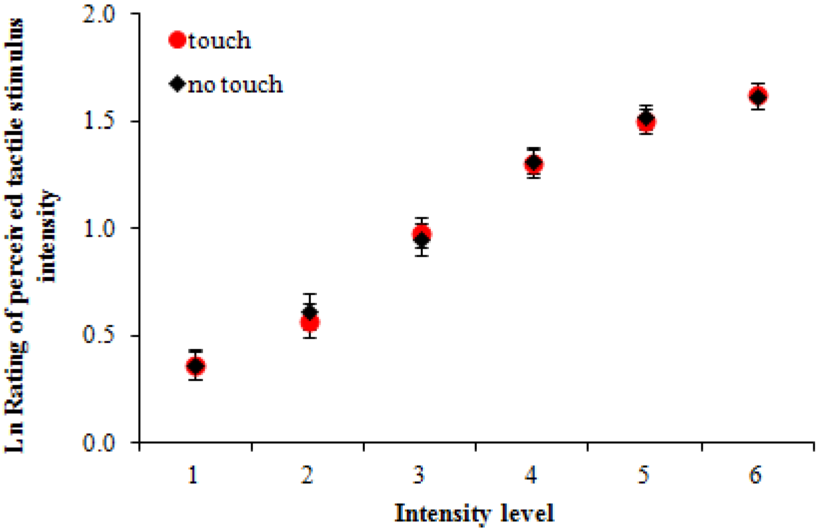


Fig. 4.1.4.b. Log transformed mean intensity ratings for each level of tactile stimulus intensity. Tactile stimuli were either accompanied by the sight of the model's index finger touch the object (red) or by the sight of the model's index finger merely move through the empty space next to the object (black). The vertical bars indicate the standard errors of the respective means.

4.1.4.4 Discussion

Unexpectedly, observing somebody else touch an object rather than the empty space next to it did not result in any systematic changes in the perceived intensity of tactile stimuli delivered to participants' corresponding index finger when participants were asked to rate the intensity of isolated tactile stimuli on a rating scale rather than directly comparing two stimuli within a trial as in Exp. 4.1.3. It can only be speculated why this type of isolated intensity judgement task did not reproduce the intensity-enhancing effect found during touch observation in Exp. 4.1.3. In the latter experiment, participants were required to select, on each trial, one of two successively presented tactile stimuli as more intense, i.e. participants had very restricted response options in the context of a 2AFC response paradigm. Rather than having to make a mere “more or less intense”- decision, participants in the present study, on the other hand, had to judge a presented tactile stimulus in a much more fine-grained fashion, having to select among eight possible responses. This possibly more time-consuming and cognitively more demanding decisional process might have interfered with measuring possibly small touch observation-related intensity modulations. Since the present intensity judgement task was not intended to analyse response latencies, no response times were recorded. In hindsight, it would be interesting to compare trials on which participants were particularly fast in assigning an intensity judgement with those trials in which participants were particularly slow in their decision so see whether the sight of touch might have affected intensity judgements after all as long as participants responded sufficiently spontaneous.

Apart from the aforedescribed differences in the task type, there were also some other factors that might have contributed to the null finding in the present study. Even though one would not necessarily expect the possible intensity-enhancing effect of observing touch to depend on the exact type of concurrently delivered tactile stimuli, it should nevertheless be noted that the bone conductor used for tactile stimulation in the present study produced a somewhat diffuse and fuzzy vibration-like sensation, quite different from the brief taps presented in Exp. 4.1.3 by driving the blunt tip of a plastic rod against participants' skin – and, for that matter, also quite different from the type of tactile sensation associated with briefly touching an object with the finger tip. The unusual nature of these stimuli might have drawn participants' attention somewhat away from the visual display. In addition, despite being repeatedly encouraged to do so, participants did not seem to make use of the full range of the 8-point rating scale – even the strongest intensity level attracted a mean intensity rating of barely above 5 (for both types of concurrently observed tactile feedback). Participants did distinguish between the different intensities as indicated by significant main effect of tactile stimulus intensity, but the range of different intensities nevertheless seemed to appear rather weak to them. While this might have been associated with the aforedescribed diffuse character of the bone conductor-produced tactile stimuli which tended to feel like a vague vibration somewhere close to the finger tip but not directly on the skin, it might also indicate that the selection of intensity levels was not ideal for the purpose of the present study. A larger selection of different intensity levels, including also less ambiguous and more tap-like high-intensity stimuli might have made an outcome similar to Exp. 4.1.3 more likely, primarily by obtaining a more spread range of responses.

All in all, an isolated intensity judgement task that has successfully been used in the past to demonstrate intensity-enhancing effects during cross-modal stimulation (Gillmeister & Eimer, 2007; Odgaard et al., 2003; Stein, London, Wilkinson, & Price, 1996) did not yield any significant changes in perceived tactile intensity in the context of touch-related visual information, in marked contrast to the findings in Exp. 4.1.3. It remains to clarify whether the absence of any systematic shifts in perceived intensity in the present study was due to the different type of intensity judgement task as compared to Exp. 4.1.3. where participants directly compared the intensities of two tactile stimuli within the same trial with very limited response options (2AFC) or whether the particular type of tactile stimuli and the selection of intensity levels in the present study might have played a role, too.

As already mentioned when discussing the intensity-enhancing effect of the sight of other's (active) touch sensation on current tactile stimuli on the observer's body in Exp. 4.1.3., the subsequently reported tactile detection task (Exp. 4.1.5) was found to be another, yet quite different task that allowed to demonstrate the modulatory effect of observing touch-related visual information. If and how the sight of others' touch experiences affects tactile processing in the observer might thus show a certain degree of task-dependence, coming out in some tasks but not in others.

Experiment 4.1.5. (Tactile detection task)

4.1.5.1 Introduction

Exp. 4.1.3 demonstrated that observing somebody else briefly touch an object with the index finger increased the perceived intensity of tactile stimuli presented to the observer's corresponding finger, as compared to observing somebody else perform the same movement without encountering touch from contact with an object. While Exp. 4.1.4 failed to re-produce this effect in the context of isolated intensity judgements, presumably reflecting a certain degree of task-dependence of touch observation-related modulations in tactile processing, the possible intensity-enhancing effect of the sight of others' active touch (see Exp. 4.1.3) raises the interesting question whether observing somebody else actively touch an object (rather than merely approach it) might also facilitate the detection of near-threshold stimuli, crucially, not in the form of a response bias but a genuine shift in perceptual sensitivity. For the sight of passive touch, it has recently been found that repeatedly observing a hand being touched on the index finger did indeed result in a significant decrease in the tactile threshold (Schaefer et al., 2005b) of the corresponding finger as measured by asking participants whether they could detect different von Frey hairs applied to their skin. Apart from the fact that the observation of others' passive and active touch sensation might, however, not necessarily evoke the same modulations in tactile perception (see Exp. 4.2.1), Schaefer et al. (2005b)'s findings have to interpreted with some caution since their study was based on a sample of only five participants and the touch observation-related modulations in tactile sensitivity were measured after (not during) presenting participants with a 15-minute video clip in which a stick was observed to unintermittently touch the depicted hand (with a "no touch"-control condition being presented in a separate 15-minute video clip). That the improvement in tactile threshold was still measurable several minutes after the presentation of the touch-related visual information hints already at how profound the effect of such a continuous exposure to the sight of touch might have been in adapting participants to the percept of touch on a hand. It is thus not only unclear what modulatory effect observing somebody actively touching something rather than being passively touched might have on the observer's sensitivity to weak tactile stimuli but also whether any touch observation-related changes in tactile sensitivity are measurable in the form of rapid sensitivity modulations in short experimental blocks in which touch-related and touch-unrelated visual information is randomly interspersed while participants are simultaneously presented with near-threshold stimuli.

The aim of the present experiment was therefore to test whether the detectability of tactile stimuli is improved by the concurrent sight of somebody else actively touch an object (rather than merely approach it) and whether this reflects an actual enhancement in perceptual sensitivity or merely a visually-induced response bias in the context of a tactile detection task in which the observed tactile feedback and the presence or absence of a weak tactile stimulus was manipulated on a trial-by-trial basis. The experimental procedure as such was an adaption of Lloyd, Mason, Brown and Poliakoff (2008)'s method used to investigate the effects of neutral, non-informative visual stimuli (light flashes) on the perceptibility of near-threshold tactile stimuli. At the end of each trial (rather than at the end of a whole block depicting a hand being either touched or merely approached as in Schaefer et al. (2005)'s study), participants had to indicate whether or not they had felt a tactile stimulus. At the end of the experiment, participants were, in addition, asked to complete a standard empathy questionnaire (EQ; Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) to allow to investigate whether the strength of any touch observation-related modulations in tactile sensitivity might be contingent on participants' individual empathic dispositions.

4.1.5.2 Methods

Participants. 24 participants (12 females and 12 males) were recruited to participate in the experiment. One female participant was excluded because her mean false alarm rate in the two experimental blocks (51.3 %) was at chance level, suggesting that she was not following instructions and merely pressed the response buttons randomly. Another four participants were excluded because their mean detection rate across the two critical blocks was so low (6.3%, 15 %, 17.5% and 25 %) that it had to be assumed that the staircase procedure had failed to establish their tactile 50% threshold reliably.[30] Similarly, the data sets of two participants whose mean hit rate was above 90 % for the two experimental blocks (without unusually high false alarm rates) were removed from the analysis. Thus, N=17 participants (10 females and 7 males) remained in the sample, ranging in age from 19 to 32 years (M = 24.06 years, SD = 4.32). All but one were right-handed and all had normal or corrected-to-normal vision by self-report. All participants gave their written consent after being informed in detail about the nature of the task and the methods involved. Procedures were approved by the Ethics Committee, City University London, and in accordance with the Declaration of Helsinki. Participants were either paid £ 7 per hour or received course credits in exchange for their participation.

Stimuli. The task-irrelevant visual stimuli consisted of the same set of colour images depicting a left hand positioned close to a neutral object superimposed on a black background as in Exp.s 3.2-3.5 as well as Exp.s 4.1.3 and 4.1.4 in the present chapter. The index finger of the observed hand was thus again shown in three different positions: In a neutral position slightly elevated from the table top and hovering over the object (neutral), in a lowered position touching the top left corner of the object (touch) and in a similarly lowered position but not touching the object (no touch). In an additional set of pictures used as task-irrelevant visual stimuli during the adaptive staircase procedure (see below), the neutral object was either shown in its default colour red or tinted in either blue or green while the depicted hand remained in its neutral position (see Fig. 4.1.5.a). An orange fixation cross was superimposed on all images slightly below the elevated index finger. All images subtended" approximately 15° x 11° of visual angle and were presented on a black background.

The task-relevant tactile stimuli were presented by means of a bone conductor (Oticon BC461-1 with a 2 pin non-polarised socket; purchased from www.connevans.co.uk) with a vibrating surface of approximately 16.9 x 24 mm attached to participants' left index finger tip with adhesive tape. The bone conductor was connected to a standard amplifier and briefly vibrated whenever a 100 Hz sine wave sound was played for a duration of 20 ms at an E-Prime-controlled volume (Psychology Software Tools Inc., version 1.1). The exact volume at which the respective sound was presented was adjusted individually for each participant such that the intensity of the perceived tactile pulse resulted in a detection rate of only 50 % (see below).

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[30] This, too, might have been associated with the rather diffuse and unusual tactile sensation produced by the bone conductor (see chapter 4.1.4.4) which might have made it difficult for some participants to stick to a initially adopted response criterion during the staircase procedure. Inconsistent response patterns can, however, lead the staircase procedure algorithm off track, resulting in an inappropriate threshold value. In a replication of this study, it should be ensured that all participants are sufficiently exposed to the unusual sensation of bone conductor-produced tactile stimuli at varying intensities prior to conducting the staircase procedure. In addition, it might be advisable to run several staircases and to average across their final intensity values to obtain a reliable threshold intensity.

Throughout the experiment, white noise was played through headphones to ensure that participants could not hear the brief buzz of the bone conductor whenever it was triggered and to attenuate any other distracting sounds. A camera positioned right next to the computer screen allowed the experimenter to continuously monitor participants' eye gaze direction to make sure they fixated on the visual stimuli as instructed.

Procedure. Participants were seated at distance of approximately 75 cm from the computer monitor where the task-irrelevant visual stimuli were to be presented during the tactile detection task. Both their arms rested on the table in front of them with the palms facing down. A wooden panel covered with black fabric was positioned over participants' hands to ensure that participants could not see them during the subsequent experiment. The bone conductor to present the near-threshold tactile stimuli was attached to the tip of the left index finger, i.e. to the finger tip that anatomically corresponded to the one to subsequently be observed to touch the object on the screen. To ensure that the vibrating bone conductor did not come into contact with the table top at any time during the experiment, participants' stimulated finger was propped up comfortably on a small foam cushion. The index and middle finger of the other hand were resting on the two response keys on a computer keyboard used to collect the responses.

In order to establish the threshold for each participant at which they perceived a weak tactile pulse in approximately 50 % of the trials, an adaptive staircase procedure was run during which the intensity of the presented tactile stimulus was systematically decrease or increased, respectively, based on whether or not participants could detect the presented tactile stimuli. A pre-programmed adaptive staircase procedure routine developed specifically for E-Prime (Hairston & Maldjian, 2008; retrievable from http://fmri.wfubmc.edu/cms/software) was adapted accordingly to adjust the volume with which a 20 ms 100 Hz square wave sound was played through the bone conductor and thus the perceived intensity of the resulting vibratory pulse on the finger tip.

Rather than determining the individual threshold intensities in the absence of any concurrent visual stimuli (see Lloyd et al., 2007), it was deemed more appropriate here to establish the intended low perceptibility stimulus intensities while participants observed the hand which they would later on also see during the actual detection task, especially since non-informative vision of a body part in itself has been found to alter tactile processing (e.g. Harris et al., 2007; Kennett et al., 2001), even if that body part actually belongs to somebody else (Haggard, 2006). To avoid, however, an immediate contamination of the established threshold intensity with the observation of finger movements that crucially either resulted in touch or not, the observed hand remained still throughout the whole staircase procedure. Instead, the neutral object next to the hand randomly changed its colour whenever a tactile stimulus was presented to control for the possible alerting effect of observing a change in the visual stimulus display.

Each trial during the adaptive staircase procedure lasted 1020 ms and started with the presentation of the model's index finger in a neutral position for 500 ms. In "tactile target present"-trials, this was followed by a the presentation of a 20 ms tactile stimulus accompanied by a colour change of the neutral object from red to green or blue which outlasted the tactile stimulus by 180 ms. The object was then depicted in its original colour for another 320 ms after which the fixation cross turned into a question mark that signalled the end of the trial and prompted participants to indicate by means of a key press whether they had felt a tactile stimulus or not. Once a response was given, the next trial started after a random delay between 500 – 700 ms presenting a tactile stimulus at an intensity adaptively adjusted in the way described below. Panel A in Fig. 4.1.5.a shows a schematic representation of the visual and tactile events in a typical trial during the adaptive staircase procedure.

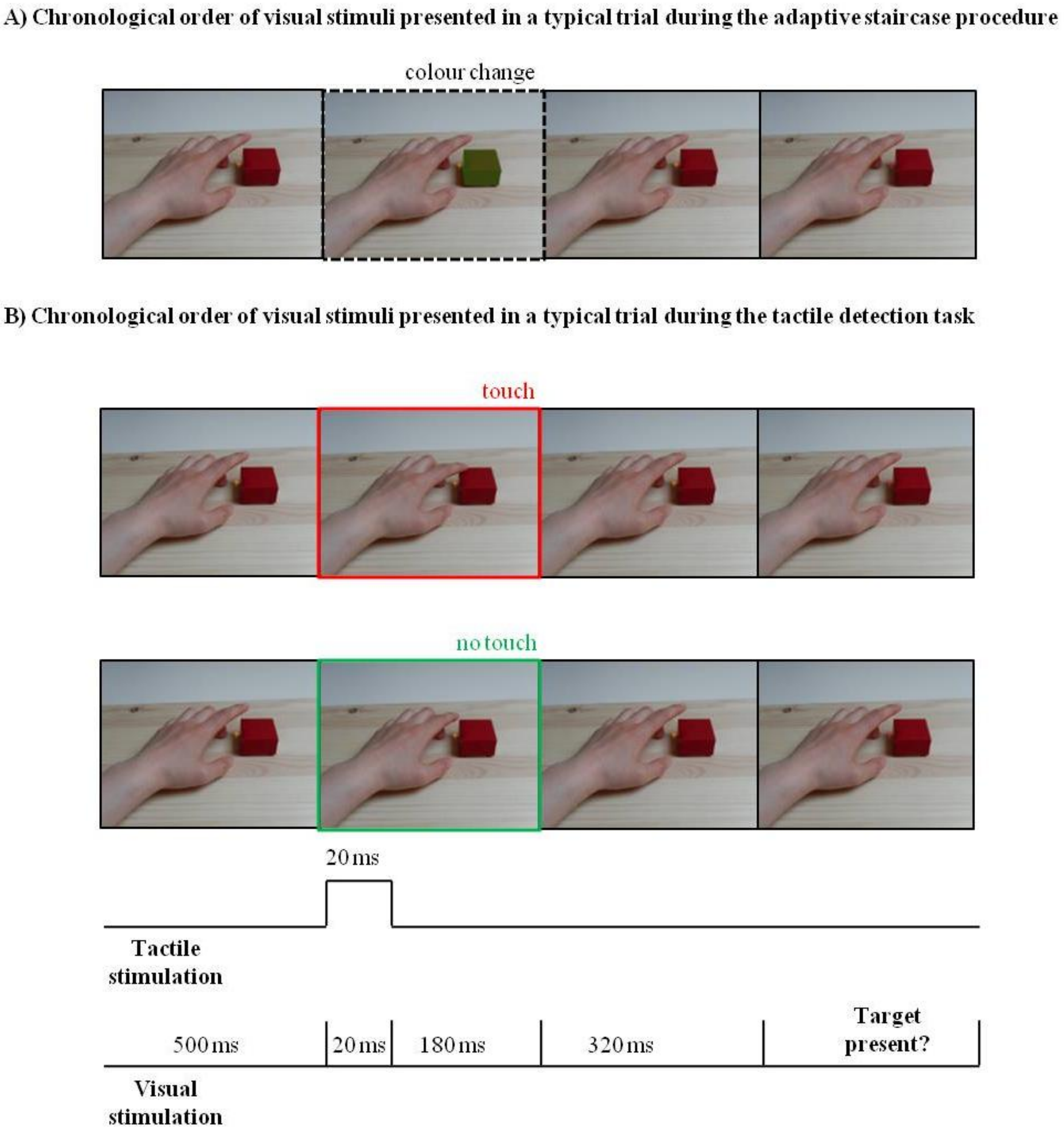

Fig. 4.1.5.a. Schematic representation of the sequence of visual and tactile events in a typical trial during the adaptive staircase procedure (A) and during the tactile detection task (B). The critical visual stimulus accompanying the onset of the tactile target is highlighted with a frame (dashed in black – neutral colour change during staircase procedure; red (touch) and green (no touch), respectively, during the tactile detection task). In "tactile target absent"- trials (not depicted here), the tactile target was replaced by an empty interval of 20 ms.

Participants were instructed to fixate on the fixation cross throughout but that the visual stimuli were otherwise completely task-irrelevant and could be ignored. When prompted at the end of each trial, they were to make a non-speeded forced-choice response, indicating by pressing either "1" or "2" on the keyboard whether they felt a tactile stimulus. The response key assignment was counterbalanced: Half of the participants pressed "1" to respond with "yes" and "2" to respond with "no" while the other half of participants pressed "2" to indicate a "yes" and "1" to indicate a "no".

Starting with a supra-threshold intensity at which most participants could clearly detect the brief tactile pulse to their finger tip (Volume -600 in E-Prime), the 50 % threshold was estimated by means of a simple 1-up/1-down rule (Levitt, 1970). Whenever participants indicated that they could feel a tactile stimulus ("yes"-response), the intensity was decreased by one step. Whenever participants indicated that they could not detect a tactile stimulus ("no"-response), the intensity was increased by one step. The initial step size by which stimulus intensity was adjusted in response to participants' performance was 100 (E-Prime volume unit). After three reversals, the step size was decreased to 50 and after 10 reversals, it was further reduced to 20. After a total number of 14 reversals, the staircase procedure auto-terminated, having converged on perceptual threshold of approximately 50 % detectability. The last two reversal intensity values were averaged and subsequently used as the threshold intensity value.

To verify the determined tactile threshold intensity, participants were subsequently presented with a block of 14 trials: In 10 of these trials, a tactile target was presented with the established threshold intensity. 4 trials did not contain a tactile target. If participants detected less than 40 % or more than 60 % of the targets in this block, the staircase procedure was re-run.

If participants' hit rate was, however, between 40% and 60 %, the actual tactile detection task was begun, replacing the concurrently observed images with the critical ones: Rather than depicting a colour change of the object, the critical image accompanying the onset of the near-threshold tactile stimulus showed the model's index finger touching either the object (touch) or merely the empty space next to it (no touch). After a practice block[31,32], participants performed two experimental blocks of 80 trials: Half of the trials of each block contained a tactile stimulus presented at the intensity level established in the adaptive staircase procedure ("target present"-trials) while the tactile target was replaced by an empty interval of 20 ms in the other half of the

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[31] While the practice block was actually equivalent to a full experimental block, it was not included in the analysis. Apart from the fact that participants were aware that this first block was to be considered practice, it was purposefully introduced to allow participants to get used to the concurrent observation of finger movements which was assumed to be more distracting than the previously observed colour changes of the object when it came to deciding whether an ambiguous near-threshold tactile stimulus was present or not. Though this could not be corroborated statistically (there was no significant interaction between block type and observed tactile feedback with respect to neither hit rates nor false alarm rates; $p > .05$), it nevertheless seemed as if there was a trend for a slightly increased false alarm rate but an unaltered hit rate during the sight of touch in the practice block. For the two experimental blocks, on the other hand, the effect of the observed tactile feedback was, reversed with increased hit rates during the observation of touch and unaffected false alarm rates (see results chapter 4.1.5.3).

[32] There was no main effect of the block type on the mean hit and false alarms (irrespective of the observed tactile feedback) for the practice block and the subsequent two experimental blocks ($\chi2(2) = .030$, $p = .985$ and $\chi2(2) = .520$, $p = .771$, respectively), suggesting that the delay in running the two critical blocks was not associated with a significant shift in the perceptual threshold as when compared to the practice block which was run immediately after establishing the threshold intensity ($M_{\text{practice block}}$ = 55.0 %, SD = 17.2; $M_{\text{block 1}}$ = 53.2 %, SD = 17.6; $M_{\text{block 2}}$ = 55.4 %, SD = 16.8 %).

trials (“tactile target absent”-trials). The onset of the tactile stimulus or the empty interval, respectively, was, in turn, accompanied by the sight of the model’s index finger touch the object on half of trials and by the sight of the model’s index finger merely move through empty space on the other half of the trials. Thus, each of the four conditions was presented 20 times per block in a random order. The timing of the visual and tactile stimuli was exactly the same as described for the adaptive staircase procedure (see Panel B in Fig. 4.1.5.a). No feedback on task performance was given.

Following the tactile detection task, participants completed the 60-item EQ questionnaire (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) which was presented in a computerised form using E-Prime, Version 1.1.

Prior to attaching the bone conductor at the beginning of the experiment, a small piece of cardboard holding the neutral object from the hand images was placed in front of the participants. They were then presented with a short visual demo of the finger movements they would later be observing during the tactile detection task (3 trials in each observational condition in random order) and asked to imitate the observed movements, i.e. to tap on the object with their left index finger tip whenever they saw it being touched on the screen and to merely lower their index finger next to the object whenever they observed the model’s index finger do so. This was to ensure that participants were aware of the different tactile consequences associated with actually performing the to-be-observed movements, though no such explanation was given to the participants.

All in all, the testing session lasted approximately 60 minutes.

Data analysis. For each participant and each observational condition, the number of *hits* (number of trials in which a tactile stimulus was presented and participants correctly said “yes”), *false alarms* (number of trials in which no tactile target was presented but participants erroneously said “yes”), *misses* (number of trials in which a tactile target was presented but participants erroneously “no”) and *correct rejections* (number of trials in which no tactile stimulus was presented and participants correctly responded with “no”) were recorded.

Especially the distribution of the false alarm rates appeared positively skewed since most participants produced only few false alarms. In an attempt to normalise the distributions of the hit and false alarm rates in both observational conditions, the respective proportions of trials were transformed using arcsine transformation of the square root of the proportion obtained in each condition for each participant (see Gillmeister & Eimer, 2007). Kolmogorov-Smirnov tests on the transformed scores, however, still indicated significant violations of normality for the false alarm rates in both observational conditions ($D(18) \leq .273$, $p \leq .037$) which is why possible differences in false alarm as well as detection rates as a function of the observed tactile feedback were analysed non-parametrically using Wilcoxon signed-rank tests on the untransformed scores.

In addition, the signal detection theory statistics d’ and c were calculated for each condition and each participant based on the respective hit and false alarm rates (Stanislaw & Todorov, 1999) with log-linear correction (Hautus, 1995).[33] These estimates of participants’ perceptual sensitivity (d’) as well as their general tendency to report tactile stimuli as present (i.e. response bias or c) were then compared for the two observational conditions by again applying two-tailed Wilcoxon signed-rank tests on the untransformed scores.

Possible relationships between the extent to which any of the computed measures described above were modulated by the observed tactile feedback and participants’ individual empathic dispositions where analysed by calculating the respective differences scores between the two observational conditions and correlating them with the obtained self-report measures of trait empathy using Spearman correlation coefficients.

4.1.5.3 Results

Table 4.1.5.a shows the obtained mean hit rates and false alarm rates in the tactile detection task as well as the computed signal detection theory statistics d’ and c for when the model’s index finger was observed to touch the object and for when it is observed to merely move through the empty space next to the object.

Combining the data from the two experimental blocks, it was found that the observation of touch significantly increased the detection rate in signal trials by 8.7 % as compared to the observation of no touch ($z = -3.136$, $p = .002$, $r = -.538$). The false alarm rate, on the other hand, remained unaffected by observed tactile feedback ($z = -.688$, $p = .491$, $r = -.118$), suggesting that the improved detection rates during the sight of touch did not merely reflect a response bias for reporting tactile stimuli whenever touch was seen.

The analysis of the signal detection theory measures corroborated this: Perceptual sensitivity for the tactile stimuli as indexed by d’ was found to be systematically enhanced when the threshold tactile stimuli were presented while participants viewed the model’s hand touch

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[33] The calculation of d’ and c both rely on the computation of the inverse-normal transform (Φ^{-1}) of the hit and false alarm rate in a given condition. Extreme proportions such as hit rate of 1 or a false alarm rate of 0, however, result in an inverse-normal transform with an infinite value and therefore have to be corrected. Rather than replacing such extreme proportions with a corrected value, the loglinear correction (see Hautus, 1995) is applied to all proportions irrespective of their extremeness: For each participant and each condition, 0.5 is added to the total number of hits in “target present”-trials and the total number of false alarms in “target absent”-trials. The total number of “target present”-trials and “target absent”-trials, respectively, is increased by 1 and used to determine the corrected hit and false alarm rates.

the object rather than the empty space next to it (z = -2.557, p = .011, r = -.439). The response criterion c – an estimate of how readily participants report the presence of a (tactile) target irrespective of whether or not a stimulus was actually delivered – did not shift as a function of the observed tactile feedback (z = - 1.633, p = .102, r = -.280), indicating yet again that the concurrent sight of somebody else's tactile sensations enhanced early sensory processing in the observer rather than inducing a response bias.

Table 4.1.5.a. Mean hit and false alarm rates as well as mean perceptual sensitivity index (d') and decision criterion index (c) for the sight of the observed index finger touch the object (touch) or merely move through the empty space next to object (no touch), separately for the two experimental blocks and averaged across both of them.

		% Hits		% False alarms		d'		c	
Block 1									
	Touch	58.2%	(17.3%)	7.9%	(12.0%)	1.73	(0.87)	0.64	(0.31)
	no touch	48.2%	(20.1%)	9.7%	(9.6%)	1.28	(0.82)	0.69	(0.31)
Block 2									
	Touch	59.1%	(19.2%)	9.1%	(11.4%)	1.64	(0.93)	0.58	(0.25)
	no touch	51.8%	(16.0%)	7.6%	(7.9%)	1.48	(0.66)	0.70	(0.29)
Overall									
	Touch	58.7%	(15.1%)	8.5%	(10.3%)	1.68	(0.83)	0.61	(0.22)
	no touch	50.0%	(13.4%)	8.7%	(8.1%)	1.38	(0.61)	0.69	(0.25)

There were no significant main effects of *block type* or any significant interactions between *block type* and the concurrently *observed tactile feedback* for any of the displayed measures (all p > .143).[34]

Table 4.1.5.b summarises the self-report measures of trait empathy obtained for this sample (N=17) by means of the EQ questionnaire (Baron-Cohen & Wheelwright, 2004; Lawrence et al., 2004) administered after the tactile detection task.

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[34] Despite the violation of the normality assumption indicated for some of the measures, the question whether there might be main effects and/or, more importantly, interaction effects involving the block type, had to be analysed parametrically using a 2 x 2 repeated measures ANOVA with the within-subject factors *block type* (1 versus 2) and *observed tactile feedback* (touch vs. no touch) since non-parametric ANOVAs are restricted to univariate analyses and thus do not allow to test for interactions between two or more factors.

Table 4.1.5.b. Mean scores and standard deviations for the self-report measures of dispositional empathy (EQ; Baron-Cohen et al. 2004).

	Empathy Quotient (EQ)			
	Total	CE	ER	SS
Sample (N=17)	48.06	14.94	13.71	6.29
	(12.25)	*(4.18)*	*(4.30)*	*(2.54)*
Normative data[a]	46.20	n/a	n/a	n/a
	(10.60)	n/a	n/a	n/a

[a)] Normative data are derived from Lawrence et al. 2004.

EQ: CE = Cognitive empathy ER = Emotional reactivity SS = Social skills

Maximal scores: Total score of EQ = 80; Cognitive empathy = 22, Emotional reactivity = 22, Social skills = 12;

Neither the systematic deviation in detection rates nor the revealed significant shift in perceptual sensitivity during the sight of touch correlated significantly with any of the empathy-related measures ($p \geq .062$ for all $r_s(17)$). The level of individuals' empathic skills was therefore not predictive of how strongly the sight of others' touch experiences modulated sensory processing of concurrent tactile stimuli to their own finger, neither for cognitive nor for as affective components of empathy.

4.1.5.4 Discussion

In the present study, participants were found to detect significantly more near-threshold tactile stimuli when the onset of such low-perceptibility stimuli was accompanied by the sight of a finger movement that involved touching an object as compared to the sight of the same finger movement that involved no such contact with the object. Importantly, this effect was not merely due to participants generally reporting feeling a tactile stimulus more readily when having concurrently observed a touch-related movement since the false alarm rate remained unaffected by the type of observed tactile feedback. The analysis of the signal detection theory statistics further corroborated that the increased detection performance reflected a genuine touch observation-related improvement in tactile sensitivity rather than a response bias: While d' – as an index of perceptual sensitivity – was found to be significantly enhanced when the observed finger actually touched the object as compared merely moving through the empty space next to it, the response criterion c – indexing participants' tendency to report a tactile stimulus as present when there was actually no tactile stimulation – was not significantly different for the sight of touch and no touch on the object. The present study thus extends previous findings on improvements in tactile sensitivity in the context of observing somebody else being passively touch on the hand (Schaefer et al., 2005b) to also the sight of others' *action-related* touch sensations, demonstrating at the same time that such touch observation-related modulations in tactile sensitivity can be measured when rapidly manipulating the type of observed tactile feedback on a trial-by-trial basis. In addition, the boosting effect of observing others' touch sensations (here from touching an object) on concurrent tactile processing further corroborates at a behavioural level the notion that actually experiencing touch on one's own body and merely observing it in others recruits (in parts) the same neural networks (e.g. Blakemore et al., 2005; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012; 2009), resulting in measurable modulations when both occurs at the same time. Interestingly enough, Lloyd et al. (2008) found that the presence of a task-irrelevant light, too, resulted in a significant increase in the number of detected near-threshold stimuli. In marked contrast to the present study, this enhanced detection rate was, however, revealed to be the consequence of a response bias (Lloyd et al., 2008), that is participants were simply more inclined to report tactile stimuli whenever they saw a light. In the present study, on the other hand, the improved detectability of weak tactile stimuli was associated with a genuine increase in perceptual sensitivity, highlighting the differential effects of touch (and body-)-related visual information as compared to neutral, modality-unspecific visual input (a "disembodied" light) during visuotactile integration.

What could not be established in the present study was a link between the strength of the touch observation-related shift in tactile sensitivity and interindividual differences in trait empathy. Neither measures of cognitive nor of affective components of empathy were found to be predictive of how strongly the sight of touch modulated the detection rates or d' in individual participants. While this might indicate that it more difficult to reveal a relationship between touch observation-related modulations in tactile processing and empathic skills at a behavioural level, possibly also contingent on the type of tactile task, it should also be taken into account that the present study might have lacked the power to detect possible subtle individual variations in the extent to which perceptual sensitivity shifted in response to the sight of touch due a relatively small sample size.

All in all, the present study demonstrated that observing touch-related visual information (observing somebody else's finger touch an object rather than the empty space next to it) genuinely enhanced tactile sensitivity in the observer instead of merely inducing a response bias. Such a modulatory effect of the sight of touch on tactile perception further corroborates the notion of shared neural representations for felt and merely observed touch.

4.2 Behavioural effects of observing others' passive touch sensations

Behavioural effects of observing others' passive touch sensations on tactile processing in the observer

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Experiment 4.2.1. (Tactile intensity discrimination task)

4.2.1.1 Introduction

So far, this chapter on the possible effects of the sight of touch on concurrent tactile processing has exclusively dealt with experiments that explored modulations in tactile perception in the context of observing others' *action-related* touch sensations (Exp.s 4.1.1-4.1.5) since this had not been investigated at all before: Both the confrontation task pioneered by Serino et al. (2008b) as well as the tactile threshold approach by Schaefer et al. (2005b) had focused on the modulatory effect of observing somebody else being passively touched rather than actively touch e.g. an object. A series of behavioural studies with different tactile tasks thus aimed to shed more light on others' touch sensations in the context of their movements and actions, probing whether it is possible to isolate the tactile component from the movement component which in itself has been found to induce modulations in somatosensory processing, at least at a neural level (Avikainen et al., 2002; Rossi et al., 2002; Voisin et al., 2011b). Ultimately, it is, however, also the effects of observing others' being passively touched on tactile processing (at a behavioural level) that are not very well understood, having so far only been investigated with the two aforementioned paradigms (Schaefer et al., 2005b; Serino et al., 2008b) that were quite different in their methodological approach. Exp. 4.2.1 thus aimed to explore the modulatory effect of the sight of others *passive* touch sensations on tactile processing in the observer with the 2-AFC direct intensity comparison task with which it had been successfully demonstrated in Exp. 4.1.3 that observing others' *haptic* touch sensations increases the perceived intensity of concurrent tactile stimuli. Again, participants were to select one of two successively presented tactile stimuli as more intense while they observed a cotton bud either touch a model's hand on the index finger or merely the empty space next to it. In an additional condition, participants observed the same cotton bud either touch or merely approach a wooden box to test the degree of body specificity of any touch observation-related modulations in task performance. At a neural level, it has previously been demonstrated that the sight of touch might actually activate the observer's somatosensory system irrespective of whether a human body or an inanimate object is seen to be touched (Ebisch et al., 2008; Keysers et al., 2004; Exp. 2.1 of this thesis; see, however, Blakemore et al., 2005). At a behavioural level, on the other hand, the sight of an inanimate object being touched was previously found to have no effect at all (Cardini et al., 2011) or a reversed effect (as compared to the sight of touch on a human face; Serino et al., 2008b) on tactile processing as indexed by a tactile confrontation task (see footnote 22). It was therefore not only of great interest if and how observing a cotton bud touch a human hand might modulate participants' intensity judgements in the context of paired intensity comparisons but also if the sight of touch on an inanimate object would have a similar effect, a qualitatively different effect or no effect at all.

4.2.1.2 Methods

Participants. 21 neurologically normal volunteers were recruited for this study. One participant was excluded from the analysis because his overall discrimination accuracy on the catch trials was only 56.5 %, possibly indicating that he did not pay sufficient attention to the task. Thus, 20 participants remained in the sample (10 females and 10 males), aged between 18 and 39 years (M = 25.8 years, SD = 6.7). All were right-handed and had normal or corrected-to-normal vision by self-report. Participants were naive as for the purpose of the study and received either the standard rate of £ 7 per hour or course credits for their participation. The procedures were approved by the local ethics committee.

Stimuli. The task-irrelevant visual stimuli comprised the same set of colour images of a left hand and a wooden box, respectively, being touched or merely approached by a cotton bud as used in Exp. 2.1. Superimposed on a blue background, the cotton bud was shown in three different position: In an neutral starting position to the right of the touch target ("neutral"), in a transitory position halfway between its starting and its subsequent end position ("approach") and finally in a position in which it either made contact with the touch target ("touch") or merely hovered in the empty space next to it ("no touch"). A green fixation cross was superimposed on all images, equidistant from the end position of the cotton bud in both observational conditions.

The tactile stimuli whose intensities participants were to compare were presented in the same way as described for Exp. 4.1.3, again achieving three different intensity levels by very subtly manipulating the tactile stimulus duration. To mask any sounds produced by the tactile stimulator attached to participants left index finger whenever it was triggered, white noise was played through loudspeakers throughout the experiment. The presentation of both the visual and the tactile stimuli was controlled by E-Prime (Psychology Software Tools Inc., version 1.1).

Procedure. The experimental procedure and instructions to participants were the same as in Exp. 4.1.3 (and Exp. 4.1.2), with the following modifications: To match the posture of the observed hand, participants were asked to rest their left arm comfortably on a table in front of the them, with their forearm slightly turned inwards toward the midline and their palms facing towards participants' body. In addition, the sequence of the visual stimuli on each trial had to be modified to ensure the perception of a smooth movement of the cotton bud towards and away from the touch target: Each trial started with a presentation of the touch target (hand vs. object) with the cotton bud in a neutral position for 500 ms which was followed by a brief 20 ms presentation of an image showing the cotton bud halfway between its initial and its final position on or next to the touch target, which was subsequently shown for a total of 200 ms (see Fig. 4.2.1.a). As in Exp. 4.1.3, the onset of this latter, critical stimulus image (touch or no touch) was simultaneous with the presentation of the first tactile stimulus for 1-3 ms. After the offset of the critical stimulus image, the cotton bud was once more shown first in its slightly retracted position for 20 ms and then back in its neutral position for 550 ms. Subsequently, the cotton bud was again depicted approaching the touch target (20 m s) and eventually either touching it or merely the empty space next to it (200 ms). The onset of the critical stimulus image was accompanied by the presentation of the second tactile stimulus for 1-3 ms. The inter-stimulus interval between the onset of the first and the onset of the second tactile stimulus was thus 790 ms, i.e. 40 ms longer than in Exp. 4.1.3, due to the insertion of two additional image showing the approaching cotton bud halfway between its neutral position and the touch target. After briefly showing the cotton bud retracted from the touch target for 20 ms, the end of the trial was signalled by depicting the cotton bud back in its neutral position. Spontaneously and without too much reflection, participants were then to indicate which one of the two tactile stimuli had felt more intense, the first one or the second one. There was no time limit for responses and the next trial was started once participants had indicated their choice by pressing either "1" or "2" on the keyboard.

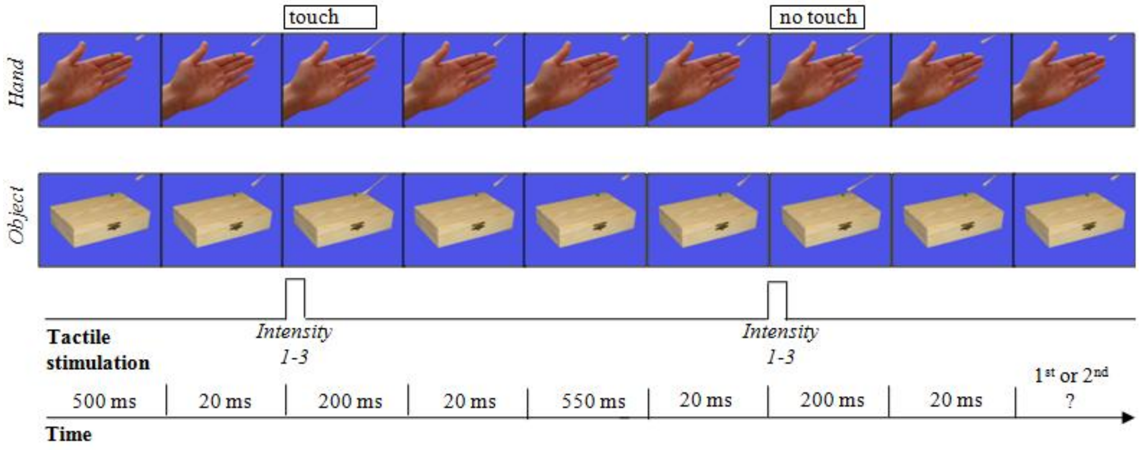

Fig. 4.2.1.a. Schematic representation of the sequence of (visual and tactile) events in a typical critical trial. In *critical trials*, the intensity of the two consecutive tactile stimuli was identical, one tactile stimulus being accompanied by the sight of the cotton bud touch the touch target touch) and the other one being accompanied by the sight of the cotton bud merely touch the

empty space next to the touch target (no touch).In *control trials*, both tactile stimuli were equally intense and accompanied by the same hand images (e.g. *touch – touch* or *no touch – no touch*). Only in *catch trials*, the tactile stimuli indeed differed in intensity, again paired with the same hand image repeated twice.

The three different types of trials (critical trials, control trials and catch trials) randomly presented in each block as well as the number of each trial type per block were the same as in Exp. 4.1.3. The order in which participants observed the two different touch targets for four consecutive blocks during the comparison task was counterbalanced: 50 % of the participants were presented with the hand images first, 50 % of the participants were presented with the object images first.

Prior to the experiment, participants were presented with a short presentation of the visual stimuli they would be observing later on (3 trials in each observational condition in random order, separately for both touch targets). The experimenter then gently touched participants' left index finger tip twice with a cotton bud. This was to casually remind participants of the tactile sensation associated with being touched with cotton bud, though no such explanation was provided to them. Subsequently, participants performed a practice block (equivalent to an experimental block with the same number of trials) to familiarise them with the direct comparison task and to establish a reasonably sufficient accuracy on the catch trials (at least 70%).

Data analysis. For the critical trials, the percentage of trials on which participants chose the tactile stimulus as more intense that was accompanied by observing the cotton bud make contact with the touch target was calculated (averaged across trials on which the first or the second tactile stimulus, respectively, was paired with the touch image), separately for the two touch targets. For the control trials, the percentage of trials on which the first stimulus was chosen as more intense was computed, separately for control trials on which both tactile stimuli were paired with a touch image and control trials on which both were paired with a no-touch image. One-sample t-tests were conducted to establish whether revealed deviations from the chance level of .5 were significant.

4.2.1.3 Results

On the catch trials where the two tactile stimuli did differ in their intensities while the visual stimuli were the same, participants correctly identified the more intense stimulus on 85.20 % (SD = 6.49 %) of the trials when they observed a hand being touched or merely approached and on 83.40 % (SD = 6.95 %) of the trials when they observed an object. The slight difference in discrimination accuracy as a function of the observed touch target was not significant (t(19) = .832, p = .461; r = .187).

On the critical trials, the two subsequently presented tactile stimuli were paired with the sight of the cotton bud either touch the model’s hand or merely approach it. The type of observed tactile feedback had, however, no effect on how participants judged the perceived intensity of the tactile stimuli: The proportion of critical trials on which participants selected the tactile stimulus accompanied by the observation of touch on the model’s hand as more intense did not differ significantly from chance (M = 50.83 %, SD = 4.62 %; t(19) = .798, p = .435, d = .180). Also the sight of an object being touched rather than merely approached did not affect the perceived intensity to the simultaneously presented tactile stimuli: Again, participants performed at chance level and did not show any tendency to select those touch stimuli as more intense that were accompanied by the sight of touch on the object (M = 51.30 %, SD = 3.46 %; t(19) = 1.681, p = .109, d = .376).

For both touch targets, the control trials in which both the tactile stimulus intensity and the touch-related visual stimuli were the same did not show a significant response bias for systematically selecting either the first or the second tactile stimulus above chance as the more intense one: Irrespective of whether the control trials showed two touch stimuli (*touch – touch*) or two no touch stimuli (*no touch – no touch*), participants guessed and randomly picked one of the two tactile stimuli as the more intense one (hand: t(19) ≤ 1.423, p ≥ .171; object: t(19) ≤ 1.190, p ≥ .249). Fig. 4.1.2.b shows the non-significant deviations from chance level for the critical as well as the two types of control trials, separately for the two touch targets.

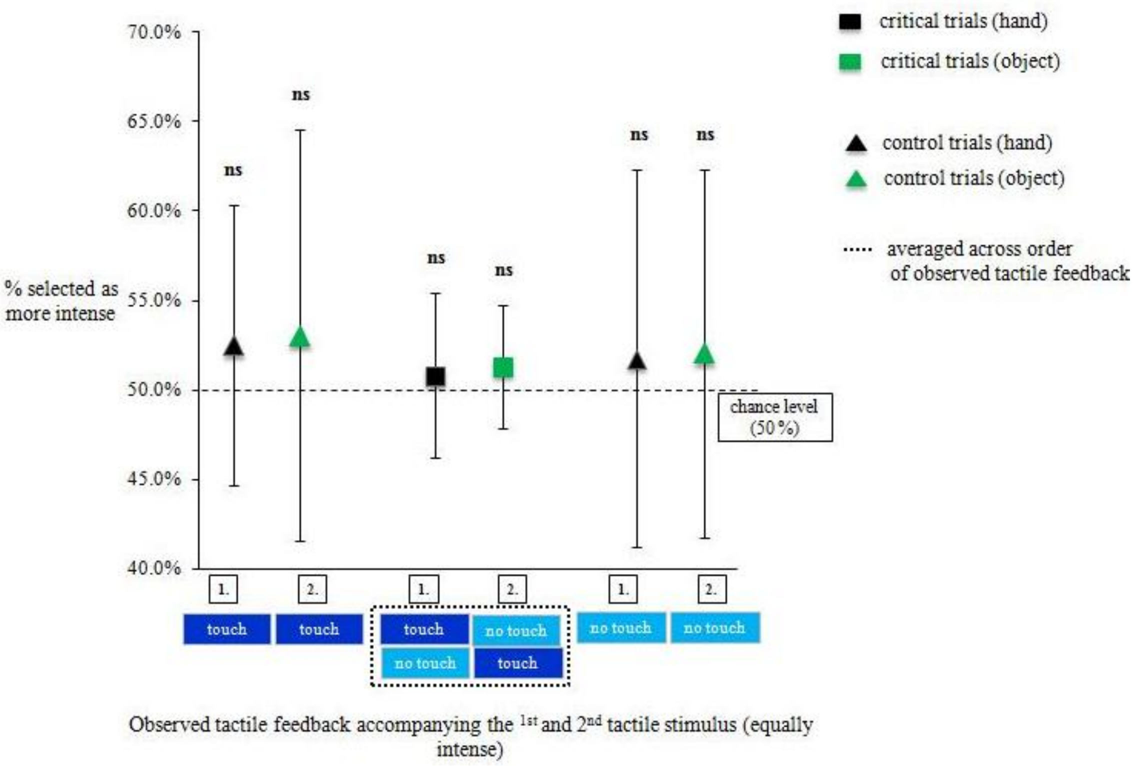

Fig. 4.2.1.b. Proportion of the critical trials on which the tactile stimulus paired with the observation of the cotton bud touch the hand/object rather than merely approach it was selected as more intense as well as the proportions of both types of control trials on which the second rather than the first tactile stimulus was chosen as more intense while the observed tactile feedback was the same.

While the statistical analyses indicated no significant deviations from chance performance in the control trials for both touch targets, visual inspection of Fig. 4.2.1.b nevertheless suggested that there might have been an ever so slight tendency to more often select the second tactile stimulus as the more intense one. To check whether such a response bias might have affected the random response pattern in the critical trials, the proportion of critical trials on which the tactile stimulus as paired with the sight of touch was re-analysed separately for the two different visual stimulus presentation orders (*touch – no touch* vs. *no touch – touch*) for both touch targets. As can be seen in Fig. 4.2.1.c, the response tendencies appeared reversed for the two subtypes of critical trials and pointed to a response bias such that participants seemed to select the second tactile stimulus as the more intense one more frequently than the first one, irrespective of whether this second stimulus was paired with the sight of touch or the sight of no touch on the touch target.

For the critical trials on which the second stimulus was paired with the observation of the cotton bud touch the touch target while the first one was paired with the observation of the cotton bud merely touch the empty space next to the touch target (*no touch – touch*), it was indeed the tactile stimulus accompanied by the sight of touch, i.e. the second one, that was more frequently selected as more intense: For both touch targets, the proportion of trials on which this second tactile stimulus was selected deviated significantly from chance (hand: M = 55.25, SD = 8.51 %; t(19) = 2.759, p = .012, d = 620; object: M = 55.80, SD = 9.40 %; t(19) = 2.761, p = .012, d = .617).

Re-analysing the critical trials on which the order of visual stimuli was reversed and the first tactile stimulus was accompanied by the sight of touch while the second one was accompanied by the sight of no touch, however, indicated that this deviation from chance did not actually reflect a touch observation-related change in perceived intensity of the second stimulus but was more likely the result of a vision-independent response bias for the second tactile stimulus: Irrespective of the fact that the second tactile stimulus was paired with the sight of no touch rather than touch in this subset of critical trials, participants yet again showed a (if non-significant) tendency to choose the second stimulus as the more intense one (hand: M = 53.60, SD = 9.25 %; t(19) = 1.740, p = .098, d = .389; object: M = 53.20, SD = 9.88 %; t(19) = 1.449, p = .164, d = .324).

Fig. 4.2.1.c shows how this response bias resulted in a below-chance portion of the "*touch – no touch*"- trials on which the first tactile stimulus was selected as more intense and an above-chance proportion of "*no touch – touch"*- trials on which the second tactile stimulus was chosen as more intense. Averaging across the two subtypes of critical trials for the main analysis thus resulted in a complete null effect for the observed tactile feedback on the perceived intensity of concurrent tactile stimuli.

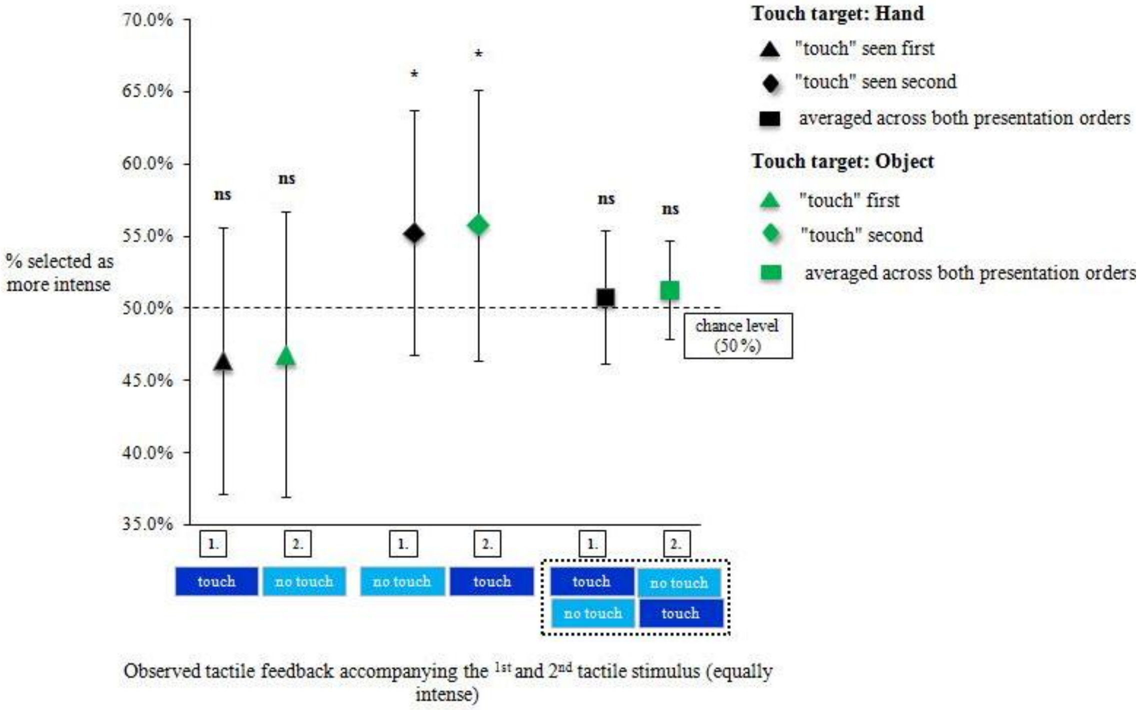

Fig. 4.2.1.c. Proportion of the critical trials on which the tactile stimulus paired with the observation of the cotton bud touch rather than merely approach the hand/object was selected as more intense separately for the two different presentation orders of the observed tactile feedback as well as collapsed across them. Asterisks indicate significant deviations from chance level = 50 %.

Interestingly, this strong response bias in the critical trials seemed to be specific for this 2AFC direct comparison task in the context of observing passive touch on a hand or an object, respectively. Here, the general tendency to select the second stimulus as more intensive irrespective of the concurrent passive touch-related visual information led to a significant deviation from chance level when collapsing across the two types of critical trials (i.e. *touch* - *no touch* and *no touch* - *touch*) (hand: M = 54.43, SD = 7.59 %; t(19) = 2.607, p = .017, d = .584; object: M = 54.50, SD = 9.00 %; t(19) = 2.237, p = .037, d = .500). For experiments 4.1.2 and 4.1.3. where the 2AFC direct comparison task was performed in the context of observing active touch, no such general preference for the second tactile stimulus was found across the critical trials (Exp 4.1.2: M = 51.94 %, SD = 6.08 %; t(19) = 1.424, p = .171, d = .319; Exp 4.1.3: M = 51.62 %, SD = 6.16 %; t(19) = 1.181, p = .252, d = .263). It should also be noted that the strong response bias in the critical trials is unlikely to be the result of extremely biased response patterns of a few specific participants. The proportions of critical trials on which participants selected the second tactile stimulus as the more intense one were all within +/- two standard deviations (39.27 % - 69.93 %) from the mean for all N=20 participants, indicating that there were no outliers that might have unduly biased the outcome of the statistical analyses.

4.2.1.4 Discussion

The present study aimed to investigate whether the sight of passive touch on somebody else's hand is associated with a similar intensity-enhancing effect on tactile stimuli concurrently presented to participants' own hand as was the sight of somebody else's hand actively touch an object in Exp. 4.1.3. It was also to be tested whether the sight of touch on an inanimate object, too, would modulate tactile perception in such a way. Given that observing passive tactile sensations does not involve the sight of body movements which in itself can modulate somatosensory processing (Avikainen et al., 2002; Rossi et al., 2002; Voisin et al., 2011b), it was assumed that associated touch observation-related modulatory effects on tactile perception might even be easier to detect and/or be more pronounced in the absence of concurrent movement observation-related changes in tactile processing.

Somewhat unexpectedly, it was, however, found that observing others' passive (rather than active) touch sensations did have no effect at all on participants' intensity comparisons: Entirely unaffected by the presence of touch-related visual information, participants appeared to randomly select one of the two successively presented tactile stimuli as the more intense one on each trial, which rendered the overall proportion of trials on which participants chose the stimulus accompanied by the sight of the cotton bud actually touch the model's hand over the stimulus paired with the sight of the cotton bud merely touch the empty space next to the hand not significantly different from chance level. The same unselective response pattern was also observed during the sight of touch on an inanimate object. Interestingly enough, it was found that participants in the present study showed a strong response bias in the critical trials which ultimately resulted in the seemingly random response pattern when averaging across both types of critical trials: Irrespective of whether participants were presented with a "*touch – no touch"* or a "*no touch – touch*" critical trial, they preferentially selected the second tactile stimulus as the more intense one on a proportion of trials significantly different from chance, possibly due to the fact that the second stimulus could still be remembered more vividly. Importantly, no such response bias was present across the critical trials in Exp. 4.1.2 and 4.1.3 when participants observed somebody else actively make contact with a solid surface rather than being passively touched. The inter-stimulus interval between the onset of the first tactile stimulus and the second tactile stimulus was 40 ms longer in the present study as compared with Exp. 4.1.2. and 4.1.3 due to the inclusion of two additional images in which the cotton bud was briefly depicted halfway between the touch target and its neutral starting position on each trial. This prolonged delay between the first and the second stimulus might explain the preferential selection of the second stimulus due to participants finding it easier to recall the perceived intensity of this second stimulus. It was, however, found that a small sample of new participants (data not reported here) still showed this preference for the second after shortening the inter-stimulus interval to match the inter-stimulus interval of 750 ms (rather than 790 ms) in Exp. 4.1.2 and 4.1.3, which suggests that the biased response pattern might be specific to the concurrent observation of passive rather than active touch sensations. It should, however, be noted that the contextual reality of the images depicting passive touch on a hand or an object, respectively, was certainly less than the contextual reality of the active touch images used previously. While the observed index finger in e.g. Exp. 4.1.3. was photographed when actually touching the object, the cotton bud administering the touch on the hand or the object, respectively, was merely superimposed over the touch target, without being genuinely contacting it. Neither the tip of the cotton nor the touch target thus showed the slight deformations that can usually be seen when a cotton bud is pressed onto the surface of the skin or another object (see, however, e.g. Cardini et al., 2011, and Serino et al., 2008b, for similarly created stimulus images). What is more, both the hand and the wooden box were themselves superimposed on a neutral background rather than a more authentic one which might have given especially the hand a somewhat “disembodied” and artificial appearance which, in turn, might have reduced the strength of touch observation-related somatosensory mirror responses (see Gu and Han, 2007, for the role of the contextual reality for the strength of pain observation-related vicarious activity in brain areas concerned with the processing of self-experienced pain).

Alternatively, the absence of any modulatory effects of the sight of passive touch (be on somebody else’s hand or on an object in the same spatial location) on forced-choice intensity comparisons in contrast to the small but highly significant shift in the proportion of trial in which a tactile stimulus accompanied by the sight of a finger actively touching an object (rather than the empty space next to it) was favoured as more intense in Exp. 4.1.3., might, indeed point to slight differences in the mechanisms that mediate the automatic sharing of others’ active and passive touch sensations and to the possibility that the present task might tap into mechanisms involved in resonating with others’ active touch sensations but not into mechanisms involved in resonating with others’ passive touch. As far as observing others’ active touch sensations is concerned, it has most certainly to be taken into account that resonating with the tactile component of an object-directed action is embedded in a more extensive mirror response triggered by the inevitable sight of movements which in itself induces not only vicarious somatosensory activity (Avikainen et al., 2002; Gazzola & Keysers, 2009; Oouchida et al., 2004; Rossi et al., 2002; Voisin et al., 2011b) but also vicarious activity in a wide-spread frontoparietal network of motor areas (Buccino et al., 2001; Chong et al., 2008a; Kilner et al., 2009; Rizzolatti et al., 1996b; Shmuelof & Zohary, 2006; 2007). For self-experienced touch, it has previously been pointed out that being touched focuses the touched individual’s attention on their own body and the evoked bodily sensation while attention shifts to the tactually explored external object during active touching (Gibson, 1962). A similar dissociation might also play a role when resonating with others' passive and active tactile sensations, possibly in the context of different functions associated with resonating with their passive and active touch sensations, such as gaining an intuitive insight into what the other person is feeling when being touched and simulating the tactile consequences of the observed touching act in an anticipatory manner in case oneself were to touch and interact with the observed object in the future or in case oneself were to respond to or evaluate others' actions based on a simulation-based prediction of the sensory outcomes of their actions. Interestingly enough, it has recently been demonstrated that predicting whether somebody else will be able to reach and touch a target object placed in front of them was associated with activity in both SI and SII (Lamm, Fischer, & Decety, 2007).

All in all, the inconsistent results obtained for the sight of others' passive versus active touch sensations with the very same 2-AFC direct comparison task highlight that it cannot necessarily be expected that the modulatory effect of observing touch is the same for both types of touch sensations. Mirror touch responses for observed passive and observed active touch might be brought about in the context of slightly different neural networks and might reveal themselves in different tactile tasks. Future studies may want to attempt to identify the task characteristics that determine if and in what way the sight of either others' passive or active touch sensations results in measurable changes in task performance and also if there are tasks that are sensitive to both types of observed touch.

Summary and discussion of chapter 4

Summary and discussion of Exp.s 4.1.1-4.1.5 and Exp. 4.2.1

Chapter 4 of this thesis presented a series of experiments aiming to explore the consequences of observing others' touch sensations at a behavioural rather than a neural level (see chapter 2 and 3). To date, behavioural correlates of shared neural representations for felt and observed touch (e.g. Blakemore et al., 2005; Bufalari et al., 2007; Ebisch et al., 2008; Keysers et al., 2004; Pihko et al., 2010; Schaefer et al., 2012; Wood et al., 2010) have barely been investigated, with only two methodologically quite different paradigms successfully demonstrating that the sight of somebody else's body being passively modulates ongoing tactile processing (Serino et al., 2008a; see also Cardini et al., 2011 and Serino et al., 2009) and improves tactile thresholds in a sustained manner (Schaefer et al., 2005b). Modulatory effects of observing others experience touch from actively making contact with a surface, on the other hand, has not been investigated at all so far. The main focus of the studies reported in this chapter was thus to establish possible changes in tactile perception during the sight of others' active touch sensations. Rather than attempting to replicate the methodological approaches pioneered by Serino et al. (2008b) and Schaefer et al. (2005b) in the context of passive touch observation, more basic tactile tasks were chosen to explore the effects of observing others touch something on tactile processing. Both an initially conducted speeded tactile intensity discrimination task (Exp. 4.1.1) and a direct intensity comparison task (Exp. 4.1.2) did yield significant effects for the sight of a movement that included a tactile component (a finger tap on the table top) as compared to a movement that did not involve touch (a finger lift into empty space) but it could ultimately not been ruled out that the results were confounded with touch-unrelated differences between the two types of observed movements, especially with regards to the opposite movement directions. When ensuring that the two types of observed movements did indeed only differ with respect to the presence or absence of a tactile component (a fingers is observed to move downwards, touching an object in one condition and merely the empty space next to it in the other condition), re-running the aforementioned 2-AFC intensity comparison task suggested that the sight of others' active touch sensations enhances the perceived intensity of concurrent tactile stimuli on the body (Exp. 4.1.3). In addition, it was also found that observing somebody else's finger touch an object rather than the empty space next to it was associated with increased sensitivity for near-threshold stimuli in a tactile detection task (Exp. 4.1.4). At the same time, a modulatory effect of observing others' active touch sensations could not be found in the context of a tactile task in which participants were to freely judge the intensity of isolated (rather than paired) tactile stimuli on a rating scale (Exp. 4.1.4). While both

Exp. 4.1.3 and 4.1.4 involved judgements on the perceived intensity of tactile stimuli, the implicated psychological processes might nevertheless be quite different and might differ in how sensitive they are to an interaction with the concurrent sight of others' touch. That the exact type of the chosen tactile task can play a crucial role has previously, for instance, been explicitly demonstrated with regards to the enhancing effect of viewing one's own body on tactile processing which was found to be measurable only for sufficiently difficult tactile tasks of a spatial nature but not for easy and/or non-spatial tasks (Press et al., 2004). The range of different tasks in the present chapter was not varied enough to allow to pinpoint which particular task characteristics determine whether the sight of others' active touch sensations interacts with the task-specific tactile processing in a measurable way and more research will be needed to clarify this. Future studies might also want to investigate at what neural processing stages the revealed behavioural modulations in Exp. 4.1.3 and Exp. 4.1.4[35] took effect by e.g. systematically interrupting activity in SI or SII with transcranial magnetic stimulation (TMS) to see how this affects the modulatory effect of observing others' active touch sensations on task performance (see Fiorio & Haggard, 2005, for a similar TMS approach in the context of identifying whether the enhancing effect of viewing one's own body on tactile processing occurs in SI or SII). In particular with regards to the ERP modulations in the context of observing others' active touch sensations reported in chapter 3, it would also be of great interest to use EEG to pinpoint the processing stages at which the sight of touch modulates somatosensory processing during a tactile task. Note that it is difficult to directly relate the SEP modulations revealed in the series of EEG studies in chapter 3 to the behavioural effects of the sight of others' active touch experiences since the tactile stimuli in all experiments in chapter 3 were completely task-irrelevant. Task-relevance of the tactile stimuli, on the other hand, might be associated with a boosted modulatory effect of the (touch-related) visual information (cf. Taylor-Clarke et al., 2002). Alternatively, touch observation-related SEP modulations in the context of task-relevant tactile stimuli might also be found to be qualitatively different and/or at different latency ranges as compared those reported in chapter 3 for task-irrelevant tactile stimuli.

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[35] In addition, it should also be tested if similar effects would have been obtained in Exp. 4.1.3 and Exp 4.1.5 if the model's hand had been replaced with an inanimate object, resulting in a scenario in which touch occurs between to inanimate objects, given that mirror touch responses have previously only at a neural level been found to be also triggered by the sight of objects touching each other (Ebisch et al., 2008; Keysers et al., 2004; Exp. 2.1 of this thesis). The "touch on object"-condition in Exp. 4.2.1. might have been able to shed more light on this at a behavioural level but since Exp. 4.2.1. yielded a null effect of the sight of passive touch on participants' paired intensity comparisons not only for the "object"-condition but also for the "hand"-condition, it would not have been appropriate to interpret the absence of a modulatory effect in the "object"-condition as an index of the body specificity of mirror touch responses.

Another aspect future studies might want to address are the possible functional differences between observing others' touch sensations in the context of object-directed actions ("active touch") and observing others' being passively touched on their body ("passive touch"). Interestingly enough, re-running the 2-AFC direct comparison task with which it had previously been found that the sight of others' active touch sensations increases the perceived intensity of tactile stimuli presented to participants' corresponding finger (Exp. 4.1.3) yielded no significant effect at all when participants observed somebody else's being *passively* touched. While it cannot be ruled out that the absence of a modulatory effect on participants' paired intensity judgements was due to the lack of contextual reality of the presented passive touch stimulus images[36], this discrepancy might also point to some differences in how others' touch sensations are processed, depending on whether they experience touch in the context of an object-related action or as a result of being passively touched. The functional purpose of resonating with either type of touch sensation might be different and this might also be associated with differences in the type of tactile task with which touch observation-related modulations in tactile perception can be detected (see above). Alternatively, it is also conceivable that action-related touch sensations are simply more salient and attract more attention than passive touch sensations (especially when those passive touch sensations are neutral rather than affectively relevant such as when they were to be occur in the form of a painful hit or a affectionate caress; see Ebisch et al., 2011), which might result in stronger mirror touch responses and ultimately in easier to detect modulations in tactile perception. In any case, if re-running Exp. 4.2.1 with more realistic and natural appearing stimulus images were again to fail to yield a significant effect of the sight of others' passive touch sensations, investigating possible differences between observing others' action-related versus passive touch sensations would most certainly be worthwhile.

All in all, the present chapter demonstrated that the sight of others' active touch sensations is associated with systematic modulations in tactile perception in the observer, even so not all types of tactile tasks might be suitable to detect such changes at a behavioural level. In addition, there was an indication that possibly suggests that modulatory effects of observing others' action-related and passive touch sensations might not always be measurable with the same type of tactile task. This latter conclusion, however, has to be considered with some caution since it was based on a single discrepancy observed in the context of the only tactile task which was actually tested for the sight of active *as well as* passive touch but which differed

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[36] While the mirror touch response induced by the sight of these touch-related images might be too subtle to be detected at a behavioural level, it should be noted that their observation was nevertheless associated with significant SEP modulations in Exp. 2.1 in chapter 2, i.e. at neural level, it was after all possible to measure an effect.

also with respect to the contextual reality of the stimulus images presented for the two types of touch (active vs. passive).

Chapter 5

General discussion

5.1 Introduction

This final chapter will attempt to briefly summarise and evaluate the key findings of the studies conducted in the course of this thesis, starting off with the investigated electrophysiological and behavioural correlates of observing others' passive and action-embedded tactile sensations (chapter 5.2), followed by the complex results regarding the links between the strength of touch observation-related modulations in somatosensory processing and interindividual differences in trait empathy (chapter 5.3). Chapter 5.4 will then propose some directions for future research, both with respect to mirror touch in particular and the phenomenon of vicarious brain activity in general.

5.2 Electrophysiological and behavioural correlates of mirror touch during the observation of others' passive and action-related tactile sensations

Chapter 2, firstly, presented a series of four ERP studies that aimed to investigate the electrophysiological correlates of vicarious somatosensory activity triggered by the sight of others' being passively touched on their body and their modulations as function of the animacy of the touch target (Exp. 2.1), the viewing perspective from which the observed-to-touched body part was observed (Exp. 2.2) and the degree to which the observer's concurrently tactually stimulated body location anatomically matched the observed-to-be-touched body location, within a given body part (Exp. 2.3) as well as across different body parts (Exp. 2.4). The obtained highly temporally resolved EEG evidence corroborated in parts previously reported fMRI evidence on touch observation-related somatosensory activity but added also new insights. Exp. 2.1, for instance, demonstrated that higher-order somatosensory processing (e.g. SII) is modulated by the sight of touch, irrespective of whether the observed touch is directed at somebody else's body or an inanimate object, in line with previous fMRI findings (Ebisch et al., 2008; Keysers et al., 2004). Importantly, this ERP-based study indicated, however, that also *primary* somatosensory processing (SI) might (under certain circumstances) be affected by the sight of touch, regardless of the animacy of the touch target, a finding that had not been reported previously. An explorative analysis indicated, however, that the strong SI modulation during the sight of an object being touched might have been somewhat contingent on having seen a hand being touched before, suggesting that being able to match the location seen to be touched on the object with a location on the observer's own body might have been important. Exp. 2.2, on the other hand, revealed that observation-related SEP modulations during early-stage somatosensory processing in SI (N80) were not further modified by whether somebody else's body part was viewed from an egocentric or an allocentric viewing perspective while later-stage modulations (SII/N140) were found to be influenced by the adopted viewing perspective in a complex fashion. While this pattern was in contradiction to fMRI-based evidence on a perspective-dependent mirror touch response in subareas of SI (BA 3a/3b and 2) and a perspective-insensitive mirror touch response in SII (Schaefer et al., 2009), it should be borne in mind that the BOLD signal in fMRI studies blurs the hemodynamic brain response over several seconds, rendering it unclear whether the revealed perspective-specific SI-response during touch observation revealed by Schaefer et al. (2009) reflected a) an early modulation of vicarious SI activity or b) a somewhat later occurring modification of touch observation-related SI activity based on feedback from higher-order cortical areas that project to SI (cf. Schubert et al., 2008). Exp. 2.2 of this thesis possibly shed more light on the possible temporal sequence of perspective-dependent modulations of touch observation-related vicarious SI activity, suggesting that the *initial* SI response might indeed be similar for both viewing perspectives and that its perspective-dependent modulation occurs only somewhat later, based on reentrant feedback to SI.

Finally, Exp.s 2.3 and 2.4 in chapter 2 suggested that the triggered mirror touch response might not be fine-grained enough to distinguish between different finger locations within a hand (a quite plausible finding given that the cortical representations of the different digits tend to overlap considerably during actual tactile stimulation; Biermann et al., 1998; Hoechstetter et al., 2001; Krause et al., 2001; Ruben et al., 2001; Simoes et al., 2001) (Exp. 2.3) but it might nevertheless be highly specific at the level of body parts (Exp. 2.4; see also Blakemore et al., 2005), at least for SI-related mirror touch responses, in line with the clear somatotopic organisation of SI responses during actual tactile stimulation (Hari et al., 1993; Nakamura et al., 1998; Yang et al., 1993). Such a pronounced body part-specific mirror touch response is thus another demonstration of how similar the processing one's own and others' tactile sensations is.

In contrast to chapter 2, chapter 3 addressed a somewhat neglected aspect of action observation-related vicarious somatosensory brain activity, investigating whether the sight of others' action-embedded and thus "active" (rather than passive) touch sensations modulates ongoing somatosensory processing in the observer in ways dissociable from the previously reported movement observation-related modulations in somatosensory processing (e.g. Avenanti et al., 2007; Avikainen et al., 2009; Voisin et al., 2011b). While it was found over a series of six ERP studies that the sight of others' active touch sensations *can* modulate somatosensory processing, it nevertheless became apparent that the revealed touch observation-related modulations in Exp. 3.2 to 3.6 were somewhat fragile and very sensitive to small changes in the experimental procedures, in particular with respect to the way people were made aware of the difference in tactile consequences associated with the observed visual stimuli. This was most likely associated with the fact that the action-embedded tactile event was rather subtle (a brief tap on a table top or on an object rather than e.g. a full-hand grasp of an object), possibly rendering any touch observation-related modulations in somatosensory processing prone to being obscured by movement observation-related modulations. In this context, it was a particularly interesting finding that several of the conducted studies (Exp.s 3.2, 3.3 and 3.5) indicated that touch observation-related SEP modulations (especially during early-stage somatosensory processing) were primarily found for the digit *adjacent* to the finger observed to move and touch, presumably because the rather finger-unspecific mirror touch response (see Exp. 2.3) was less subjected to interference by (possibly more finger-specific) movement observation-related somatosensory activity when the tactually stimulated finger did not match the observed-to-move-and-touch finger. This also highlights that while the observation of others' active touch sensations seems to evoke a distinct somatosensory resonance response just like the observation of others' passive tactile sensations does, this mirror touch response nevertheless occurs in the context of inevitably seeing (and simulating) also movements. Future research might want to investigate in more detail how the simulation processes of the motor and proprioceptive action components interact with and shape the simulation processes of the tactile action components.

Lastly, chapter 4 attempted to establish behavioural correlates of touch observation-related vicarious somatosensory activity, primarily in the context of witnessing others' active rather than passive touch sensations. While it was found that observing somebody else touch an object rather than the empty space next to it increased the perceived intensity of concurrently presented tactile stimuli in a 2-AFC direct comparison task and improved tactile sensitivity in a tactile detection task, it became also apparent that the exact type of task might play an important role as to whether or not behavioural consequences of shared neural representations for felt and observed touch can successfully be measured.[37] Such a task-dependency has also been found for other types of interactions between body-related visual information and tactile processing (Press et al., 2004) and future research will have to clarify what task properties tap into touch observation-related modulations in tactile perception. In this context, it is also interesting to note

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[37] Given that the ERP evidence on the effects of observing others' active touch sensations on somatosensory processing in the observer suggested that touch observation-related modulations were sometimes more reliable for the adjacent rather than the anatomically congruent finger, it should be noted here that the behavioural studies in chapter 4 exclusively involved tactile stimulation of the anatomically homologous finger. It cannot be ruled out that touch observation-related effects on tactile task performance might have been more pronounced or easier to detect had also the adjacent finger been tested.

that what kind of task is suitable might differ as a function of whether others' active or passive touch sensations are observed (see Exp. 4.1.2). Regardless of what type of touch is ultimately witnessed, it most certainly appears somewhat "easier" to demonstrate shared neural representations for experienced and felt touch at a neural rather than at a behavioural level. While touch observation-related vicarious somatosensory activity might still be clearly detectable directly in brain activity (irrespective of whether it is registered by e.g. fMRI or EEG), the consequences of such possibly rather subtle resonance activity (cf. Pihko et al., 2010) might be much harder to measure in the form of a behavioural effect that emerges at the end of a long chain of sensory and cognitive processes during which a number of unknown factors might influence the outcome. While future studies might nevertheless be able to identify a range of tactile tasks with which touch observation-related modulations in self-related tactile perception can studied reliably, it should also be noted that given the putative role of visuotactile mirror-matching mechanisms in understanding others' tactile experiences, it might actually be more interesting to investigate behavioural effects of being able to resonate with others' touch sensations in this way not with respect to how this might change how we perceive our own touch but how it actually influences (and possibly facilitates) how we perceive the touch sensations of others: Bolognini et al. (2011a), for instance, demonstrated that a TMS-induced interruption of SI activity significantly impaired individuals' capacity to recognise whether an observed finger actually touched somebody else's hand or not. Such approaches are vital for shedding more light on the functional role of shared neural representations for felt and observed touch (see further below).

All in all, most experiments presented in chapters 2, 3 and 4 nevertheless implicated the observer's own somatosensory cortex (both SII and often also SI) in the perception of others' tactile sensations, be it from seeing them being passively touched or actively touch e.g. an object. Rather than being a merely visual process, the touch we observe in others is automatically embodied by triggering a somatosensory brain response that is in parts similar to the one evoked by actual touch on our own body. Importantly, while both attentional processes and tactile imagery can modulate or trigger, respectively, somatosensory activity in both SI and SII (Eimer & Forster, 2003; Forster & Eimer, 2004; García-Larrea et al., 1995; Yoo et al., 2003; Zopf et al., 2004), it is seems unlikely that the revealed modulations in somatosensory processing in chapters 2, 3 and 4 merely reflected attention- or imagery-related rather than touch observation-related effects on somatosensory activity. Firstly, with the only exception of Exp. 3.5, the visual stimuli in all conducted experiments were task-irrelevant and participants were instructed to pay no attention to the depicted visual display (apart from monitoring the task-relevant fixation cross). While it could still be argued that visual stimuli that involve a tactile component might have been more salient and might thus have attracted more attention than similar visual stimuli without a tactile event, it would nevertheless be difficult to explain e.g. the body part-specificity of the SEP modulations in Exp. 2.4 or the finger-specificity of the SEP differences in Exp.s 3.2, 3.3, 3.5 and 3.6 with such an unspecific attentional bias. It seems also implausible that the revealed modulations merely reflected mental imagery of touch. Participants might have *occasionally* imagined being touched or touching the seen object, respectively, themselves but since there was no instruction or task-related incentive to do so, it is rather unlikely that participants engaged in tactile imagery systematically and continuously enough to induce the observed modulations in somatosensory processing. Instead, the observed effects on tactile processing, revealed both at a neural and a behavioural level, are much more likely to be the genuine result of the brain's tendency to map others' touch sensations onto the observer's own somatosensory system. Linking the touch we observe in others with our own experience of touch in this way might be a mechanism that shapes in a fundamental way how we perceive and understand others' tactile sensations. Interestingly enough and as previously mentioned, interrupting such vicarious somatosensory activity has been found to indeed interfere with the accurate perception of others' touch: Bolognini et al. (2011a) recently demonstrated that TMS over SI impaired participants' ability to discriminate whether an observed index finger touched somebody else's hand or not, causally linking visuo-tactile mirror-matching mechanisms to how we recognise and understand others' touch. Such a "virtual lesion"-based impairment in coding others' touch sensations bears some resemblance to how actual damage in e.g. the insula, a cortical structure that contains shared neural representations for experienced and merely observed disgust (Wicker et al., 2003), impairs the ability to recognise disgusted facial expressions in others (Adolphs, Tranel, & Damasio, 2003; Calder, Keane, Manes, Antoun, & Young, 2000). Future studies might want to study the consequences of e.g. stroke-related brain damage in SI and SII for processing visual stimuli that depict tactile event in the context of other people's bodies (see Bolognini et al., 2011b), since disruptions in how accurately others' tactile sensations are perceived would provide important and powerful evidence for the functional role of vicarious somatosensory brain activity in our capacity to intuitively understand others' somatic experiences.

An important question in the context of shared neural representation for felt and observed touch which has so far not been addressed concerns how the touch-related visual input reaches the somatosensory cortices in the first place to trigger the portrayed vicarious activity in response to observing somebody else being touched. Anatomical connections to various relevant areas in posterior parietal cortex (as identified in monkey studies) might be essential here. The somatosensory cortices maintain, for instance, direct connections to ventral intraparietal area (VIP; Lewis & Van Essen, 2000), a cortical region which has been implicated in multisensory processing containing not only unimodal visual neurons but also bimodal visuotactile neurons as well as seemingly unimodal neurons whose response is nevertheless modulated by input from the other modality (Avillac, Ben Hamed, & Duhamel, 2007; Duhamel, Colby, & Goldberg, 1998). Interestingly, VIP (along with area 7b) also seems to contain visuo-tactile mirror neurons responding both when a monkey was touched and when it observed the experimenter touch himself on the corresponding body part (Ishida et al., 2010). In addition, some bimodal visuo-tactile VIP neurons have been described as "body-matching" neurons firing not only when the monkey is touched or a visual stimulus enters the visual receptive field anchored to the monkey's corresponding body part, but also when a visual stimulus moves in the vicinity of the experimenter's matching body part (Ishida et al., 2010). These body-matching neurons seem to create a reference for others' bodies based on one's own body (i.e. shared body presentations; see Thomas, Press and Haggard, 2006, for (behavioural) evidence on shared body representations in humans) and this body-part related information may be vital for mirror matching mechanisms in e.g. motor- and somatosensory-related areas (Ishida et al., 2010). Another important area in posterior parietal cortex somatosensory cortices (more specifically: BA 2) are connected with is the inferior parietal lobule (IPL; Rozzi et al., 2006) where visual, somatosensory and, importantly, motor mirror neurons can be found (Fogassi et al., 2005; Rozzi et al., 2008). This latter link seems important since a connection to parietal mirror neurons might explain somatosensory activations during the observation of others' movements (e.g. Avikainen et al., 2002; Gazzola & Keysers, 2009; Möttönen et al., 2005; Oouchida et al., 2004; Raos et al., 2004; 2007; Rossi et al., 2002).

While the described connections (provided they exist in a similar way in humans) elucidate how visual input might reach the somatosensory cortices, they do not explain how or why the somatosensory cortices become a recipient of touch-related visual information in the first place. Rather than assuming that vicarious somatosensory activity is an innate predisposition with a pre-wired neural circuit (cf. Gallese, 2001; Rizzolatti & Craighero, 2004), it seems more likely that the tendency to map observed touch onto one's own somatosensory system is a (by-) product of associative or Hebbian learning in the context of observing touch on *one's own* body (cf. Heyes, 2010, and Keysers and Perrett, 2004, for respective accounts, originally formulated for motor mirror neurons): Feeling one's own body being touched and observing the applied touch at the same time results in a co-activation of somatosensory and visual representations of the experienced tactile event. The repeated temporal contiguity and contingency of those visuo-tactile experiences strengthens initially weak and unsystematic synaptic connections between visual- and somatosensory-related areas, eventually allowing visual input to activate somatosensory representations in the absence of actual touch, ultimately even when the visual input refers to somebody else's body. The pronounced morphological similarities between our own body and those of others might be crucial in allowing such a generalisation from “touch on one’s own body” to “touch on somebody else’s body”. That *repeated* correlated visuo-tactile experience, presumably from an early age on, might be the key to the development of automatic somatosensory mirror touch responses whenever somebody else is observed to experience a tactile sensation appears crucial with respect to a certain methodological aspect that was part of almost all studies reported in this thesis: With the exception of Exp.s 3.2 and 4.1.1, participants were presented with a short demo of the touch-related visual stimuli at the beginning of the experimental session and were then either briefly touched on their own hand with a cotton bud (chapter 2) or asked to imitate the observed movements several times (chapters 3 and 4). This was done to ensure that participants were sufficiently aware of the rather subtle tactile content in the visual stimulus displays, although no such explanation was given to participants. It appears, however, highly unlikely that the touch observation-related modulations in somatosensory processing revealed at both a neural and a behavioural level in the studies of the present thesis reflected a newly formed visuo-tactile association between observing touch and feeling touch learnt at the beginning of the testing session instead of a pre-existing one, based on a lifelong experience with observing and feeling touch at the same time. The initial demonstration of the tactile consequences in the presented studies (e.g. participants being touched with a cotton bud only *twice*) would most certainly have been much too short to induce the formation of any entirely new association. Moreover, especially the sight of a hand being touched or touching an object (be it one’s own or somebody else’s) is a rather common and highly familiar situation with which most individuals have had ample experience with from an early age, given that our own hands rarely operate outside our own visual range. In this context, it would nevertheless be of great interest to study vicarious somatosensory activity in the context of observing touch on body parts for which individuals have only a limited experience of seeing the touch they feel on their own body, such as the back of the neck. (Tipper et al., 2001), for instance, demonstrated that the enhancing effect of viewing one’s own body on tactile processing of stimuli presented to the viewed body part was decreased for body sites (the back of the neck) which cannot be viewed directly. If the formation of visuo-tactile mirror-matching mechanisms depends on a sufficient correlated experience of feeling touch on one’s body and observing this touch at the same time (cf. Heyes, 2010), it is conceivable that mirror touch responses might be less pronounced when touch on somebody else’s body is observed in a location which the observer has never been able to directly see touched on their own body.

Another aspect that should not remain unmentioned when discussing shared neural representations for touch is the question of how an efficient self-other distinction is maintained: If we systematically activate our own somatosensory cortex whenever we see somebody else experience touch, how come we are not constantly confused as to whether we were just touched ourselves or whether we merely observed somebody else being touched? Firstly, somatosensory activity (in SI) in response to the sight of others' touch has in one study been found to be less strong and also delayed as compared to the somatosensory activity triggered by actual touch (Pihko et al., 2010); note that mirror touch synaesthetes who do sometimes confuse felt and merely observed touch (Banissy & Ward, 2007) are thought to have an overactive tactile mirror system (Blakemore et al., 2005). Furthermore, it has also been pointed out that observing touch results not only in overlapping but also differential activations in somatosensory-related brain areas: Ebisch et al. (2011) demonstrated that the BOLD response in the posterior insular cortex (pIC) increased during the experience of touch but decreased during the mere sight of (albeit social or affective) touch, indicating that the overlap between self and other is not complete. In addition, shared neural representations not only for touch in particular but also in general do not operate in isolation but are likely to be embedded in different neural networks. Zaki, Ochsner, Hanelin, Wager and Mackey (2007), for instance, demonstrated that overlapping brain areas for self- and other-related pain (here the AI and ACC, respectively) showed an enhanced connectivity with the midbrain and the periaqueductal gray during the actual experience of pain while the mere observation of others' pain was associated with an increase in connectivity to the dorsolateral prefrontal cortex as well as to the STS, posterior cingulate cortex and the precuneus. While the functional connectivity of the somatosensory cortices during feeling touch and observing has not been investigated yet, it seems quite conceivable that SII and SI might also be found to be distinctly connected with different higher-order brain areas in the two conditions and that this differential connectivity might be vital in maintaining a sense of self.

5.3 Electrophysiological correlates of mirror touch during the observation of others' touch sensations and interindividual differences in trait empathy

Important (albeit indirect) evidence on the role of mirror-matching mechanisms as the neural basis of empathy comes from studies that show that the extent to which certain brain areas are vicariously activated during the observation of others' actions, emotions and somatic sensations (pain, touch) correlates positively with individuals' self-reported empathic dispositions (Avenanti et al., 2009; Cheng et al., 2008; Gazzola et al., 2006; Gazzola & Keysers, 2009; Saarela et al., 2007; Schaefer et al., 2012; Singer et al., 2004). In particular with respect to vicarious somatosensory activity triggered by the sight of touch, Schaefer et al. (2012) recently reported that participants who scored high on the IRI's *perspective-taking* scale tended to show stronger SI activity (as revealed by fMRI) during touch observation. For this reason, participants in almost of all experiments in chapters 2 and 3 of this thesis were asked to complete standard empathy questionnaires after the EEG testing to explore possible links between interindividual differences in trait empathy the strength of touch observation-related SEP modulations in the context of temporally highly resolved *electrophysiological* correlates of mirror touch. Interpreting the resulting empathy-related correlations revealed in the different studies proved overall challenging, given that, from study to study, the correlations tended to be found at different latency ranges, at different electrodes and for different empathy scales. In addition, depending on the specific research question in a given study and the results of the statistical analyses of the touch observation-related ERP modulations, the correlational analyses were conducted on SEP amplitude differences that were averaged across two or more experimental conditions and, depending on where significant effects of the sight of touch were found, for quite different electrode clusters. When considering the empathy-related findings across all studies, it nevertheless emerged that the variations in the strength of the identified SEP modulations as a function of individuals' empathic skills seemed to follow certain patterns: If correlations between the size of touch observation-related ERP changes and empathy measures were found, the implicated empathy scales tended to tap primarily (but not exclusively) the emotional rather than the cognitive dimension of empathy, involving the EQ's *emotional reactivity* subscale and/or the IRI's *empathic concern/personal distress* scales. This was somewhat unexpected, given that the strength of vicarious somatosensory responses during action, touch or pain observation is usually found to correlate with subscales for *cognitive* empathy (Avenanti et al., 2009; Cheng et al., 2008; Gazzola et al., 2006; Schaefer et al., 2012). The high temporal resolution of the EEG data obtained in this thesis might have allowed to reveal short-lived variations in somatosensory mirror touch responsiveness as a function of individuals' *emotional* empathy levels that might not be detectable in e.g. fMRI approaches where neural activity is lumped together over several seconds and where it is often somewhat unclear whether parts of the measured brain activity might not already be influenced by feedback from higher-order brain areas (cf. Schubert et al., 2008). In addition, there are also findings that do link vicarious somatosensory activity to the tendency for emotional empathic responses: Mirror touch synaesthetes, for instance, whose somatosensory cortex responds unusually strong to the sight of touch on others' bodies (Blakemore et al., 2005) score significantly higher on the EQ's *emotional reactivity*-subscale than non-synaesthetic controls (Banissy & Ward, 2007), linking the tendency to resonate strongly with observed somatic sensations of others' (even if it is just a neutral touch sensation) with the tendency to respond emotionally to others' mental and emotional states.

In this context, it is important to note that the nature of emotional responses deemed empathic by the implicated empathy scales in the experiments of this thesis was rather diverse: The EQ's *emotional reactivity* subscales quantifies more broadly the "tendency to have an emotional reaction in response to others' mental states" (Lawrence et al., 2004, p. 918), based on items that directly tap individuals' emotional responsiveness ("I get upset if I see people suffering on news programmes.") as well as items that probe individuals' capability of understanding others' emotions ("Other people tell me I am good at understanding how they are feeling and what they are thinking."). The IRI's *empathic concern* scale, on the other hand, targets specifically the tendency to react with "feelings of warmth, compassion and concern" (Davis, 1983, p. 6) to others' negative experiences with items such as "I often have tender, concerned feelings for people less fortunate than me" or "When I see someone being taken advantage of, I feel kind of protective towards them.". Finally, the IRI's *personal distress* scale measures "feelings of fear, apprehension and discomfort at witnessing the negative experiences of others." (Davis, 1983, p. 12), involving items such as "When I see someone who badly needs help in an emergency, I go to pieces." or "In emergency situations, I feel apprehensive and ill-at-ease.". While this latter scale has been criticised for measuring self- rather than other-oriented emotional responses and thus for not tapping genuine empathic emotional reactions (Baron-Cohen & Wheelwright, 2004), it nevertheless probes the tendency to be emotionally affected by witnessing others' misfortunes. The findings of the present thesis thus link touch observation-related vicarious somatosensory activity to a broad range of complex and reactive emotional responses that go beyond merely sharing the observed emotion and that are not necessarily congruent (but at least appropriate) with the perceived psychological state. The challenging task for future research will be to clarify precisely how the somatosensory cortices, traditionally thought of as being exclusively concerned with processing tactile and proprioceptive input from one's own body, might contribute to the occurrence of such other-related emotional empathic responses. While it should be borne in mind that the experience of (emotional) empathy is a highly complex and multi-faceted psychological phenomenon which is likely to be mediated by a complex and wide-spread network of brain areas (Decety, 2010), with low-level simulation mechanisms in sensorimotor areas as only one (albeit important) contributor, it seems nevertheless interesting that the somatosensory cortices have previously been implicated in decoding others' emotions based on facial expressions (Adolphs et al., 2000; Pitcher, Garrido, Walsh, & Duchaine, 2008; Pourtois et al., 2004), whole-body emotional expressions (Heberlein et al., 2004; Heberlein & Saxe, 2005) and vocal signals (Adolphs, 2010; Banissy et al., 2010) as well as with predicting others' future emotional states (Hooker, Verosky, Germine, Knight, & D'Esposito, 2008). The generation of a somatosensory representation of what displaying a certain emotional facial expression or body posture must feel like in terms of the underlying muscle contractions or of a more general vicarious representation of the body state associated with a certain emotion (cf. Heberlein & Atkinson, 2009) might be important for being able to recognise others' emotions, possibly even through directly producing the corresponding affective state in the observer (Goldman & Sripada, 2005). It could be speculated that such a somatosensorically mediated accurate and intuitive understanding of others' emotions is a crucial prerequisite for showing the above described types of appropriate empathic emotional responses that go beyond merely sharing the observed emotion. For instance, simulating what it would proprioceptively feel like to make a sad face might help the observer to recognise and understand that the other person is sad which might, in turn, provide vital input to processes that bring about an appropriate emotional response of e.g. concern and compassion. Importantly, future studies in this context should distinguish much clearer between the different types of emotional empathic responses to be able to establish the extent to which they might be distinct but yet related to each other. To date, it is not always clear whether the term "emotional empathy" refers to the emotional sharing of the observed emotion only (e.g. Duan, 2000; Shamay-Tsoory, 2011) or whether it more broadly targets other types of appropriate, other-related emotional response (cf. Baron-Cohen & Wheelwright, 2004).

Albeit to a lesser extent, some of the studies in the present thesis suggested also links between the extent of vicarious somatosensory activity at early- (N80; Exp.s 2.4 and 3.5) as well as mid- (P100; Exp. 3.3) and late-latency (N140; Exp. 2.2) processing stages during the observation of others' touch sensations and cognitive dimensions of empathy, implicating the EQ's *cognitive empathy* subscale and the EQ's *social skills* subscale. The latter measures individuals' intuitive social understanding along with the tendency to spontaneously use socials skills as compared to over-relying on social rules (Lawrence et al., 2004). Since the EQ's *social skills* subscale has been previously been found to correlate (albeit weakly) with the IRI's *perspective taking* scale (Lawrence et al., 2004) as well as with the EQ's *cognitive, empathy* scale (Exp. 3.3 in the present thesis), it is assumed that this subscale taps aspects of interpersonal social behaviour that rely on cognitive rather than affective dimensions of empathy (Lawrence et al., 2004). It therefore appears as if vicarious somatosensory activity is related to both affective as well as cognitive components of empathy and that there is no clear dissociation (cf. Hooker et al., 2010). As mentioned above, future studies will have to address the question how low-level resonance mechanisms in e.g. the somatosensory cortices interact with mentalising processes in higher-order brain areas to shape both cognitive and affective aspects of responding empathically to others.

Apart from the fact that the temporally highly resolved electrophysiological data from the ERP studies in chapters 2 and 3 provided evidence for an involvement of vicarious somatosensory activity in both affective and cognitive components of empathy, there was also another important finding in the context of trait empathy-related variations in the strength of touch observation-related modulations of somatosensory processing which has not been discussed so far: Surprisingly enough, vicarious activity in SI (but not in higher-order somatosensory areas such as SII) was repeatedly found to be linked to interindividual differences in empathy in a negative rather than a positive fashion: In Exp. 2.1, 2.3, 2.4 and 3.5, touch observation-related ERP modulations at early latency ranges (P50 and N80, respectively) associated with SI processing (Allison et al., 1992; Hämäläinen et al., 1990) were found to be the least pronounced for participants who scored high on either emotional or cognitive empathy scales. This was a surprising finding since previous research commonly links high trait empathy with stronger observation-induced mirror responses in brain areas with overlapping representations for self and other (Gazzola et al., 2006; Kaplan & Iacoboni, 2006; Saarela et al., 2007; Schaefer et al., 2012; Schulte-Rüther et al., 2007; Singer et al., 2004; see, however, Costantini et al., 2008, and Perry et al., 2010). While it might again have been the high temporal resolution of the EEG technique that allowed to detect such a counterintuitive relationship for touch observation-related modulations during early-stage somatosensory processing, this finding has important implications in that it might point to possible top-down influences on mirror touch responses, e.g. in the context of maintaining self-other distinction. As discussed in chapter 2.5, particularly empathic participants might generally be more prone to a reduced self-other differentiation (Asai et al., 2011) which they might, however, be able to counteract in a situation in which they are explicitly instructed to ignore somebody else’s body part and what happens to it, as it was the case in all studies in the present thesis (see Exp. 3.5 for an exception). Interestingly enough, Decety, Yang and Cheng (2010) recently demonstrated that physicians, as compared to matched controls, are capable of down-regulating stimulus-driven mirror pain responses in the context of observing others’ bodily pain at very early processing stages, suggesting that vicarious brain activity can be inhibited by top-down processes. Also in normal individuals, it has recently be found that more empathic participants showed less activity in somatosensory areas in response to perceived pain in others, presumably due to their attempt to control the extent to which the vicariously shared the seen pain (Costantini et al., 2008). While the findings in the present thesis are the first to suggest that individual might also be able to inhibit vicarious somatosensory activity (in SI) when observing others’ non-painful and entirely neutral somatic experiences, presumably in the context of attempting to comply with an instruction to completely ignore the other-related visual information, there is already some empirical evidence that mirror touch can, in general, be subject to top-down influences from higher-order processes: Similar to findings by Xu, Zuo, Wang and Han (2009) who demonstrated that the strength of pain observation-related vicarious brain activity decreases when painful stimulation is observed to be applied to faces of other races, Serino et al. (2009) showed that the enhancing effect of observing somebody else being touched on their face on tactile perception in the observer was, too, modulated by the perceived similarity between the observed person and the observer in terms of racial and political group membership. Future studies may want to shed more light on the effects of higher-order factors on automatic vicarious somatosensory activity in general as well as on the specific role of individual personality traits such as empathic dispositions in shaping mirror touch responses in particular.

The findings of the present study suggest that such top-down influences might affect resonant somatosensory activity differentially, depending on the somatosensory processing stage (SI vs. SII).

All in all, the correlational analyses conducted in the experiments in chapter 2 and 3 of this thesis suggest links between the strength of vicarious somatosensory activity in both SII and SI during the observation of others' touch sensations (be they passive or active) and interindividual differences in primarily affective but also cognitive empathy, indicating that the somatosensory cortices might play an important role in social perception. While the revealed associations should not be interpreted without caution, given that they tended to be found for different latency ranges, different electrode sites and different empathy-related scales and given the general limitations of self-report measures, it is also important to note that correlational evidence nevertheless leaves open the question of the direction of the (causal) relationship between the amount of vicarious somatosensory brain activity and individual differences in empathic skills. Do individuals tend to respond more emotionally to others and find it easier to mentally put themselves into others' shoes, respectively, *because* they tend to recruit their own somatosensory system more when perceiving others, e.g. due to a more efficient visuotactile connectivity (cf. Schaefer et al., 2012), or do individuals use their own somatosensory system to simulate others' bodily states more readily *because* they are highly empathic and e.g. pay more attention to social cues regarding others' somatic states? Whether interindividual differences in neural connectivity or responsiveness determine empathic tendencies or whether individuals' empathic capacities depend on other factors but also shape the activity in brain areas with shared neural representations will be an intriguing topic for future research.

5.4 Future research directions

The findings of this thesis's electrophysiological and behavioural studies corroborated the notion of an automatic embodied simulation of others' tactile sensations, both in the context of observing others being passively touched and witnessing others actively touch e.g. an object. As already suggested earlier in this general discussion, interesting directions for future research concern questions such as whether somatosensory mirror touch responses might be less pronounced for body parts such as the back of the neck for which individuals have only limited and indirect experience of observing being touched in this location themselves (see chapter 5.2), based on the assumption that visuotactile mirror-matching mechanisms might be a by-product of associative learning (cf. Heyes, 2010) and might thus depend on a sufficient amount of correlated sensory experience of being touched and seeing this touch being applied at the same time. If the sight of touch on a visually less accessible body part were indeed to be found to be less effective in evoking a somatosensory resonance response, it would be highly interesting to test if and what amount of a systematic provision of appropriate visual feedback during being touched in such a location (e.g. through mirrors) might be able to establish a mirror touch response that is comparable to a somatosensory resonance response triggered by the sight of touch on a more accessible body location, an outcome that would strongly corroborate the notion that (initially self-related) associative learning might be important for mirror-matching mechanisms to emerge. Another important question that has already been mentioned briefly and that needs to be addressed in future research relates to the functional connectivity of the somatosensory cortices during the actual experience as compared to the mere observation of touch (see Zaki et al., 2007, for such an approach in the context of shared pain), an important aspect which will help to clarify how an effective sense of self is maintained despite the pronounced overlaps in how our own and others' tactile sensations are processed. While the similarities between self- and other-related processing of bodily states are highly intriguing, it is also important to investigate the differences to establish how we nevertheless distinguish between e.g. our own touch experiences and those of others. Finally, in analogy to the beneficial effects of action observation training in the rehabilitation of motor impairments in stroke patients (e.g. Ertelt et al., 2007), it will also be of great interest to explore possible clinical applications of mirror touch in future research. The sight of others' touch sensations might, for instance, be able to boost the onlooker's somatosensory system in a way that facilitates the detection of tactile stimuli (see Serino et al., 2008b, as well as Exp. 4.5 in this thesis) in patients with somatosensory deficits after e.g. a stroke, helping them to re-gain tactile sensitivity in the affected body part. Also patients with amputations might benefit from observing others' being touched: Ramachandran and Brang (2009) found that seeing somebody else being touched on their hand evoked a tactile sensation in the corresponding phantom hand of amputees. Interestingly enough, one of the tested amputees in this study reported in this context that merely observing his wife massage her own corresponding hand alleviated the phantom pain in his missing hand, pointing to a simple yet effective therapeutic intervention for this kind of pain. Based on this anecdotal finding, the authors even speculated whether the sight of soothing tactile stimulation on somebody else's corresponding body part might not even relieve actual pain in the "real" limbs of non-amputees. Investigating such rehabilitative and therapeutic applications of the automatic tendency to activate the somatosensory cortex in response to the sight of touch more systematically will most certainly be worthwhile, especially due to the ease with which such interventions could be implemented in clinical settings as well as in daily life.

Finally, another important direction for future research relates to the revealed links between vicarious somatosensory activity and both affective and cognitive aspects of empathy (see chapter 5.3). Vicarious brain activity not only in response to the sight of others' touch sensations in particular but also in response to the sight of others' actions, emotions and somatic sensations in general is thought to be the neural basis of empathy and the human capacity to intuitively understand what others do and feel (Gallese, 2003; 2007; 2004; Keysers & Gazzola, 2006). Importantly, empathy as such is, however, a highly complex psychological construct that entails but also goes beyond merely sharing others' emotions and their observed bodily states. Assuming that an interpersonal phenomenon as intricate and multi-facetted as empathy might be contingent on a small number of brain regions with shared neural representations is, however, clearly overly simplistic (see Decety, 2010). A large part of empathically understanding others depends indeed on complex cognitive processes such as purposefully adopting somebody else's perspective and consciously inferring their mental and emotional states (cf. Baron-Cohen & Wheelwright, 2004), processes that are typically associated with neural activity in brain areas such as e.g. the mPFC, the TPJ, the (posterior) STS and the temporal poles (Carrington & Bailey, 2009; Frith & Frith, 2003; Van Overwalle, 2009) that do not have mirror properties. A major challenge for future research will be to elucidate how low-level mirror-matching mechanisms in sensorimotor and para-limbic areas might interact with higher-order reasoning processes in bringing about an empathic understanding of others in given situation. Currently, most studies focus on either mirroring or mentalising processes and thus try to isolate the two processes from each other in their experimental designs: In studies on shared neural representations, the stimulus material usually involves the passive observation of body parts in motion, being touched or subjected to pain while investigations on mentalising typically present participants with written stories, cartoons etc. and encourage participants to actively reflect upon others' mental states (cf. Van Overwalle & Baetens, 2009). The use of stimulus material that in itself reflects more the multimodal and dynamic nature of social signals in everyday life situations and is thus more likely to activate both mirroring and mentalising areas (see e.g. Hooker et al., 2010; Schulte-Ruether et al., 2007; Zaki, Weber, Bolger, & Ochsner, 2009) along with functional connectivity analyses between those cortical regions will be crucial in shedding more light on the complex interplay between shared neural representations and inferential processes. Such approaches might also help to elucidate the direction of the causal relationship between variations in the strength of vicarious brain activity and interindividual differences in complex cognitive and affective aspects of dispositional empathy as repeatedly observed in the studies of the present thesis.

5.5 Final conclusion

The present thesis investigated electrophysiological and behavioural correlates of the automatic embodied of others' tactile sensations, both in the context of observing others' being passively touched and witnessing others' actively touch e.g. an object. Despite some inconsistencies, the findings on the whole corroborated the notion of shared neural representations for experienced and merely observed touch in SII and under certain circumstances also in SI. In addition, the strength of touch observation-related vicarious somatosensory activity was found to co-vary in a highly complex fashion with interindividual differences in primarily affective but also cognitive dimensions of trait empathy. Rather than being exclusively concerned with processing tactile and proprioceptive signals from our own bodies, the somatosensory cortices might therefore not only play a vital role in intuitively sharing and understanding others' somatic states, but also in contributing to highly complex social phenomena such as empathy.

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