
Citation: Gillmeister, H., Sambo, C.F. & Forster, B. (2010). Which finger? Early effects of attentional selection within the hand are absent when the hand is viewed. EUROPEAN JOURNAL OF NEUROSCIENCE, 31(10), pp. 1874-1881. doi: 10.1111/j.1460-9568.2010.07195.x

This is the submitted version of the paper.

This version of the publication may differ from the final published version.

Which finger? Early effects of attentional selection within the hand are absent when the hand is viewed.

Journal:	*European Journal of Neuroscience*
Manuscript ID:	EJN-2009-09-16104.R1
Manuscript Type:	Research Report
Date Submitted by the Author:	
Complete List of Authors:	Gillmeister, Helge; University of Essex, Psychology Sambo, Chiara; Institute of Psychiatry, King's College London, Psychological Medicine Forster, Bettina; City University London, Psychology
Key Words:	somatosensory, spatial attention, event-related potentials (ERPs), vision, hand

Running title: Vision abolishes early within-hand selection

Section: Cognitive Neuroscience

Associate Editor: Martin Sarter / Douglas P. Munoz

Which finger? Early effects of attentional selection within the hand are absent when the hand is viewed.

Helge Gillmeister[1,3,*], Chiara F. Sambo[2,3], and Bettina Forster[3]

[1]Department of Psychology, University of Essex

[2]Institute of Psychiatry, King's College London

[3]Department of Psychology, City University London

*Correspondence:

Department of Psychology, University of Essex, Wivenhoe Park, CO4 3SQ, UK

E-mail: helge@essex.ac.uk

Tel.: +44 (0) 1206 87 3533

Fax.: +44 (0) 1206 87 3801

Abstract

The sight of a hand can bias the distribution of spatial attention, and recently it has been shown that viewing both hands simultaneously can facilitate spatial selection between tactile events at the hands when these are far apart. Here we directly compared the electrophysiological correlates of within- and between-hand tactile-spatial selection to investigate whether within-hand selection is similarly facilitated by viewing the fingers. Using somatosensory event-related potentials (ERPs), we show that effects of selection between adjacent fingers of the same hand at early somatosensory components P45 and N80 were absent when the fingers were viewed. Thus, we found a detrimental effect of vision on tactile-spatial within-body part (i.e. hand) selection. In contrast, effects of tactile-spatial selection between hands placed next to each other, which were first found at the P100 component, were unaffected by vision of the hands. Our findings suggest that (a) within- and between-hand selection can operate at different stages of processing, and (b) the effects of vision on within- and between-hand attentional selection may reflect fundamentally different mechanisms.

Introduction

Our successful interaction with the world around us, that is, our ability to grasp, manipulate, or defend ourselves against external objects, is greatly facilitated by orienting attention to those selective regions of space where interactions with external objects are likely to occur. Visual targets appearing in the space near a hand, for example, are prioritised for attentional processing over targets appearing outside of reach (Reed, Grubb, & Steele, 2006). Peripersonal space around the hand is encoded by bimodal visuo-tactile neurons in hand-centred coordinates (see Graziano & Gross, 1998), in similar frontoparietal neural networks as those supporting spatial attention and action preparation (e.g. Corbetta, 1998; Graziano, Hu, & Gross,1997; Kalaska & Crammond, 1995; Macaluso, Frith, & Driver, 2002; Rushworth, Johansen-Berg, Göbel, & Devlin, 2003). Attentional prioritisation occurs because the presence of a hand recruits additional neural substrates representing peripersonal space near the hand, which increases the salience of that region of space, compared to other locations less relevant for future actions.

Viewing the hand(s) can have profound effects, not only on visual-spatial attention, but also on tactile-spatial selective processing. For example, seeing one's own hand can ameliorate deficits in both visual-spatial selection (di Pellegrino & Frassinetti, 2000) and in tactile-spatial selection between the hands (Làdavas, Farnè, Zeloni, & di Pellegrino, 2000). If viewing a hand increases the salience of nearby regions of space, tactile-spatial attention may also benefit from viewing both hands because the same process would enhance information about the *relative* location of the hands. Indeed, the development of somatosensory spatial representations in such external coordinates depends on the availability of visual information early in life (e.g. Röder, Rösler, & Spence, 2004). In line with this, viewing both hands during sustained attention to tactile targets on one hand was found to facilitate tactile-spatial selection (Sambo, Gillmeister, & Forster, 2009) and to activate parietal regions involved in multimodal spatial representations (Macaluso, Frith, & Driver, 2000).

At present it is not known whether viewing one's own hand also facilitates tactile-spatial selection between fingers of the same hand. It has been suggested that within- and between-hand selection may operate at different stages of processing (Eimer & Forster, 2003a), and two recent studies have reported earlier effects of within-hand selection but delayed effects of between-hand selection in congenitally blind, compared to sighted, observers (Forster, Eardley, & Eimer, 2007; Röder, Föcker, Hötting, & Spence, 2008). This suggests that putative differences between these attentional mechanisms may be linked to the recruitment of external (visual-)spatial frameworks and/or to vision-related differences in the tuning of somatosensory representations. The present study tested the effects of viewing the hand(s) on within- and between-hand selection in sighted observers. In sustained tactile-spatial attention tasks, observers selected between adjacent fingers of the same hand (within-hand task) and between homologous fingers of both hands placed at an equivalent distance (between-hand task). Fingers were either both visible (fingers visible) or covered from view (fingers covered) throughout separate blocks. We compared ERPs to touch at attended and unattended fingers as a function of task and vision.

Methods

Participants

Sixteen participants (nine men; all right-handed; mean age = 26.3) gave informed written consent and were paid for their participation. The study was approved by the local ethics committee and conducted in accordance with the 1964 Declaration of Helsinki.

Stimuli and Materials

Participants' hands were covered by a wooden board with a viewing window, which was either open (fingers visible) or closed (fingers covered). Tactile stimuli were presented using two 12-volt solenoids, masked by white noise (65 dB SPL). The rod of the solenoid contacted the fingertip for 200ms for tactile non-targets (single taps), and the 200-ms contact was interrupted for 4 ms half-way through presentation for tactile targets (double taps). Vocal responses to targets at attended locations were recorded with a free-standing microphone.

Design and Procedure

Participants placed index and middle fingers of their left or right hand (within-hand task), or their left and right index fingers (between-hand task), on two tactile stimulators placed 2 cm to the left and right of a central fixation point, with the fingertips pointing away from the body (see Figure 1). In separate blocks they continually attended to either the left or the right finger to detect and vocally respond ("pa") to infrequent tactile targets (double taps) at that finger, ignoring tactile stimuli at the other finger (see Table 1). **They were instructed to maintain fixation on a white marker, which was**

located midway between attended and unattended fingers (fingers visible), or at an equivalent location on the closed viewing window (fingers covered).

Figure 1 about here

Table 1 about here

Each trial consisted of the 200-ms presentation of a tactile stimulus at either the attended or unattended finger, followed by a 1000-ms blank interval (total response time window: 1200ms), followed by a random intertrial interval (200-600 ms). Each participant completed two blocks of 72 trials of each combination of task (within- and between-hand), vision (fingers visible and fingers covered) and attended side (left and right), in counterbalanced order (see Table 1). Each of the 16 blocks was composed of 60 non-target trials (30 non-targets at the attended and 30 at the unattended finger), and twelve target trials (8 targets at the attended finger, requiring a vocal response, and 4 at the unattended finger).

<u>EEG recording and ERP analysis</u>

EEG was recorded with Ag/AgCl electrodes from Fp1, Fp2, F3, Fz, F4, FC5, FC1, FCz, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, O1 and O2 (subset of the international 10-10 system), referenced to the earlobes. Horizontal

EOG was recorded bipolarly from the outer canthi of both eyes; vertical EOG from above and below the right eye. EEG was amplified, band-pass filtered at 0.01 – 100 Hz, digitised at 500 Hz, and filtered off-line with a low pass filter of 40 Hz. EEG, HEOG and VEOG were epoched for a period from 100 ms before to 400 ms after the onset of the tactile stimulus. Trials with horizontal or vertical eye movements (HEOG or VEOG exceeding ± 40 µV relative to the 100-ms pre-stimulus baseline), eye blinks or other artefacts (a voltage exceeding ± 70 µV at any electrode relative to pre-stimulus baseline) measured in this interval were excluded from analysis. ERPs to non-targets were averaged relative to pre-stimulus baseline for all combinations of attention (attended vs. unattended finger), task (within-hand vs. between-hand task), vision (fingers visible vs. fingers covered), and stimulated hand (left vs. right). **ERP mean amplitudes were computed within separate, component-centred measurement windows from 45 ms to 340 ms post-stimulus onset (see Figure 3), covering P45 (45 - 65 ms), N80 (65 - 90 ms), P100 (95 - 125 ms), N140 (125 - 175 ms) components. For waveforms at late processing stages, ERP mean amplitudes were computed for two measurement windows, Nd1 (200 - 270 ms) and Nd2 (270 - 340 ms), with Nd1 overlapping with the N200 component.** Within each measurement window statistical analyses of ERP mean amplitudes were conducted for the nine electrodes situated close to and over somatosensory cortex (i.e. FC1, FCz, FC2, C3, Cz, C4, CP1, Pz, CP2). Repeated-measures ANOVAs were conducted for the factors attention (attended vs. unattended finger), task (within- vs. between-hand), vision (fingers visible vs. fingers covered), and electrode (see above). Follow-up ANOVAs were conducted for each time window in which effects of task or vision on attention were found. When appropriate, Greenhouse-Geisser adjustments to the degrees of freedom were applied.

Results

Figures 2 **and 3** show somatosensory ERPs at attended and unattended fingers for each vision condition in within- and between-hand tasks, **for the set of nine electrodes analysed (Figure 2), and enlarged for illustrative purposes for one example electrode (Figure 3).** In order to compare ERPs across tasks, figures and statistical analyses consider ERP waveforms to tactile stimuli on the index fingers only. That is, for the within-hand task attended waveforms were elicited by tactile stimulation to the index finger when this finger was attended, and unattended waveforms were elicited by tactile stimulation of the index finger when the middle finger was attended (i.e. index finger unattended).

Figure 2 about here

Figure 3 about here

Effects of tactile-spatial selection (differences between attended and unattended waveforms) were present at earlier stages of processing (45 - 90 ms post-

stimulus) for the within- than the between-hand task, but only when fingers of the same hand were covered from view (see top right panel in Figures 2 and 3). This was tested in an overall ANOVA for the factors attention (attended vs. unattended finger), task (within- vs. between-hand), vision (fingers visible vs. fingers covered), and electrode (FC1, FCz, FC2, C3, Cz, C4, CP1, Pz, CP2), in which there were significant three-way interactions between attention, task, and vision in the time windows of the first two somatosensory components, P45 (45 - 65 ms) and N80 (65 - 90 ms) (P45: $F(1,15) = 13.50$, $P = .002$; N80: $F(1,15) = 17.41$, $P = .001$). To test whether there were differences in tactile-spatial attention within and between hands, separate ANOVAs were conducted for each task. For the within-hand task, there were interactions between attention and vision (P45: $F(1,15) = 6.99$, $P = .018$; N80: $F(1,15) = 11.64$, $P = .004$). For the between-hand task, there were no attentional effects (P45: $F(1,15) < 1$, $P = .349$; N80: $F(1,15) < 1$, $P = .611$) or interactions between attention and vision (P45: $F(1,15) < 1$, $P = .416$; N80: $F(1,15) < 1$, $P = .967$). To test whether viewing the fingers affected within-hand selection, separate ANOVAs were conducted for each vision condition. These confirmed that effects of attention were present only when fingers were covered (main effect of attention: P45: $F(1,15) = 5.15$, $P = .038$; N80: $F(1,15) = 9.79$, $P = .007$), and not when fingers were visible (main effect of attention: P45: $F(1,15) = 2.44$, $P = .139$; N80: $F(1,15) < 1$, $P = .426$)[1]. There were no interactions between attention and electrode in either vision condition for the P45 ($F(8,120) < 1$, $P \geq .405$). There were no such interactions for the N80 when fingers were visible ($F(8,120) = 1.57$, $P = .214$), but there was a reliable interaction between attention and electrode when fingers were

covered (*F*(8,120) = 5.03, *P* = .010). Pairwise comparisons showed that attentional effects were somewhat stronger for central-parietal electrodes (C3/4c, Cz, CP1/2i, Pz, CP1/2c: *P* ≤ .010) than for frontal-central electrodes (C3/4i, FC1/2c, FCz, FC1/2i: *P* ≤ .042).

Effects of tactile-spatial selection in the between-hand task were first present for the P100 component (95 - 125 ms). An overall ANOVA showed an interaction between attention, task, and electrode (*F*(8,120) = 6.68, *P* = .003). Separate ANOVAs for each task showed that there were no attentional effects in the within-hand task (attention: *F*(1,15) < 1, *P* = .585; attention x vision: *F*(1,15) = 1.38, *P* = .258), except for an interaction between attention and electrode (*F*(8,120) = 10.32, *P* < .001), and pairwise comparisons showed that there were no attentional effects for any electrode (*P* ≥ .080) except C3/4c (*P* = .027). For the between-hand task, there was an overall effect of attention (*F*(1,15) = 5.13, *P* = .039), but this was independent of whether the fingers were visible or covered (attention x vision: *F*(1,15) < 1, *P* = .962). There was also no interaction between attention and electrode (*F*(8,120) = 2.19, *P* = .128).

There were no effects of, or task- or vision-related interactions with, attention for the N140 component (125 - 175 ms) in the overall ANOVAs (*F* ≤ 3.3, *P* ≥ .067).

For the time range of the early Nd (Nd1: 200 - 270 ms), an overall ANOVA showed that effects of attention (*F*(1,15) = 58.41, *P* < .001) did not differ as a

function of task or vision (attention x task: *F*(1,15) = 2.00, *P* = .178; attention x vision: *F*(1,15) < 1, *P* = .414; attention x task x vision: *F*(1,15) < 1, *P* = .489).

For the late Nd (Nd2: 270 - 340 ms), however, the overall ANOVA showed that effects of attention (*F*(1,15) = 14.82, *P* = .002) differed as a function of task (attention x task: *F*(1,15) = 4.74, *P* = .046). Separate ANOVAs for each task showed that, for the within-hand task, effects of attention (*F*(1,15) = 26.17, *P* < .001) were independent of vision (attention x vision: F(1,15) = 1.58, P = .224), but differed as a function of electrode (attention x electrode: F(8,120) = 20.00, P < .001). Pairwise comparisons showed that attentional effects were present for all electrodes (P ≤ .014). There were no attentional effects in the ANOVA for the between-hand task (attention: F(1,15) = 4.01, P = .064; attention x vision: F(1,15) < 1, P = .960) except for an interaction between attention and electrode (F(8,120) = 16.87, P < .001). Pairwise comparisons showed that there were attentional effects at frontal-central electrodes (FC1/2c, FCz, FC1/2i: P ≤ .017), marginal effects at electrode C3/4i (P = .051), but no effects at central-parietal electrodes (C3/4c, Cz, CP1/2i, Pz, CP1/2c: *P* ≥ .068).

Discussion

Previous studies have shown that tactile-spatial attention can be facilitated by viewing the hand(s) (e.g. Làdavas et al., 2000; Sambo et al., 2009). Using somatosensory ERPs as indices of tactile-spatial attention, we tested whether attentional selection between fingers of the same hand is affected by vision in the same way as selection between fingers of different hands. We found that viewing the fingers had dramatically different effects on tactile-spatial selection between fingers of the same and of different hands. **Effects reflecting attentional selection between adjacent fingers of the same hand were first found at early somatosensory ERP components P45 and N80 when fingers were covered, but only as a later negative difference (Nd) when fingers were visible. Effects reflecting between-hand selection were first found at the mid-latency P100 component, as well as at later Nd stages of processing, regardless of vision. In other words, viewing adjacent fingers of the same hand led to an absence of tactile-spatial attention effects at early somatosensory ERP components P45 and N80. Viewing fingers of different hands placed at an equivalent distance from one another, however, did not modulate ERP effects of attentional selection at any time range.**

Within- and between-hand tactile-spatial attention modulates different stages of processing

We found that within-hand selection led to earlier effects of tactile-spatial attention (45-90 ms) than between-hand selection (95-125 ms), at least when no vision of the hand(s) was available. In line with previous suggestions (Eimer & Forster, 2003a), this indicates that within- and between-hand selection may operate at different stages of processing. Importantly, our study is the first to directly compare the ERP signature of the processes involved in within- and between-hand tactile-spatial selection.

In tasks of sustained tactile attention, between-hand selection most consistently affects N140 and Nd stages of processing (e.g. Adler, Giabbiconi, & Müller, 2009; Desmedt & Robertson, 1977; Eimer and Driver, 2000; Eimer and

Forster, 2003b; Garcìa-Larrea, Lukaszewicz, & Mauguière, 1995; Hötting, Rösler, & Röder, 2003; Michie, 1984; Sambo et al., 2009; Zopf, Giabbiconi, Gruber, & Müller, 2004). Similar effects are less often shown in the time range of earlier somatosensory components such as P45 (e.g. Garcìa-Larrea, Bastuji, & Mauguière, 1991; Schubert, Ritter, Wüstenberg, Preuschhof, Curio, Sommer, & Villringer, 2008), N80 (e.g. Desmedt & Robertson, 1977; Eimer & Forster, 2003b; Hötting et al., 2003; Michie, Bearpark, Crawford, & Glue, 1987; Schubert et al., 2008), and P100 (e.g. Desmedt & Robertson, 1977; Eimer and Forster, 2003a; Michie et al., 1987; Schubert et al., 2008). Similar to previous findings, our study has shown that selecting between fingers of different hands affects P100 (95-125 ms) as well as later stages of processing (Nd1; 200-270 ms). Interestingly, and unlike most studies of between-hand selection, the N140 was found to be unaffected by attention. This may be because our observers' hands were placed in close spatial proximity, which is not typical in studies of between-hand selection. This suggests that the N140 may be modulated by spatial-selective attention primarily when the hands are sufficiently distant in external space. This is consistent with effects of hand distance on attentional modulations of the N140 (Eimer, Forster, Fieger, & Harbich, 2004), and is in line with the suggestion that this component is linked to the external spatial aspects of attention (Garcìa-Larrea et al., 1995).

Very few studies have investigated effects of attentional selection between fingers of the same hand. In a study most closely comparable to our own, Eimer & Forster (2003a) found that within-hand selection modulated P100 and Nd, but not other stages of processing. Attentional modulations in the time range of the Nd were

also found for within-hand selection regardless of vision in the present study. This suggests that attentional effects at these later stages are unaffected both by vision (see also Sambo et al., 2009) and by whether selected fingers are on the same or on different hands (see also Eimer & Forster, 2003a). However, there was some indication that selected body parts may play a role in attentional modulations at latencies beyond the N200 component: Effects of within-hand selection were stronger than those of between-hand selection in the latest time window (Nd2; 270-340 ms). This shows for the first time that attentional effects at later processing stages can persist for longer in within- than between-hand selection, which may reflect greater in-depth processing of task-relevant features of attended stimuli when selecting between adjacent fingers of the same hand. Importantly, and unlike Eimer & Forster (2003a), we show that within-hand selection can affect somatosensory components thought to reflect earlier, and possibly distinct, stages of tactile processing than P100 (i.e. P45 and N80) (e.g. Hämäläinen, Kekoni, Sams, Reinikainen, & Näätänen, 1990). Differences in experimental set-up may account for these latency differences - the stimulated hand, though never directly viewed, was visible to observers in Eimer & Forster's study, but it was completely covered in the present task. In line with this, and similar to our findings, attentional modulations in the time range of P45 have previously been demonstrated in observers who did not see the stimulated hand (Desmedt, Huy, & Bourget, 1983; Garcìa-Larrea, Bastuji, & Mauguière, 1991; but see Josiassen, Shagass, Roemer, Ercegovac, & Straumanis, 1982, for an absence of early ERP effects in a comparable task). In these studies, however, ERPs at attended and unattended fingers were each

compared to a control condition (rest) in which no attentional task was performed, rather than directly with one another. Therefore, the present study is the first to explicitly report spatial-selective attentional modulations for within-hand selection at time ranges overlapping, not only with P45, but also with the N80 component.

Taken together, the findings of the present study suggest that the modulation of early somatosensory components P45 and N80 through spatial-selective attention may be specific to selecting between adjacent fingers of the same hand. Although some studies have suggested that P45 and N80 can also be affected by selecting between fingers of different hands (e.g. Garcìa-Larrea et al., 1991; Michie et al., 1987; Schubert et al., 2008), this was not replicated in the present study, in which within- and between-hand selection were compared directly. Within-hand selection may be primarily associated with processing in primary somatosensory cortex (SI) because SI contains separate representations of the fingers, a distinctiveness that is not preserved in secondary somatosensory cortex (SII) (e.g. Ruben, Schwiemann, Deuchert, Meyer, Krause, Curio et al., 2001). Attentional selection between different hands has also been shown to modulate processing in SI (e.g. Noppeney, Waberski, Gobbelé, & Buchner, 1999; however, other studies have associated between-hand selection with processing in numerous areas including SI and SII, **intraparietal sulcus, parietal operculi, and left frontal regions** (e.g. De Santis, Spierer, Clarke, & Murray, 2007; **Macaluso et al., 2002; Schubert et al., 2008**). While their precise cortical origins remain speculative, our findings nevertheless provide a direct demonstration that within-hand selection can operate at earlier stages of processing than between-hand selection.

Effects of viewing fingers on within- and between-hand tactile attentional selection

We found that **tactile-spatial attentional effects at early somatosensory components were absent when viewing adjacent fingers of the same hand**, while ERP effects of between-hand attentional selection were unaffected by vision. Effects of within-hand spatial selection were present at early stages of processing when fingers were covered (**P45 and N80**; 45-90 ms post-stimulus), but these attention effects were only present at substantially later stages (**Nd**; 200-340 ms) when fingers were visible. Effects of spatial selection between index fingers of different hands placed at equivalent locations were first present for the mid-latency **P100 component** (95-125 ms) and were also found at later stages (**Nd1**; 200-270 ms), irrespective of vision. At least with regard to the effects of viewing the hand(s), these findings may indicate that there are fundamental differences between tactile-spatial attention mechanisms operating within- and between-hands. This is in line with the observation that the (un)availability of visual information early in life may have fundamentally different effects on tactile-spatial attention within and between hands. **Selection between tactile events at the two hands was found to have a later onset in congenitally blind (Nd) than sighted (P100) observers** (Röder et al., 2008), suggesting that the external spatial framework provided by developmental vision may facilitate tactile-spatial selection between the hands. However, blind observers were also shown to **have effects of within-hand selection at earlier stages of somatosensory processing (P100, N140) than sighted observers (Nd)** (Forster et al., 2007). Since somatosensory representations in the congenitally blind may be more fine-tuned than in the sighted (see Röder et al., 2008), and since the location of adjacent fingers can be described along purely somatotopic, rather than external spatial, coordinates (Haggard, Kitadono, Press, & Taylor-Clarke, 2006; Röder, Spence, & Rösler, 2002; but see Shibuya, Takahashi, & Kitazawa, 2007), improved within-hand selection may be due to superior somatosensory representations of the fingers whenever spatial selection occurs within somatotopic frameworks (i.e. within-hand). Taken together with the results of the present study, this suggests that, in the sighted, on-line visual information may facilitate between-hand selection by reinforcing tactile localisation in external spatial frames of reference, but **interfere with** within-hand tactile-spatial selection by affecting the somatosensory representations of the fingers. In the following, we will discuss how these different mechanisms may account for our findings.

<u>Effects of viewing both hands on between-hand tactile-spatial selection depend on hand distance in external space</u>

Since the hands are represented in external spatial coordinates, visual information about their relative locations may be expected to enhance tactile-spatial selection. Indeed, our earlier study (Sambo et al., 2009) showed that viewing the hands (placed at some distance from each other) led to effects of attentional selection **at earlier somatosensory components (P100, N140) than not viewing the hands (Nd)**. This effect was not replicated in the present study, where viewing the hands (placed close together) had no effects on tactile-spatial attentional modulations **(P100, Nd)**. Taken together, these observations suggest that the interactions between spatial attentional mechanisms and those subserving the representation of peripersonal space near the hand(s) can be profoundly affected by the distance between the two hands in external space. Specifically, the facilitatory effects of viewing the hands on tactile-spatial selection arise only when the hands are sufficiently separated in external space, and this visual facilitation is diminished or altogether absent when selecting between hands in close spatial proximity. Tactile selection is generally more effective at greater distances between the hands (e.g. Driver & Grossenbacher, 1996; Eimer et al., 2004) because more distant tactile event locations are more likely to represent separate sources of information (Gillmeister, Adler, & Forster, 2009). Similarly, temporal order judgments (TOJs) for tactile events on the hands improve not only for greater distances between hands (Shore, Gray, Spry, & Spence, 2005), but also when greater distances are merely illusory by providing false visual feedback (Gallace & Spence, 2005). Thus, tactile-spatial selection may be facilitated by the availability of additional (visual) spatial information about the relative distance of the hands in external space, possibly through interactions between the frontoparietal networks involved in spatial attention and the (visual-tactile) representation of peripersonal space around the hands, respectively. Such interactions may also reinforce the remapping of tactile information into references frames based on external spatial coordinates (see Röder et al., 2004). Intriguingly, our results suggest that such remapping, or other facilitatory interactions between spatial attention and hand-centred peripersonal spatial networks, may not necessarily take place when the hands are close. This may be because any visually-induced increase in salience of space near one hand would essentially serve to facilitate spatial attention and future actions also with the other hand. Further studies may clarify the precise mechanisms underlying these interactions between vision and hand position effects.

Effects of viewing adjacent fingers on within-hand tactile-spatial selection

If similar tactile-attentional mechanisms supported the selection of fingers within and between hands, it might be expected that, like between-hand selection, within-hand selection would be unaffected by vision, since the viewed fingers were in close spatial proximity in both cases. **Instead, we found that viewing adjacent fingers of the same hand abolished the attentional modulations observed at early somatosensory components P45 and N80 when fingers were covered.** Importantly, this is the first study to show that viewing adjacent fingers of the same hand can have detrimental effects on tactile-spatial selection.

Several mechanisms may be proposed to explain this adverse effect of vision. First, a conflict between tactile- and visual-spatial selection processes brought about by attending selectively to touch on one finger while both fingers were visible may account for **the absence of early-latency effects of** tactile-spatial within-hand selection when fingers were visible. Similarly, TOJs for touch on fingers of the same hand can be adversely affected by incongruent spatiotemporal dynamics of visual events presented close to the touched fingers (Shibuya et al., 2007), similar to comparable visual-tactile congruency studies (e.g. Yamamoto & Kitazawa, 2001). If this were the case, however, one would expect a similar conflict to arise also during vision of the fingers in our between-hand task. Instead, we found that vision had detrimental effects on tactile-spatial within-hand selection, but not on between-hand selection, suggesting that these adverse effects are specific to fingers of the same hand.

Alternatively, simultaneous visual exposure to adjacent fingers may modulate tactile-spatial selection by affecting their (adjacent) somatosensory representations. Since the fingers engage in a myriad of sensorimotor functions, somatosensory cortex may need to continuously adapt to the demands of specific tasks and stimulation patterns in order to optimally process afferent inputs. For example, selective attention between adjacent fingers typically causes instantaneous changes in SI that sharpen the contrast between the representations of attended and unattended (unseen) fingers through lateral inhibitory processes (Braun, Haug, Wiech, Birbaumer, Elbert, & Roberts, 2002; Iguchi, Hoshi, & Hashimoto, 2001), which enables the more efficient filtering of tactile inputs at selected locations. When adjacent fingers of the same hand are viewed, however, this filtering of attended inputs may be **absent until later processing stages**, as shown in our study. Since such visual-tactile interactions arise in a bimodal system, vision and touch may be both independently and jointly capable of inducing similar exposure effects on the processing of touch in SI (Harris, Arabzadeh, Moore, & Clifford, 2007). In line with this, both vision of the hand and tactile exposure have been shown to lead to changes in the cortical organisation of SI (e.g. Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Schäfer, Heinze, & Rotte, 2005a; Taylor-Clarke, Kennett, & Haggard, 2002), and to concomitant improvements in tactile spatial acuity at the stimulated finger(s) (e.g. Kennett, Taylor-Clarke, & Haggard, 2000; Pleger, Dinse, Ragert, Schwenkreis, Malin, & Tegenthoff, 2001; Schäfer, Heinze, & Rotte, 2005b). Interestingly, however, SI cortical reorganisation due to temporally correlated tactile exposure (Braun, Schweizer, Elbert, Birbaumer, & Taub, 2000; Braun, Wilms, Schweizer, Godde, Preissl, Birbaumer, 2000; Godde, Spengler, & Dinse, 1996; Rockstroh, Vanni, Elbert, & Hari, 1998; Sterr, Müller, Elbert, Rockstroh, Pantev, & Taub, 1998), can also compromise observers’ ability to localise tactile stimuli to the correct finger (Braun, Schweizer et al. 2000; Rockstroh et al., 1998; Sterr et al., 1998). We propose that the effects of viewing both index and middle finger on tactile-spatial attention may be similar to the effects of temporally correlated tactile exposure. That is, correlated visual exposure to adjacent body parts may lead to changes in their cortical organisation in SI, and to a concomitant decrease in the effective isolation of tactile sensations on one finger from those on another. **While SI is known to instantaneously adapt to spatial attentional demands and to the properties of tactile stimulation (Braun et al., 2002; Braun, Schweizer, et al., 2000; Iguchi et al., 2004), it is unclear how rapidly the proposed effects of visual exposure may interact with tactile-attentional filtering mechanisms. In our study, effects of vision on attentional selection were obtained from observers who viewed their fingers for no more than a few minutes during each experimental block. Similarly, prolonged viewing of the body is typically not necessary to show vision-related improvements of tactile spatial acuity (e.g. Schäfer et al., 2005a; Taylor-Clarke et al., 2002). Therefore, the effects of visual exposure on tactile attentional selection and spatial acuity are likely to be as instantaneous as the effects of attentional selection themselves.** Future research may clarify the specific changes to SI mechanisms that are induced by visual exposure to body parts and how they relate to those brought about by selective attention and tactile exposure.

Conclusion

In summary, the findings of our study indicate that the mechanisms underlying the effects of viewing the hand(s) on tactile-spatial attention can dramatically differ depending on whether the selected locations are on the same or on different hands. In addition, this is the first study to show that viewing the hand can adversely affect tactile-spatial selection between adjacent fingers. We have proposed candidate mechanisms that may underlie each of these effects.

Acknowledgments

This research was supported by a grant from the Biotechnology and Biological Sciences Research Council (BBSRC) to B.F.

References

Adler, J., Giabbiconi, C. M., & Müller, M. M. (2009). Shift of attention to the body location of distracters is mediated by perceptual load in sustained somatosensory attention. *Biol. Psychol.,* **81**, 77-85.

Braun, C., Haug, M., Wiech, K., Birbaumer, N., Elbert, T., & Roberts, L. E. (2002). Functional organization of primary somatosensory cortex depends on the focus of attention. *Neuroimage,* **17**, 1451-1458.

Braun, C., Wilms, A., Schweizer, R., Godde, B., Preissl, H., & Birbaumer, N. (2000). Activity patterns of human somatosensory cortex adapt dynamically to stimulus properties. *Neuroreport,* **11**, 2977-2980.

Braun, C., Schweizer, R., Elbert, T., Birbaumer, N., & Taub, E. (2000). Differential activation in somatosensory cortex for different discrimination tasks. *J. Neurosci.,* **20**, 446-450.

Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: identical independent or overlapping neural systems? Proc. Natl. Acad. Sci. U.S.A., **95**, 831–8.

di Pellegrino, G., & Frassinetti, F. (2000). Direct evidence from parietal extinction of enhancement of visual attention near a visible hand. *Curr. Biol.,* **10**, 1475–1477.

De Santis, L., Spierer, L., Clarke, S., & Murray, M. M. (2007). Getting in touch: segregated somatosensory what and where pathways in humans revealed by electrical neuroimaging. *Neuroimage,* **37**, 890-903.

Desmedt, J. E., Huy, N. T., & Bourget, M. (1983). The cognitive P40, N60 and P100 components of somatosensory evoked potentials and the earliest electrical signs of sensory processing in man. *Electroencephalogr. Clin. Neurophysiol.,* **56**, 272-282.

Desmedt, J. E., & Robertson, D. (1977). Differential enhancement of early and late components of the cerebral somatosensory evoked potentials during forced-paced cognitive tasks in man. *J. Physiol.,* **271**, 761–782.

Driver, J. & Grossenbacher, P. (1996). Multimodal constraints on tactile spatial attention. In Innui, T. & McClelland, J. (eds), *Attention and Performance* (XVI ed.). MIT Press, Cambridge, MA, pp. 209-235.

Eimer, M., & Driver, J. (2000). An event-related brain potential study of cross-modal links in spatial attention between vision and touch. *Psychophysiology,* **37**, 697-705.

Eimer, M. & Forster, B. (2003a). The spatial distribution of attentional selectivity in touch: evidence from somatosensory ERP components. *Clin. Neurophysiol.,* **114**, 1298-1306.

Eimer, M., & Forster, B. (2003b). Modulations of early somatosensory ERP components by transient and sustained spatial attention. *Exp. Brain Res.,* **151**, 24–31.

Eimer, M., Forster, B., Fieger, A., & Harbich, S. (2004). Effects of hand posture on preparatory control processes and sensory modulations in tactile-spatial attention. Clin. Neurophysiol., **115**, 596–608.

Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science,* **270**, 305-307.

Forster, B., Eardley, A.F. & Eimer, M. (2007). Altered tactile spatial attention in the early blind. Brain Res., **1131**, 149–154.

Gallace, A. & Spence, C. (2005). Visual capture of apparent limb position influences tactile temporal order judgments. *Neurosci. Lett.,* **379***,* 63-68.

Garcìa-Larrea, L., Bastuji, H., & Mauguière, F. (1991). Mapping study of somatosensory evoked potentials during selective spatial attention. *Electroencephalogr. Clin. Neurophysiol.,* **80**, 201-14.

Garcìa-Larrea, L., Lukaszewicz, A. C., & Mauguière, F. (1995). Somatosensory responses during selective spatial attention: the N120 to N140 transition. *Psychophysiology,* **32**, 526–537.

Gillmeister, H., Adler, J., & Forster, B. (in press, 2009). Object-based Spatial Attention in Touch: Holding the Same Object with Both Hands Delays Attentional Selection. *J. Cogn. Neurosci.*, doi:10.1162/jocn.2009.21265.

Godde, B., Spengler, F., & Dinse, H. R. (1996). Associative pairing of tactile stimulation induces somatosensory cortical reorganization in rats and humans. *Neuroreport,* **8**, 281-285.

Graziano, M. S., Hu, X. T., & Gross, C. G. (1997). Visuospatial properties of ventral premotor cortex. *J. Neurophysiol.,* **77***,* 2268–2292.

Haggard, P., Kitadono, K., Press, C., & Taylor-Clarke, M. (2006). The brain's fingers and hands. *Exp. Brain Res.,* **172**, 94–102.

Hämäläinen, H., Kekoni, J., Sams, M., Reinikainen, K., & Näätänen, R. (1990). Human somatosensory evoked potentials to mechanical pulses and vibration: contributions of SI and SII somatosensory cortices to P50 and P100 components. *Electroencephalogr. Clin. Neurophysiol.,* **75**, 13-21.

Harris, J. A., Arabzadeh, E., Moore, C. A., & Clifford, C. W. (2007). Noninformative vision causes adaptive changes in tactile sensitivity. *J. Neurosci.,* **27**, 7136-7140.

Hötting, K., Rösler, F., & Röder, B. (2003). Crossmodal and intermodal attention modulate event-related brain potentials to tactile and auditory stimuli. *Exp. Brain Res.,* **148**, 26-37.

Iguchi, Y., Hoshi, Y., & Hashimoto, I. (2001). Selective spatial attention induces short-term plasticity in human somatosensory cortex. *Neuroreport,* **12**, 3133-3136.

Josiassen, R. C., Shagass, C., Roemer, R. A., Ercegovac, D. V., & Straumanis, J. J. (1982). Somatosensory evoked potential changes with a selective attention task. *Psychophysiology,* **19**, 146– 159.

Kalaska, J. F., & Crammond, D. J. (1995). Deciding not to GO: Neuronal correlates of response selection in a GO/NOGO task in primate premotor and parietal cortex. *Cereb. Cortex,* **5***,* 1047–3211.

Kennett, S., Taylor-Clarke, M., & Haggard, P. (2001). Noninformative vision improves the spatial resolution of touch in humans. *Curr. Biol.,* **11***,* 1188-1191.

Làdavas, E., Farnè, A., Zeloni, G., & di Pellegrino G. (2000). Seeing or not seeing where your hands are. *Exp. Brain Res.,* **131**, 458-467.

Macaluso, E., Frith, C., & Driver, J. (2000). Selective spatial attention in vision and touch: unimodal and multimodal mechanisms revealed by PET. *J. Neurophysiol.,* **83**, 3062-3075.

Macaluso, E., Frith, C. D., & Driver, J. (2002). Supramodal effects of covert spatial orienting triggered by visual or tactile events. *J. Cogn. Neurosci.,* **14***,* 389–401.

Michie, P. T. (1984). Selective attention effects on somatosensory event-related potentials. *Ann. N. Y. Acad. Sci.,* **425**, 250–255.

Michie, P. T., Bearpark, H. M., Crawford, J. M., & Glue, L. C. T. (1987). The effects of spatial selective attention on the somatosensory event-related potential. *Psychophysiology,* **24**, 449–463.

Noppeney, U., Waberski, T. D., Gobbelé, R., & Buchner, H. (1999). Spatial attention modulates the cortical somatosensory representation of the digits in humans. *Neuroreport,* **10***,* 3137-3141.

Pleger, B., Dinse, H. R., Ragert, P., Schwenkreis, P., Malin, J. P., & Tegenthoff, M. (2001). Shifts in cortical representations predict human discrimination improvement. *Proc. Natl. Acad. Sci. U. S. A.,* **98***,* 12255-12260.

Reed, C. L., Grubb, J. D. & Steele, C. (2006). Hands up: Attentional prioritization of space near the hand. J. Exp. Psychol. Hum. Percept. Perform., **32**, 166–177.

Rockstroh, B., Vanni, S., Elbert, T., and Hari, R. (1998). Extensive somatosensory stimulation alters somatosensory evoked fields. In Aine, C., Okada, Y., Stroink, G., Swithenby, S., & Wood, C. (eds), *Advances in Biomagnetism Research: Biomag96 International Conference on Biomagnetism*. Springer, New York, pp. 848-851.

Röder, B., Föcker, J., Hötting, K., & Spence, C. (2008). Spatial coordinate systems for tactile spatial attention depend on developmental vision: evidence from event-related potentials in sighted and congenitally blind adult humans. Eur. J. Neurosci., **28**, 475-483.

Röder, B., Spence, C. & Rösler, F. (2002) Assessing the effect of posture change on tactile inhibition-of-return. Exp. Brain Res., **143**, 453–462.

Röder, B., Rösler, F., & Spence, C. (2004). Early vision impairs tactile perception in the blind. *Curr. Biol.,* **14**, 121-124.

Ruben, J., Schwiemann, J., Deuchert, M., Meyer, R., Krause, T., Curio, G. et al. (2001). Somatotopic organization of human secondary somatosensory cortex. *Cereb. Cortex,* **11**, 463-473.

Rushworth, M. F. S., Johansen-Berg, H., Göbel, S. M., & Devlin, J. T. (2003). The left parietal and premotor cortices: Motor attention and selection. *Neuroimage,* **20**, S89–S100.

Sambo, C. F., Gillmeister, H., & Forster, B. (2009). Viewing the body modulates neural mechanisms underlying sustained spatial attention in touch. *Eur. J. Neurosci.,* **30**, 143-150.

Schäfer, M., Heinze, H. J., & Rotte, M. (2005a). Seeing the hand being touched modulates the primary somatosensory cortex. *Neuroreport,* **16**, 1101-1105.

Schäfer, M., Heinze, H. J., & Rotte, M. (2005b). Viewing touch improves tactile sensory threshold. *Neuroreport,* **16**, 367-370.

Schubert, R., Ritter, P., Wüstenberg, T., Preuschhof, C., Curio, G., Sommer, W., & Villringer, A. (2008). Spatial attention related SEP amplitude modulations covary with BOLD signal in S1 - a simultaneous EEG-fMRI study. *Cereb. Cortex*, **18**, 2686-700.

Shibuya, S., Takahashi, T., & Kitazawa, S. (2007). Effects of visual stimuli on temporal order judgments of unimanual finger stimuli. *Exp. Brain Res.,* **179***,* 709-721.

Shore, D. I., Gray, K., Spry, E., & Spence, C. (2005). Spatial modulation of tactile temporal-order judgments. *Perception,* **34***,* 1251-1262.

Sterr, A., Müller, M. M., Elbert, T., Rockstroh, B., Pantev, C., & Taub, E. (1998). Perceptual correlates of changes in cortical representation of fingers in blind multifinger Braille readers. *J. Neurosci.,* **18***,* 4417-4423.

Taylor-Clarke, M., Kennett, S., & Haggard, P. (2002). Vision modulates somatosensory cortical processing. *Curr. Biol.,* **12**, 233-236.

Yamamoto S, Kitazawa S (2001). Reversal of subjective temporal order due to arm crossing. Nat. Neurosci., **4**, 759–765.

Zopf, R., Giabbiconi, C. M., Gruber, T., Müller, M. M. (2004). Attentional modulation of the human somatosensory evoked potential in a trial-by-trial spatial cueing and sustained spatial attention task measured with high density 128 channels EEG. *Cogn. Brain Res.,* **20**, 491-509.

Footnotes

[1] The same was found when we included attended and unattended ERP waveforms to tactile stimuli on the middle finger in the analyses: Effects of attentional selection were present only when fingers were covered (main effect of attention: 45-65 ms: $F(1,15) = 8.8$, $P = .009$; 65-90 ms: $F(1,15) = 23.1$, $P < .001$), and not when fingers were visible (main effect of attention: 45-65 ms: $F(1,15) < 1$, $P = .761$; 65-90 ms: $F(1,15) = 1.7$, $P = .216$). **Note that this also indicates that task-related differences in ERP effects of attentional selection are unlikely to be due to the index finger crossing over the midline and into the opposite hemispace in within-hand but not in between-hand tasks.**

Tables

Table 1. Experimental conditions defined by task and attended / unattended finger, and the number of experimental blocks completed in fingers visible / fingers covered conditions. Left and Right refer to left hand and right hand, respectively.

Task	*Attended finger*	*Unattended finger*	*Number of blocks*
Within-hand	Left index	Left middle	2 (1 fingers visible, 1 fingers covered)
	Left middle	Left index	2 (1 fingers visible, 1 fingers covered)
	Right index	Right middle	2 (1 fingers visible, 1 fingers covered)
	Right middle	Right index	2 (1 fingers visible, 1 fingers covered)
Between-hand	Left index	Right index	4 (2 fingers visible, 2 fingers covered)
	Right index	Left index	4 (2 fingers visible, 2 fingers covered)

Figure legends:

Figure 1. Participants' view of their fingers in within-hand (A) and between-hand (B) tasks. Hands and arms were covered by a black wooden board with a viewing window. In fingers visible conditions, this window was open and observers fixated on a white marker located between attended and unattended fingers. In fingers covered conditions (separate blocks, not shown), observers fixated on a white marker at an equivalent location on the closed viewing window.

Figure 2. Grand-averaged ERP waveforms to tactile stimuli at attended (black lines) and unattended (grey lines) fingers in within-hand (A) and between-hand (B) tasks in fingers visible (left panel) and fingers covered (right panel) conditions, shown for nine analysed electrodes.

Figure 3. Grand-averaged ERP waveforms to tactile stimuli at attended (black lines) and unattended (grey lines) fingers in within-hand (A) and between-hand (B) tasks in fingers visible (left panel) and fingers covered (right panel) conditions. Waveforms are shown for one example electrode (C3/4c, located over somatosensory cortex contralateral to the stimulated hand). Left panel in A shows the measurement windows for which analyses were conducted in ms. Significant main effects of attention per condition and measurement window are denoted by asterisks.

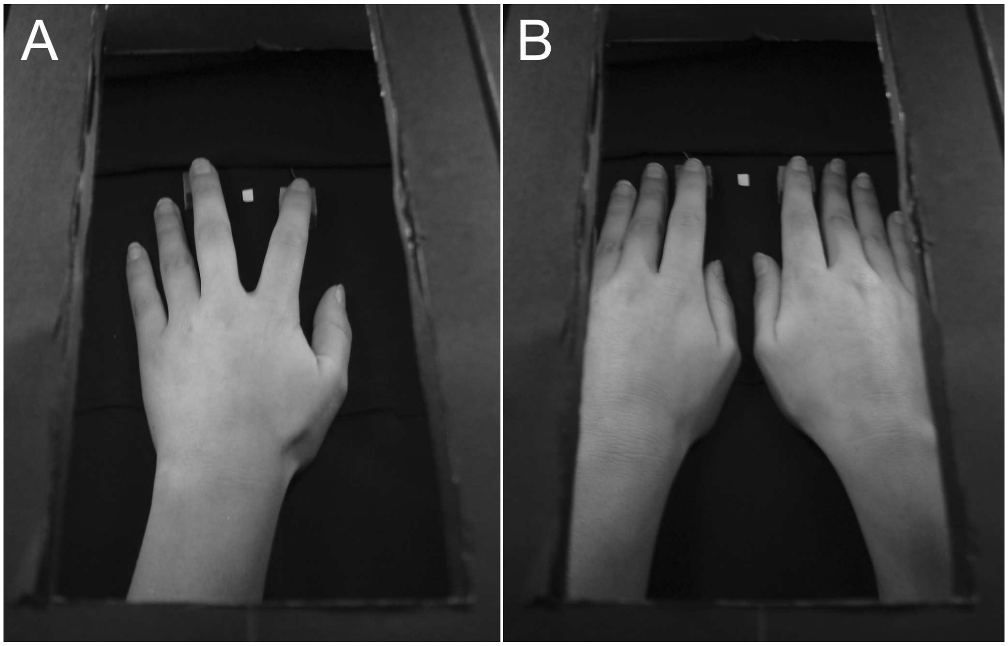

Figure 1. Participants' view of their fingers in within-hand (A) and between-hand (B) tasks. Hands and arms were covered by a black wooden board with a viewing window. In fingers visible conditions, this window was open and observers fixated on a white marker located between attended and unattended fingers. In fingers covered conditions (separate blocks, not shown), observers fixated on a white marker at an equivalent location on the closed viewing window.
150x95mm (350 x 350 DPI)

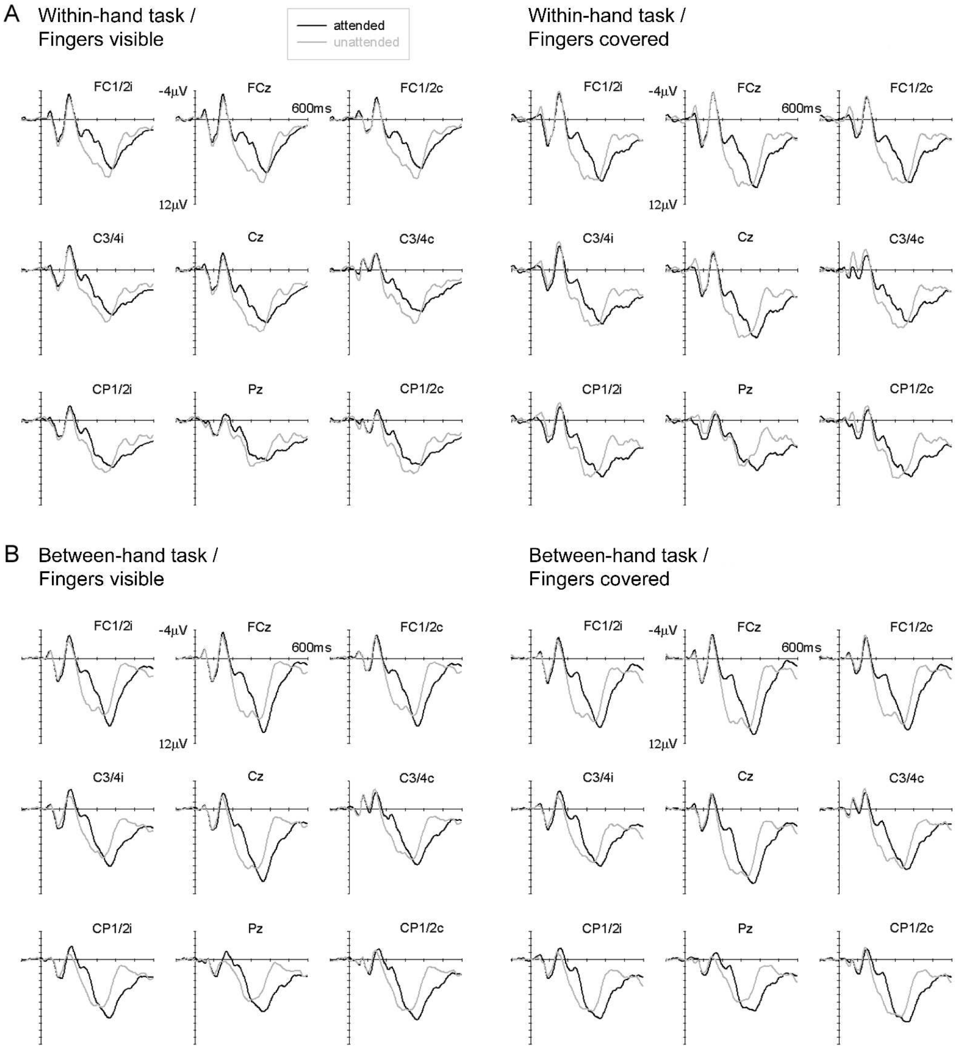

Figure 2. Grand-averaged ERP waveforms to tactile stimuli at attended (black lines) and unattended (grey lines) fingers in within-hand (A) and between-hand (B) tasks in fingers visible (left panel) and fingers covered (right panel) conditions, shown for nine analysed electrodes.
249x270mm (500 x 500 DPI)

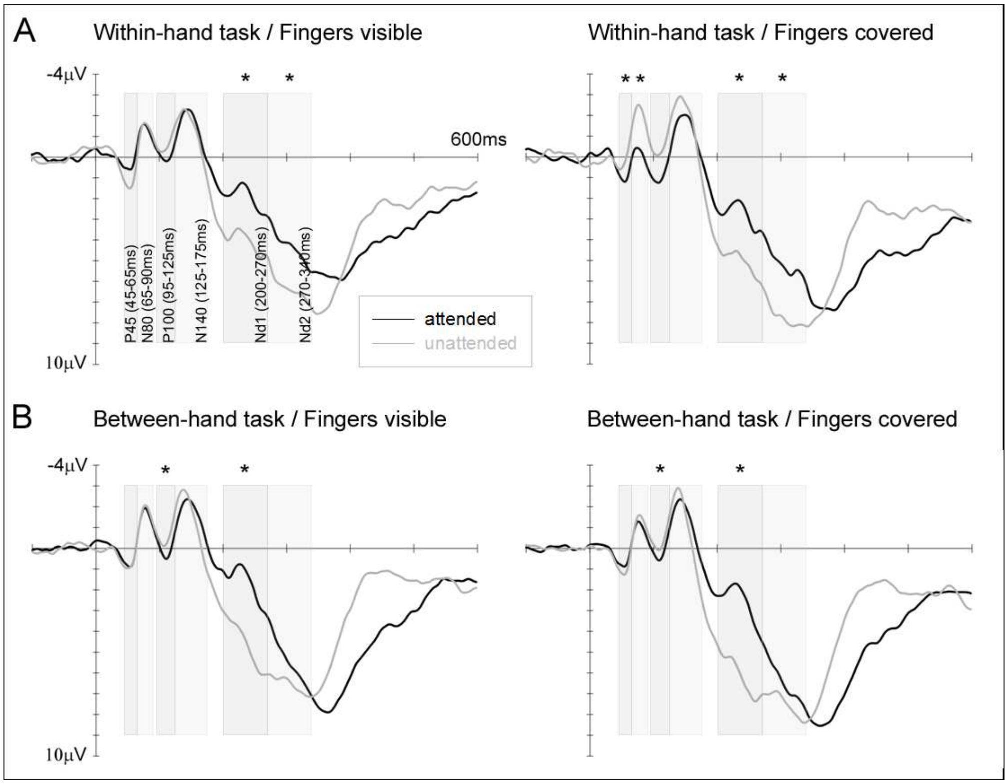

Figure 3. Grand-averaged ERP waveforms to tactile stimuli at attended (black lines) and unattended (grey lines) fingers in within-hand (A) and between-hand (B) tasks in fingers visible (left panel) and fingers covered (right panel) conditions. Waveforms are shown for one example electrode (C3/4c, located over somatosensory cortex contralateral to the stimulated hand). Left panel in A shows the measurement windows for which analyses were conducted in ms. Significant main effects of attention per condition and measurement window are denoted by asterisks.
188x146mm (150 x 150 DPI)