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Cue-locked lateralized components in a tactile spatial attention task: evidence for a functional dissociation between ADAN and LSN

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Abstract

ERP studies investigating the control processes responsible for spatial orienting in touch have consistently observed that the anterior directing attention negativity (ADAN) elicited by an attention directing cue is followed by a sustained negativity contralateral to the cued hand. Recent evidence suggested that the later negativity, labelled late somatotopic negativity (LSN), might reflect distinct neuro-cognitive processes from those associated with the ADAN. To investigate the functional meaning of the ADAN and LSN components, we measured event-related brain potentials elicited by bilateral tactile cues indicating to covertly shift tactile attention to the left or right hand. Participants performed two spatial attention tasks which differed only for the difficulty of the target/nontarget discrimination at attended locations. The LSN but not the ADAN was sensitive to our experimental manipulation of task difficulty, suggesting that this component might reflect sensory-specific preparatory processes prior to a forthcoming tactile stimulus.

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Cue-locked lateralized components in tactile attention tasks

Introduction

A distributed network of highly interconnected brain areas including the dorsolateral-prefrontal and posterior parietal cortex are involved in the control of visual spatial attention (e.g. Corbetta & Shulman, 2002; Gitelman et al., 1999; LaBerge, 1990; Mesulam, 1981). While the brain structures activated during orienting of spatial attention have been well described (for a recent review see Ptak, 2012), the specific functional contributions of the different areas and the time course of their activations remains poorly understood. Electrophysiological studies have started to elucidate the temporal dynamics of these control processes by systematically investigating brain activity elicited by attention directing cues and its change over time. In cuing studies of visual attention, in which the cue indicates the likely location of a forthcoming target, ERPs elicited during the cue-target interval are characterized by a series of lateralized components which are thought to reflect different phases in the covert orienting of spatial attention[1]. The anterior directing attention negativity (ADAN), is an enhanced negativity over anterior electrodes contralateral to the direction of the attentional shifts typically observed between 300-500 ms post cue onset (e.g. Hopf & Mangun, 2000; Nobre, Sebestyen & Miniussi, 2000; Eimer, Forster & Van Velzen, 2003; but see also Eimer, 1993; 1995 for a first description of the ADAN). This lateralized componenthas been initially interpreted as reflecting the top down control processes responsible for the direction of attention in space (e.g. Nobre et al., 2000; Eimer, Van Velzen, & Driver, 2002). The time course and amplitude of the ADAN are linked to both the physical characteristics of the cue and the information it conveys. For instance, the onset of the ADAN is delayed when it is more difficult to derive cue meaning (Jongen, Smulders, & Van Der Heiden, 2007). The amplitude of this component is also sensitive to other cue characteristics like the certainty with which it predicts target location (Seiss, Gherri, Eardley & Eimer, 2007; Green, Conder & McDonald, 2008). In addition, the amplitude of the ADAN is increased by spatial attention task demands when task irrelevant distractors are presented simultaneously with the target (Seiss, Driver & Eimer, 2009). The

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[1] In studies of visual attention, the ADAN is typically followed by the late directing attention positivity, LDAP, which is an enhanced positivity contralateral to the cued location observed over posterior electrodes from about 500 ms post cue onset (albeit the exact onset time of this component can vary across studies). The LDAP has been suggested to reflect attentional control processes in posterior parietal areas which are based on representations of visually mediated external space (e.g. Van Velzen et al., 2006). However, because this component is not always reliably present in tactile attention tasks (e.g. Forster, Sambo & Pavone 2009; Gherri & Eimer, 2008), including the present study, this component will not be discussed further.

observation that the ADAN is elicited not only during instructed shifts of visual attention but also during auditory and tactile attention tasks (e.g. Gherri, Driver & Eimer, 2008; Forster, Sambo & Pavone, 2009) led to the suggestion that it might reflect supramodal attentional control processes independent of the sensory modality of the task-relevant stimulus (e.g. Eimer et al., 2002). However, the exact functional significance of this component is still a matter of debate and some authors have challenged the idea that the ADAN observed in the different modalities reflects the same neuro-cognitive processes (c.f. Green & McDonald, 2006; Green et al., 2008).

While the vast majority of ERP studies investigating the ADAN have been carried out within the visual and auditory modalities, there is now consistent evidence that a reliable ADAN is also elicited when attention is oriented towards a cued location on the body during tactile attention tasks (Eardley & Van Velzen, 2011; Eimer & Van Velzen, 2002; Eimer, Forster & Van Velzen, 2003; Gherri & Eimer, 2008; Gherri & Forster, 2012; Jones & Forster, 2012; Forster et al., 2009; Van Velzen, Forster & Eimer, 2006). Because different cue types were used in these studies, the onset time of the tactile ADAN varied accordingly. For instance, the ADAN was elicited around 300 ms post cue following central visual arrows (e.g. Gherri & Forster, 2012) or central auditory cues involving simple pitch-to-hand mappings (e.g. Gherri & Eimer, 2008; Eardley & Van Velzen, 2011), but its onset time was delayed up to 600 ms post cue-onset for bilateral tactile cues requiring difficult frequency-to-location mappings (e.g. Forster et al., 2009). Despite this wide variability in the ADAN onset time, one consistent finding in these studies is a sustained negativity contralateral to the cued hand present over fronto-central electrodes in the last part of the cue-target interval, typically the last 200 ms (Eardley & Van Velzen, 2011; Eimer & Van Velzen, 2002; Eimer et al., 2003; Gherri & Eimer, 2008; Gherri & Forster, 2012; Jones & Forster, 2012; Forster et al., 2009; Van Velzen et al., 2006). Given its polarity and scalp distribution, this late negativity was labelled ‘late’ ADAN in line with the assumption that analogous cognitive processes were responsible for both the ‘early’ and ‘late’ ADAN. Crucially, however, the ‘late’ ADAN is elicited towards the end of the cue-target interval (CTI) *regardless* of the CTI duration, suggesting that this component might not be cue-locked, unlike the ‘early’ ADAN. Thus, distinct processes might be responsible for the generation of the ‘early’ and ‘late’ ADAN observed in touch.

The first systematic evidence for a functional dissociation between the early and late ADAN came from a recent ERP study in which the same tactile attention task was performed under uncrossed and crossed hands postures (Gherri & Forster, 2012). In this study, lateralized components were computed relative to the location of the cued hand in external space (e.g. a left cue indicated the hand placed on the left hemi-space, which under crossed hands conditions was the right hand). Thus, the polarity of these lateralized components in the crossed hand condition would reveal the reference frame according to which the underling cognitive processes operate (enhanced negativity contralateral to the position of the hand in external space or to the anatomical side of the hand). No difference was observed between uncrossed and crossed hand conditions for the early ADAN (measured between 300 and 500 ms post cue over fronto-central electrodes and elicited by a visual arrow), while the late ADAN (measured between 700 and 900 ms post cue onset over fronto-central electrodes) reversed polarity when participants crossed their hands. Thus, the early ADAN reflects processes that operate according to the body's position in external space. In contrast, the processes underlying the late negativity operate according to a somatotopic reference frame, based on the position of the stimulated sensory receptors on the skin and their representation in the cortex[2]. This dissociation between the early and late ADAN suggests that these lateralized components reflect distinct processes related to tactile attention. To differentiate the late from the early negativity associated with the ADAN, the late negativity was labelled 'Late Somatosensory Negativity' (LSN), given its late onset and somatotopic reference frame (Gherri & Forster, 2012). While the ADAN might reflect attentional control processes elicited by the cue, such as the encoding and selection of the task-relevant location, the LSN might reflect the activation of sensory-specific attentional processes in preparation for the forthcoming tactile stimulus.

The aim of the present study was to investigate further the functional differences between the ADAN and the LSN. In particular, we asked whether the ADAN and LSN elicited during a unimodal tactile attention task are differentially modulated by task difficulty – defined by the difficulty of the perceptual target-nontarget discrimination performed at the cued body location. In this study, bilateral tactile cues (single or double taps) signalled participants to focus attention on the left or right hand and were followed by a unilateral tactile stimulus, either a target or a nontarget (high or low frequency vibrations). Participants had to discriminate between target and nontarget stimuli presented to the cued hand in order to respond only to infrequent target stimuli, while ignoring all stimuli to the uncued hand. Lateralized ERPs

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[2] Note that earlier studies (e.g. Eimer, Forster & Van Velzen, 2003; Eardley & Van Velzen, 2011) which first carried out an analogous hand posture manipulation during a tactile attention task, observed a somatotopic reference frame for the 'late' ADAN. While our findings (Gherri & Forster, 2012) are in line with these observations, we interpreted these results as evidence that early and late ADAN are distinct ERP components. We believe it was the short CTI used in these previous studies (resulting in largely overlapping 'early' and 'late' ADAN components) which prevented the authors from individuating the early and late ADAN as independent components. Please refer to the general discussion of this manuscript and of Gherri & Forster, 2012, for an in-depth discussion of this topic.

elicited in the cue-target interval were measured and compared in two different tasks in which the difference between the frequencies of target and nontarget stimuli was pronounced (easy task) or subtle (difficult task). If the ADAN reflects the selection of the to-be-attended cued hand, it should not be modulated by our task difficulty manipulation. In line with this hypothesis, one previous ERP study demonstrated that the ADAN elicited during a visual attention task was not sensitive to the difficulty of the perceptual discrimination between target and nontarget stimuli (Hopf & Mangun, 2000). In contrast, increased perceptual difficulty of the target/nontarget discrimination should selectively modulate the LSN, if this component reflects preparatory activation for somatosensory processing.

Methods

Participants

Twenty paid volunteers participated in the experiment. Five participants were excluded due to poor eye fixation control in the cue-target interval (see details below) and one was unable to complete the study because of a technical problem with the tactile stimuli, leaving 14 participants (10 women, 4 men; aged 18-35) in the sample. All participants were right-handed and had normal or corrected-to-normal vision. The study was approved by the Psychology Research Ethics Committee, Department of Psychology, Edinburgh, and was conducted in accordance with the Declaration of Helsinki.

Stimuli, apparatus and procedure

Participants were tested in a sound-attenuated cabin fixating on a cross centrally presented on a computer screen and resting their hands on a table with their index fingers 20 cm to the left and right of the body midline. To mask the sounds made by tactile stimulators, one speaker was positioned on the table close to the hands and presented white noise (65 dB SPL) throughout the experimental blocks. Tactile stimuli were presented using 12 V solenoids (Heijo Research Electronics, UK) that were driving a metal rod with a blunt conical tip. The tip of the tactile stimulators touched the skin whenever a current was passed through the solenoid. Two tactile stimulators were used, each attached with adhesive medical tape to the left and right index finger. They were positioned so that the metal rod made contact with the inner side of the top phalanx.

On each trial, a tactile cue (S1, 60 ms duration) presented simultaneously to both hands was followed after an interval of 950 ms by a target or a nontarget tactile stimulus (S2, 205 ms duration) presented to the left or the right hand. The cues consisted of either a single or double tap and indicated which hand to covertly attend. For half the participants, a single tap (60 ms continuous stimulation) indicated the left hand and double taps (two 5 ms stimulations separated by a 50 ms interval) the right hand, while the remaining half followed the opposite tap-to-hand mapping. Target and nontarget stimuli were characterized by a high or a low frequency vibration, respectively. Each participant performed two discrimination tasks, the easy and the difficult tasks, which were identical except for the target frequencies (100 Hz for the easy and 40 Hz for the difficult task targets; 25 Hz for nontargets in both), thus making it harder to discriminate between targets and nontargets in the difficult task.

Six blocks of 80 trials each were run for both tasks. On 60 of these trials, tactile nontargets were preceded with equal probability by a left or right cue and presented with equal probability to the left or right hand, requiring no vocal response. On the remaining 20 trials, target stimuli were presented. Target stimuli were delivered to the cued hand on 12 trials requiring a vocal response. On 8 target trials per block, target stimuli were delivered to the hand on the uncued side, requiring no vocal response. The inter-trial interval randomly varied between 1200 and 1300 ms. The order of the easy and difficult tasks was counterbalanced across participants.

In both easy and difficult tasks, participants were instructed to vocally respond to targets presented to the cued hand while ignoring nontargets to the cued hand as well as all tactile stimuli (both target and nontargets) to the opposite uncued hand. To further encourage participants to focus fully their attention on the task relevant hand, cued targets which required a response were more likely to be presented than uncued ones (15% of all trials cued target, 10% uncued targets).

Recording and data analysis

EEG was recorded from 70 active electrodes (Biosemi ActiveTwo system; impedance kept below 15 kO; 512 Hz sampling rate; 40 Hz upper cut-off frequency with a high-pass filter of 0.53 Hz and a notch filter of 50 Hz). Eye movements were monitored by bipolar horizontal and vertical EOG derivations. EEG was digitally re-referenced to the average of the left and right earlobes and epoched into 1100 ms periods, starting 100 ms before cue onset. Trials with eye blinks (VEOG exceeding ±60 µV), horizontal eye movements (HEOG exceeding ±40 µV) or other artifacts (a voltage exceeding ±80 µV at any other electrode) were excluded.

To detect systematic deviations of eye position indicating residual tendencies to move the eyes toward the side of the cued response, averaged HEOG waveforms in the cue-target interval in response to left versus right cues were examined for each participant. HEOG deviations exceeding ±3.5 µV led to the disqualification of 5 participants.

ERPs to tactile cues were averaged for all combinations of task (easy vs. difficult), cued hand (left vs. right) and hemisphere (left vs. right). Mean amplitude values were computed at lateral anterior sites (F1/2, F3/4, F5/6, F7/8, Fc1/2, Fc3/4, Fc5/6, FT7/8), lateral central sites (C1/2, C3/4, C5/6, T7/8, Cp5/6, Cp1/2, Cp3/4, TP7/8), and lateral posterior sites (P1/P2, P3/4, P5/6, P7/8, PO3/4, PO7/8) within three successive latency windows (400–600, 600–800 and 800–1000 ms relative to cue onset), and these values were analyzed separately for anterior, central, and posterior electrodes by repeated measures ANOVAs for the factors of task(easy vs. difficult), lateralization (electrode ipsilateral vs. contralateral to the cued hand) and electrode site.

The latency of vocal responses was measured with a voice key relative to the onset of the tactile high or low frequency vibrations. Mean reaction times (RTs) for correct vocal responses obtained in the easy and difficult tasks were compared with paired t-tests. To characterize participants' overall performance, the mean accuracies measured in the easy and difficult tasks were compared with t-tests. Furthermore, mean percentage errors (PEs) were calculated separately for the different types of errors on the cued and uncued side of each task. 'Failure to respond' indicated the absence of a vocal response on *cued target* trials while 'false alarms' referred to responses that were incorrectly given on *uncued target*, *cued target* or *uncued nontarget* trials. These different PE measures measured in the easy and difficult tasks were compared with t-tests.

For all analyses, Greenhouse–Geisser adjustments to the degrees of freedom were applied where appropriate. Unless specifically stated otherwise, nonsignificant results were not reported.

Results

Behavioral performance

Overall, participants' performance was more accurate in the easy than in the difficult task (97.9% and 93.9% accuracy, respectively, t(13)= 5.5, p < .001). To further investigate participants' performance on the cued and uncued side, mean PEs were also calculated and analyzed separately for the different types of trials. When a tactile stimulus was presented to the cued hand, PEs were significantly higher in the difficult than in the easy task for both missed responses to targets (t (13) = 6.17, p < .001, d = 1.34) and false alarms to nontargets (t (13) = 2.52, p < .03, d = 0.93). In contrast, when a tactile stimulus was presented to the uncued hand, no difference was observed between PEs in the easy and difficult tasks for false alarms to targets as well as false alarms to nontargets (both t (13) <1.2, both p > .25). The analysis of vocal responses to target stimuli at cued locations revealed faster RTs in the easy task compared to the difficult task (t (13) = 3.77, p < .003), see Table 1 for a summary of the behavioural results.

Lateralized ERP components in the cue-target interval

General ERP analysis

Figures 1 and 2 show ERPs to tactile cues ipsilateral and contralateral to the cued hand at lateral electrodes F3/4, F5/6, F7/8, FC3/4, FC5/6, FT7/8, C3/4, C5/6 T7/8, CP3/4, CP5/6, TP7/8 in the difficult and easy tasks respectively. Figure 3 shows the same ERPs averaged across all lateral anterior and central electrodes (left and right columns), for the difficult (top panels) and easy task (central panels) together with their corresponding difference waveforms (bottom panels).

The presence of reliable lateralized components was observed between 400 and 1000 ms post cue. Significant main effects of lateralization at *anterior* sites (Figure 3, left panels) emerged in the 400 - 600 ms (F(1, 13) = 5.3, p < .039, η^2_p = 0.29) and 600 - 800 ms (F(1, 13) = 6.9, p < .021, η^2_p = 0.35) intervals. The main effect of lateralization was not present over lateral central electrodes in the 400-600 ms interval and failed to reach significance in the 600-800 ms time window (F(1, 13) = 3.2, p = .097, η^2_p = 0.2). Between 400 and 800 ms post cue onset, the amplitude of these lateralized components over anterior electrodes, did not differ between the easy and the difficult task (for both time intervals, and both anterior and central electrodes, task x lateralization, all F(1, 13) < 1). In contrast, in the final time window (800-

1000 ms post cue) lateralized components elicited over anterior electrodes were not only reliably present (F(1, 13) = 6.3, p < .026, η^2_p = 0.33) but also modulated by task (task x lateralization, F(1, 13) = 5.03, p < .043, η^2_p = 0.28). As can be observed in Figures 1, 2 and 3, in the 800-1000 ms interval enhanced negativities contralateral to the side indicated by the cue were stronger in the difficult than the easy task. Follow-up analyses demonstrated significant lateralizations at anterior electrodes in the difficult task (F(1, 13) = 7.5, p < .017, η^2_p = 0.37) but not in the easy task (F(1, 13) = 2.5, p > .13, η^2_p = 0.16).

At *central* electrodes (Figure 3, right panels), the main effect of lateralization was not present in the 400-600 ms interval while it failed to reach significance in the 600-800 ms (F(1, 13) = 3.2, p = .097, η^2p = 0.2) and 800-1000 ms (F(1, 13) = 3.4, p = .087, η^2p = 0.2) intervals. No task x lateralization interactions were observed in any of the time windows considered (all F(1, 13) < 1.7, p > .2, η^2p < 0.11). Importantly, however, in the 800-1000 ms interval a significant lateralization x electrode interaction (F(7, 91)=2.56, p < .049, η^2p = 0.17) revealed systematic differences between the reliability of the lateralized components elicited at the different electrode sites (see Figure 4). Follow-up analyses showed significant lateralizations at central electrodes (C3/4, C5/6 and T7/8, all F(1, 13) > 4.7, all p < .049, approaching significance at C1/2 F(1, 13) =3.5, p = .086), but not at centro-parietal sites (CP1/2, CP3/4, CP5/6, and TP7/8, all F(1, 13) < 1). To further investigate possible differences between the lateralized components elicited in the easy and difficult tasks at central electrodes in the 800-1000 ms time window, additional analyses were carried out separately for C3/4, C5/6 and T7/8 where significant lateralizations were observed. A task x lateralization interaction emerged at T7/8 (F(1, 13) = 4.9, p < .046) and follow up analyses showed the presence of significant lateralized components in the difficult task at C3/4, c5/6 and T7/8 (all F(1, 13) > 5.3, all p < .039) but not in the easy task (all F(1, 13) < 3.8, all p > .073).

No reliable lateralization main effects or task x lateralization interactions were observed over lateral *posterior* electrodes in any of the time windows considered.

Data-driven ERP analysis

In the analyses reported above three distinct regions of interest (lateral anterior, central and posterior areas) were chosen and analyzed in line with previous studies investigating the lateralized components elicited in the cue-target interval of spatial cuing attention tasks (e.g. Eimer et al., 2003; Eardley & Van Velzen, 2011; Gherri & Forster, 2012). However, results indicate that the lateralized components elicited in the present study were primarily focused over frontal, frontocentral and central electrodes. Furthermore, two distinct clusters of electrodes showed lateralized activity between 400 and 1000 ms post-cue as can be seen in Figure 4 where the scalp distribution of the lateralized components elicited in the difficult and easy tasks is represented. One of these cluster encompassed medial frontal and fronto-central electrodes whereas the other included more lateral fronto-central and central electrodes. Thus, to further explore the activity of these newly defined regions of interest additional analyses were carried out separately for '*medial frontal electrodes*' (F3/4, F5/6 and FC3/4), and for '*lateral central electrodes*' (T7/8, C5/6 and FC5/6) for the three different time interval previously considered (400-600 ms; 600-800 ms; 800-1000ms). These analyses included the factors task (easy vs. difficult), laterality (electrode contralateral vs ipsilateral to the cued hand) and electrode sites (F3/4, F5/6 and FC3/4, for medial frontal; T7/8, C5/6 and FC5/6, for lateral central). Figure 5 shows ERPs to tactile cues ipsilateral and contralateral to the cued hand averaged across medial frontal and lateral central electrodes (left and right columns, respectively), for the difficult (top panels) and easy task (central panels) together with their corresponding difference waveforms (bottom panels). Figure 6 show the average amplitude and the statistical reliability of the lateralized components elicited in the CTI over medial frontal (F3/4, F5/6 and FC5/6) and lateral central electrodes (C5/6, T7/8 and FC5/6) in the three different time windows considered.

At *medial frontal electrodes* (F3/4, F5/6 and FC5/6, see Figure 5, left panels), a significant main effect of laterality was observed for all the time windows considered (400 - 600 ms post-cue onset, ($F(1, 13) = 10.9$, $p < .006$, $\eta^2p = .5$); 600 – 800 ms, ($F(1, 13) = 8.7$, $p < .011$, $\eta^2p = .4$); 800 – 1000 ms, ($F(1, 13) = 4.8$, $p < .047$, $\eta^2p = .3$). However, these lateralized components were not modulated by task (task x laterality, $F(1, 13)$ for both 400 – 600 and 600 - 800 ms intervals; $F(1, 13) = 2.7$, $p = .12$, for the 800-1000 ms interval).

At *lateral central electrodes* (C5/6, T7/8 and FC5/6, see Figure 5, right panels), reliable ERP lateralizations were observed between 600 and 1000 ms post-cue onset (both 600 – 800 and 800 – 1000 ms intervals, $F(1, 13) > 6.4$, both $p < .025$, $\eta^2p > .3$) but not in the initial 400 – 600 ms time window ($F(1, 13) = 2.7$, $p = .12$). Importantly, the task x lateralization interaction was not significantly present between 400 and 800 ms post-cue (both intervals, $F(1, 13) < 1$) but emerged to be significant in the final time window, 800 – 1000 ms ($F(1, 13) = 5.2$, $p < .040$, $\eta^2p = .3$). Follow-up analyses showed a significant laterality main effect in the difficult task

($F(1, 13) = 9.5$, $p < .009$, $\eta^2p = .4$) but not in the easy one ($F(1, 13) = 3.1$, $p = .1$)

Discussion

This study investigated whether task difficulty - defined by the discriminability of tactile stimuli - selectively modulates the lateralized components elicited in the cue-target interval of a unimodal tactile attention task. Participants were instructed to covertly attend to the cued hand to respond to infrequent tactile targets while ignoring frequent nontargets presented to that hand. They also had to ignore all stimuli to the uncued hand. Thus, the task required a tactile discrimination between target and nontarget stimuli on the cued hand. The difficulty of this discrimination was manipulated in different tasks by decreasing the physical difference between target and nontargets in the ‘difficult’ as compared to the ‘easy’ task, so that participants were strongly encouraged to allocate increased attentional resources to the cued hand in the difficult task. Participants’ behavioural performance confirmed the effectiveness of the task difficulty manipulation, as demonstrated by slower responses and increased error rates for stimuli presented to the cued hand in the difficult task.

The general analysis of the lateralized ERP components elicited in the cue-target interval revealed the presence of enhanced negativities over anterior electrodes contralateral to the cued hand from 400 ms post cue onset until the presentation of the tactile stimulus, 1000 ms after cue onset. Crucially, while similar lateralized components were measured in the easy and difficult tasks between 400 and 800 ms post cue, systematic differences between tasks were observed in the final 800 - 1000 ms interval. The observation that the late but not the early phase of these anterior negativities is sensitive to task difficulty demonstrates a functional dissociation between these ERP components. Based on this dissociation and in line with our previous study (Gherri & Forster, 2012), we suggest that the ERP lateralization measured in the last 200 ms of the cue-target interval (800 - 1000 ms post cue onset) is the late somatosensory negativity (LSN), while the enhanced negativity contralateral to the cued hand elicited between 400 and 800 ms is the ADAN.

The ADAN has been suggested to reflect supramodal mechanisms responsible for the encoding and selection of the task-relevant location in spatial attention tasks (Eimer et al., 2002). This component appears to be independent from the sensory modality of the target (cf.

Green & McDonald, 2006; Green et al., 2008 for an in-depth discussion of the ADAN elicited during auditory tasks) and to the duration of the cue-target interval (Van Velzen, Forster & Eimer, 2002). However, the time course of the ADAN is affected by the properties of the cue, with delayed onset when it is difficult to derive cue meaning (e.g. Jongen et al. 2007). In the present study, in which cue meaning was relatively easy to extract (bilateral single vs. double taps associated with the left or right hand), a reliable ADAN was observed starting from 400 ms post cue onset. Important for the aim of this study, no difference emerged between the lateralized components elicited over anterior electrodes between 400 and 800 ms post cue in the easy and difficult tasks. The tasks of the present study differed only with respect to the physical characteristics of the tactile targets, while all the other task parameters, including task requirements, were identical. Our results provide the first indication that during instructed shifts of tactile attention, the ADAN is not modulated by the expected difficulty of the target/nontarget discrimination. These findings are in line with previous evidence suggesting that the ADAN elicited during visual attention tasks is not sensitive to manipulations of the perceptual load of the target identification at cued locations (Hopf & Mangun, 2000).

In contrast to the ADAN, the LSN was systematically modulated by task difficulty, with stronger LSN components in the difficult compared to the easy task. These quantitative changes between the amplitude of the LSN and, as a consequence, the neural activity elicited in the last part of the cue-target interval in the easy and difficult tasks reflect differences in the degree of engagement of the cognitive processes indexed by the LSN. The crucial question is what are exactly the cognitive processes associated with the LSN? Previous cuing studies of spatial attention suggest that the LSN is exclusively observed during the cue-target interval of tactile attention tasks (e.g. Eardley & Van Velzen, 2011; Eimer et al., 2003; Eimer & Van Velzen, 2002; Forster et al., 2009; Gherri & Eimer, 2008; Gherri & Forster, 2012; Jones & Forster, 2012; Van Velzen et al., 2006). Furthermore, the LSN is typically elicited in the last 200 ms of the cue-target interval, regardless of the interval duration, and does not return to baseline before target presentation. Thus it appears to be time-locked to the anticipated presentation time of the task-relevant tactile stimulus rather than to the cue. In addition, the observation that the LSN is elicited contralateral to the task-relevant body part regardless of that body part's position in external space (Gherri & Forster, 2012; see also Eardley & Van Velzen, 2011 and Eimer et al., 2003, for analogous results interpreted as 'late ADAN' rather than LSN) suggests that this component operates according to a somatotopic reference frame. Taken together, these pieces of evidence are in line with the hypothesis that the LSN reflects sensory-specific preparatory processes for the presentation of the task-relevant tactile stimulus. More specifically, this LSN component might reflect the differential excitability of the brain areas involved in the processing of somatosensory events at expected locations. Anticipating the appearance of a tactile stimulus at a specific body location may produce an increment in brain activity which primes the response of sensori-specific areas already before stimulus onset. While the earlier ADAN may reflect control processes that encode and select the task-relevant location as indicated by the cue, based on this information the processes reflected by the LSN may upregulate the activity of the brain areas involved in somatosensory processing in preparation for stimulus presentation at the expected body location.

Results of the present study provide direct evidence for a functional dissociation between the ADAN and LSN lateralized components. It seems therefore reasonable to assume that such functional dissociation between ERP components might also be reflected by a clear anatomical difference between their neural generators. The distribution of brain activity over the scalp (Figure 4) shows a gradual shift during the cue-target interval from medial-frontal areas in the time intervals in which the ADAN is maximal to lateral-central areas of the scalp when the LSN peaks. This slow change in the scalp distribution is further shown in Figure 6, where the mean amplitude of the lateralized components elicited over medial-frontal and latera-central electrodes are represented separately for the three different time windows investigated (and averaged across the easy and difficult task). As described in the Data Driven ERP Analysis, brain activity over frontal areas was reliably present across all time windows. In contrast, brain activity over more central regions showed an increasing pattern with maximal amplitudes at the end of the cue-target interval. This different time-course of activation between frontal and central brain areas suggests some degrees of independence between the underlying neural generators. However, it is relevant to note that these qualitative changes do not provide direct evidence that the ADAN and LSN components are characterized by distinct neural generators and, to date, no study has attempted to localize the neural generators of the lateralized components elicited during the cue-target interval of tactile spatial attention tasks. Studies on visual attention localized the ADAN in the lateral premotor cortex using dipole source modeling (Mathews, Dean& Sterr, 2006; Praamstra, Boutsen & Humphreys, 2005; van der Lubbe, Neggers, Verleger & Kanemans, 2006). However, it has been suggested that multiple neural generators are in fact responsible for the visual ADAN, including areas in the inferior frontal regions as well as motor areas (e.g. Green et al., 2008). Despite the fact that it is particularly challenging to perform source localization analyses on the lateralized components elicited during the cue-target interval, due to their small amplitude and their lateralized nature, future studies should directly investigate whether shared neural generators are responsible for the ADAN observed during visual and tactile attention tasks, and whether a different set of generators is responsible for the LSN component.

The finding that the LSN but not the ADAN is modulated by task difficulty (defined by target discriminability) provides novel evidence that these components reflect distinct cognitive processes. This conclusion may appear surprising, given the number of studies that considered the ADAN and LSN (previously labelled 'late ADAN') as reflecting similar processes (e.g. Eimer et al., 2003; Forster et al., 2009; Gherri & Eimer, 2008). However, the previous conflation of the ADAN and LSN may have resulted from the extreme difficulty in dissociating these components. Both ADAN and LSN are enhanced negativities contralateral to the cued hand elicited over fronto-central electrodes. For this reason, there is often substantial overlap between them, especially with shorter cue-target intervals (SOA between 600 and 700 ms; e.g. Eimer et al., 2003; 2004; Eardley & Van Velzen, 2001) and/or when the onset of the ADAN is delayed because of difficult cue-to-body part mappings (e.g. Forster et al., 2009). However, if the cue-target interval is sufficiently long (SOA around 1000 ms), and the onset of the ADAN is relatively early (e.g. following symbolic arrow cues), it is possible to isolate the relative contribution of these components. Because the ADAN is triggered by cue onset while the LSN appears to be determined by the anticipated presentation time of the task-relevant tactile stimulus, future studies should be able to shed light on the relative timing of these components by systematically varying the duration of the cue-target interval.

In summary, the present experiment has shown for the first time that the LSN but not the ADAN is sensitive to task difficulty defined by the discriminability of tactile stimuli. Our findings provide direct evidence that the ADAN and LSN are functionally distinct lateralized ERP components reflecting different aspects of endogenous tactile orienting. Whereas the ADAN appears to reflect supramodal processes involved in the encoding and selection of the spatial information conveyed by the cue (e.g. Eimer et al., 2003; Eimer et al., 2002; Mathews et al., 2006), the LSN may reflect brain activity in preparation for somatosensory processing that depends on the attributes and timing of the expected stimuli instead of the cue.

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Table 1

Type of trial:			**Easy Task**	**Difficult Task**	**p value**
Cued hand	***Targets*** (15% of all trials)	RTs (ms) Responses	636 (95.2)	694 (106.5)	.003
		PE (%) Missed responses	9.1 (6.9)	24.4 (14.4)	.001
	Nontargets (37.5% of all trials)	PE (%) False alarms	0.2 (0.4)	4.6 (6.6)	.024
Uncued hand	***Targets*** (10% of all trials)	PE (%) False alarms	5.8 (5.5)	5.5 (4.9)	n.s
	Nontargets (37.5% of all trials)	PE (%) False alarms	0.1 (0.2)	0.4 (0.7)	n.s.

Note. Means and standard deviations (in brackets) of reaction times and percentage errors are reported separately for the different types of trials in the easy and difficult task. The right column shows the p values for the paired comparisons across tasks. RT = reaction time; PE = percentage error.

Figures

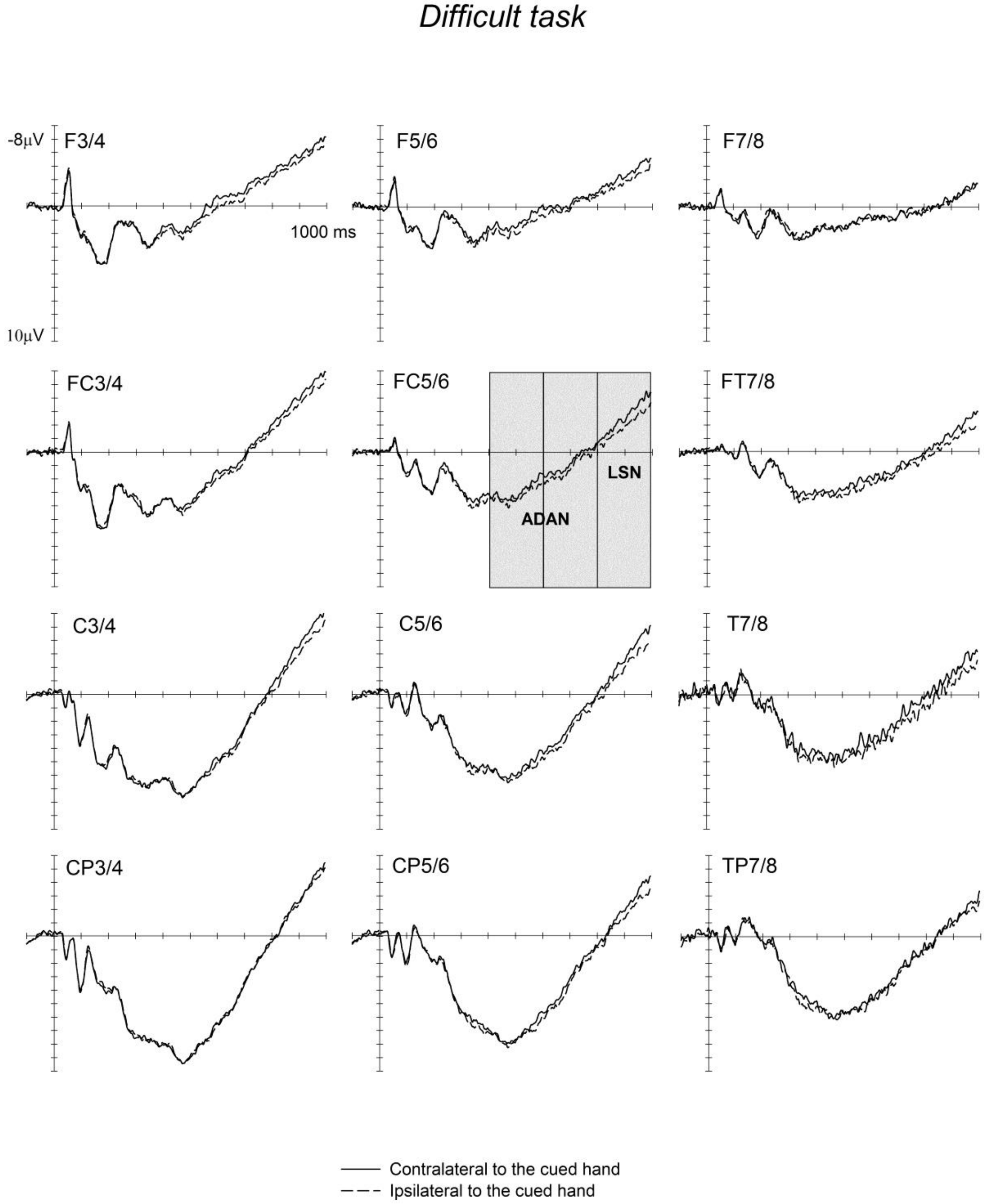

Figure 1. ERPs elicited in the difficult task in the 1000 ms interval following cue onset at lateral electrodes F3/4, Fc3/4, F5/6, Fc5/6, F7/8, FT7/8, C3/4, C5/6, T7/8, Cp5/6, Cp3/4 and TP7/8 ipsilateral and contralateral to the cued hand.

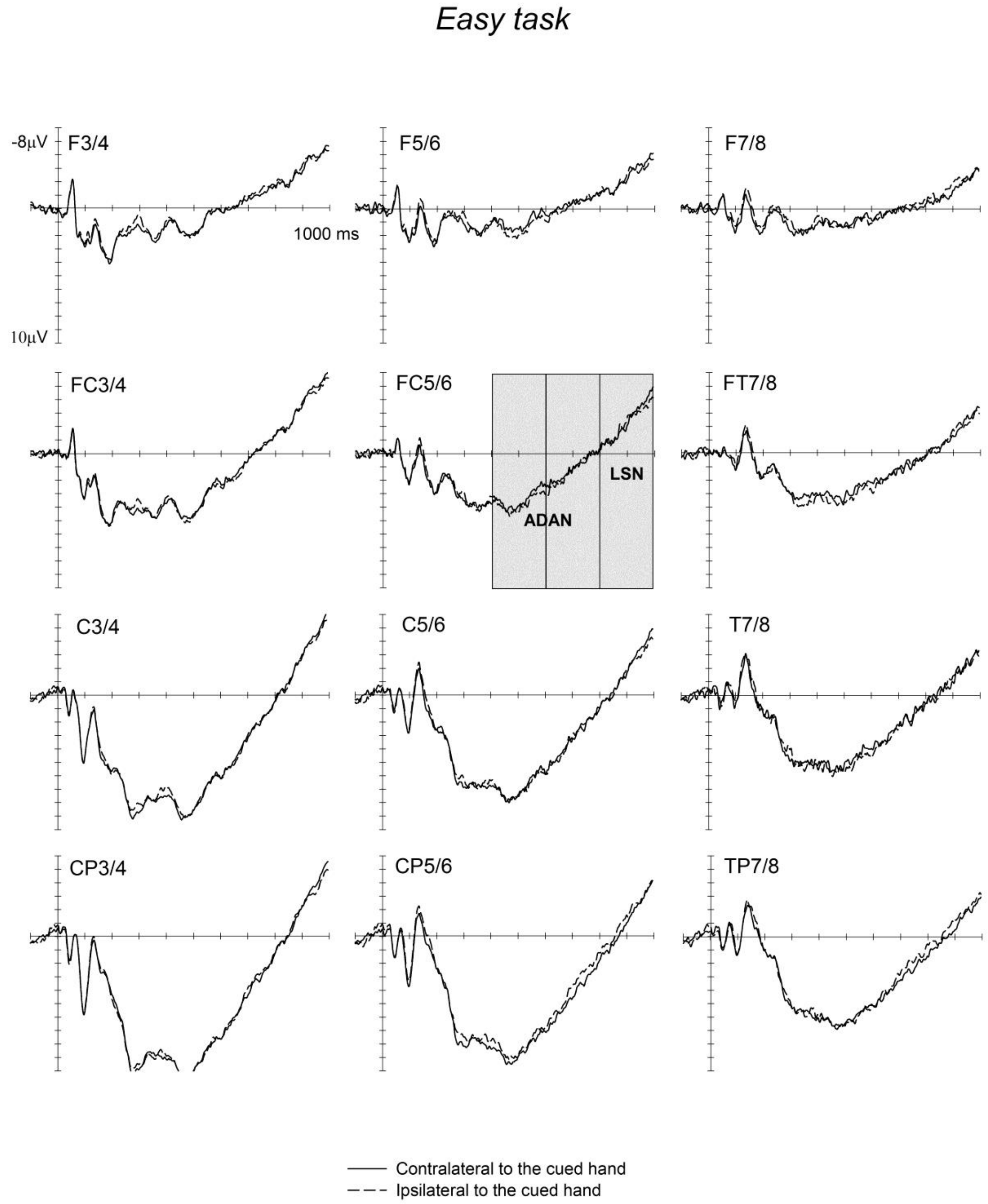

Figure 2. ERPs elicited in the easy task in the 1000 ms interval following cue onset at at lateral electrodes F3/4, Fc3/4, F5/6, Fc5/6, F7/8, FT7/8, C3/4, C5/6, T7/8, Cp5/6, Cp3/4 and TP7/8 ipsilateral and contralateral to the cued hand.

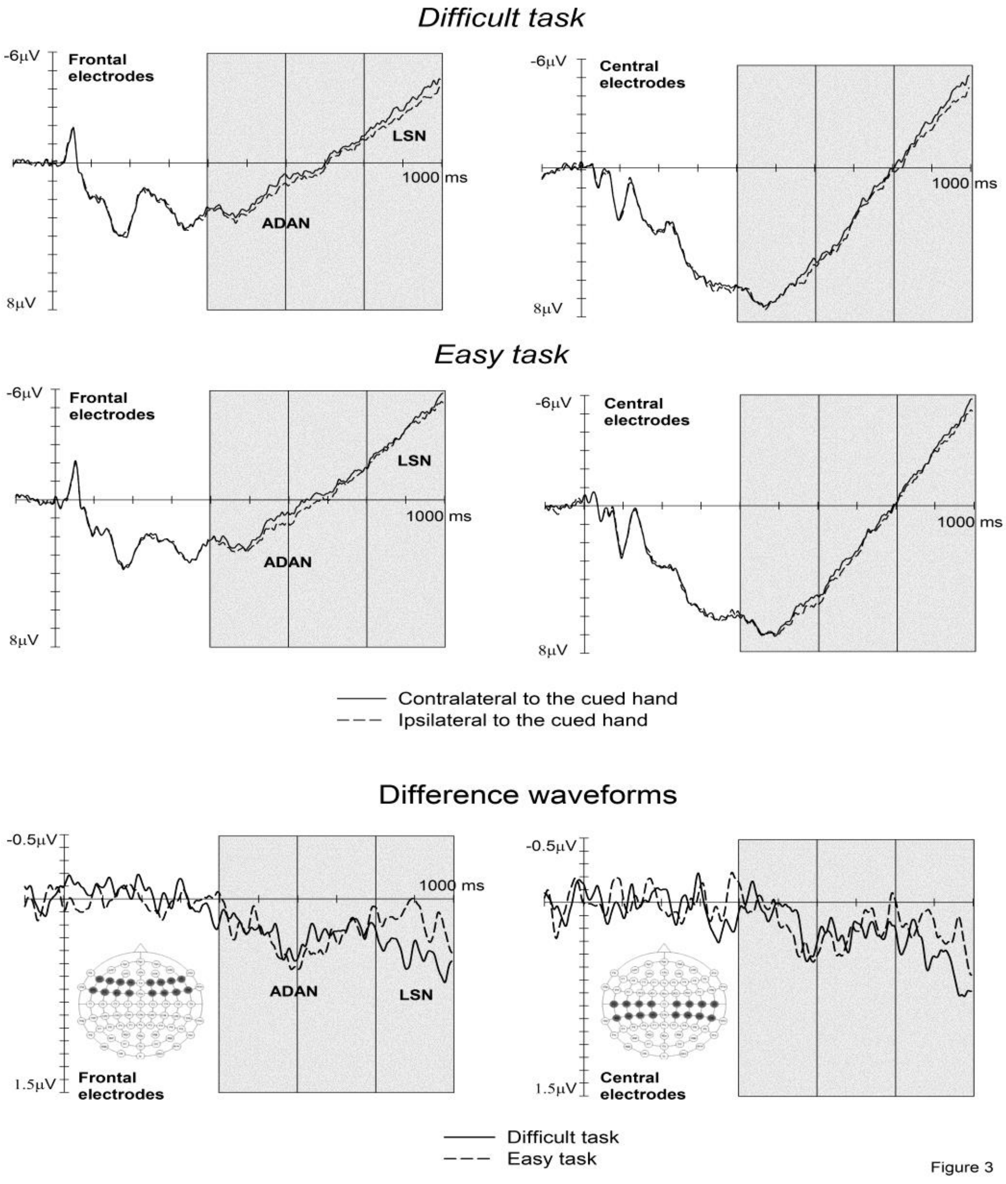

Figure 3

Figure 3. ERPs elicited in the 1000 ms following cue onset at pooled anterior (F1/2, F3/4, F5/6, F7/8, Fc1/2, Fc3/4, Fc5/6, FT7/8**)** and central (C1/2, C3/4, C5/6, T7/8, Cp5/6, Cp1/2, Cp3/4, TP7/8) electrodes ipsilateral and contralateral to the cued hand, for the difficult and easy tasks (top and central panels, respectively). Relevant time intervals included in the analyses (400 - 600, 600 - 800, and 800 - 1000 ms) are highlighted in the gray boxes. The corresponding double subtraction waveforms are represented in the bottom panels separately for the difficult (solid line) and easy (dashed line) tasks. Here, enhanced negativities contralateral to the cued side are reflected by positive values (downward deflections).

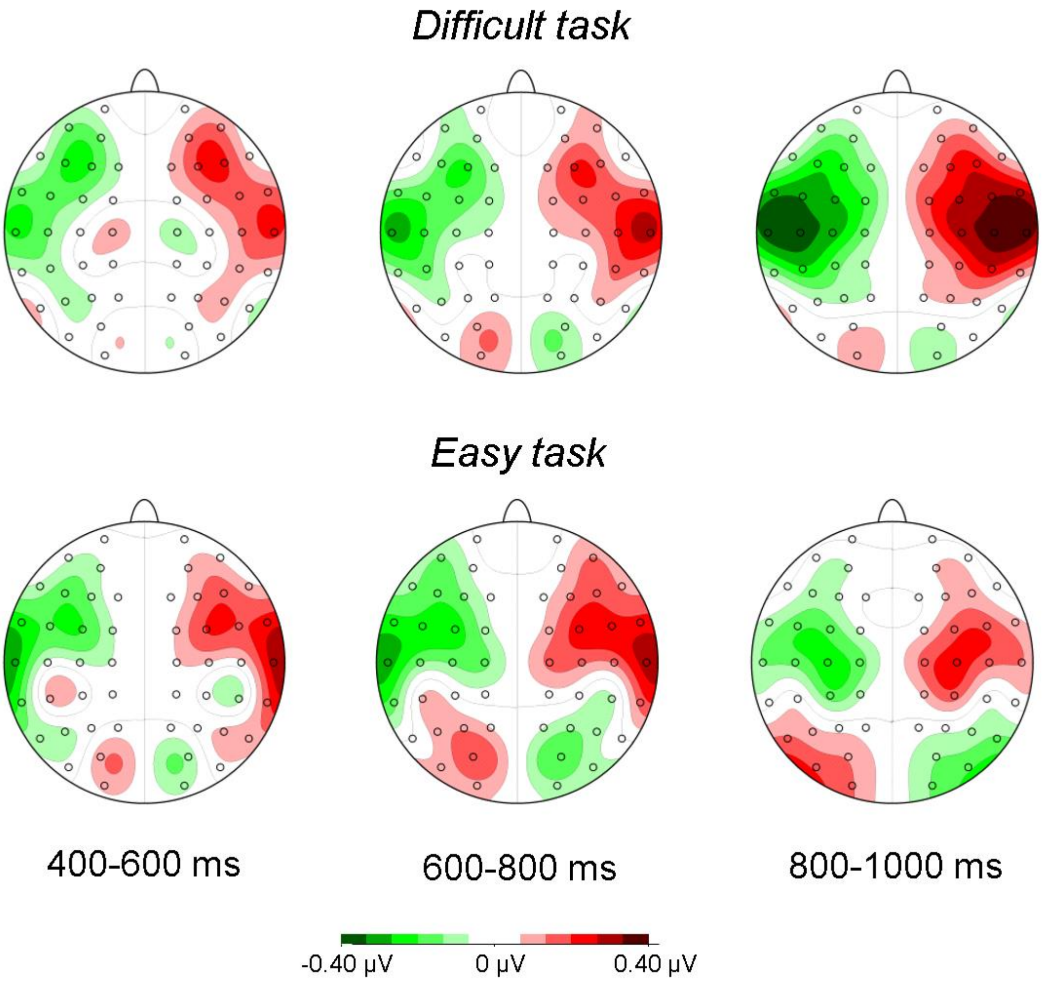

Figure 4. Topographical voltage maps of lateralized ERP components elicited in the cue–target interval in response to bilateral tactile cues. Maps are shown separately for the 400 – 600 ms, 600 - 800 ms and 800 – 1000 ms intervals after cue onset, separately for the difficult task (top panels) and the easy task (bottom panels). They were computed by spherical spline interpolation (number of splines = 3) of difference waves (see Perrin, Pernier, Bertrand, & Echallier, 1989), which were obtained by subtracting ERPs at electrodes ipsilateral to the cued hand from those at contralateral electrodes, and then mirroring the difference waveforms to the opposite hemisphere to obtain symmetrical, but inverse, voltage values for both hemispheres. Amplitude scales range from −0.4 to 0.4 µV.

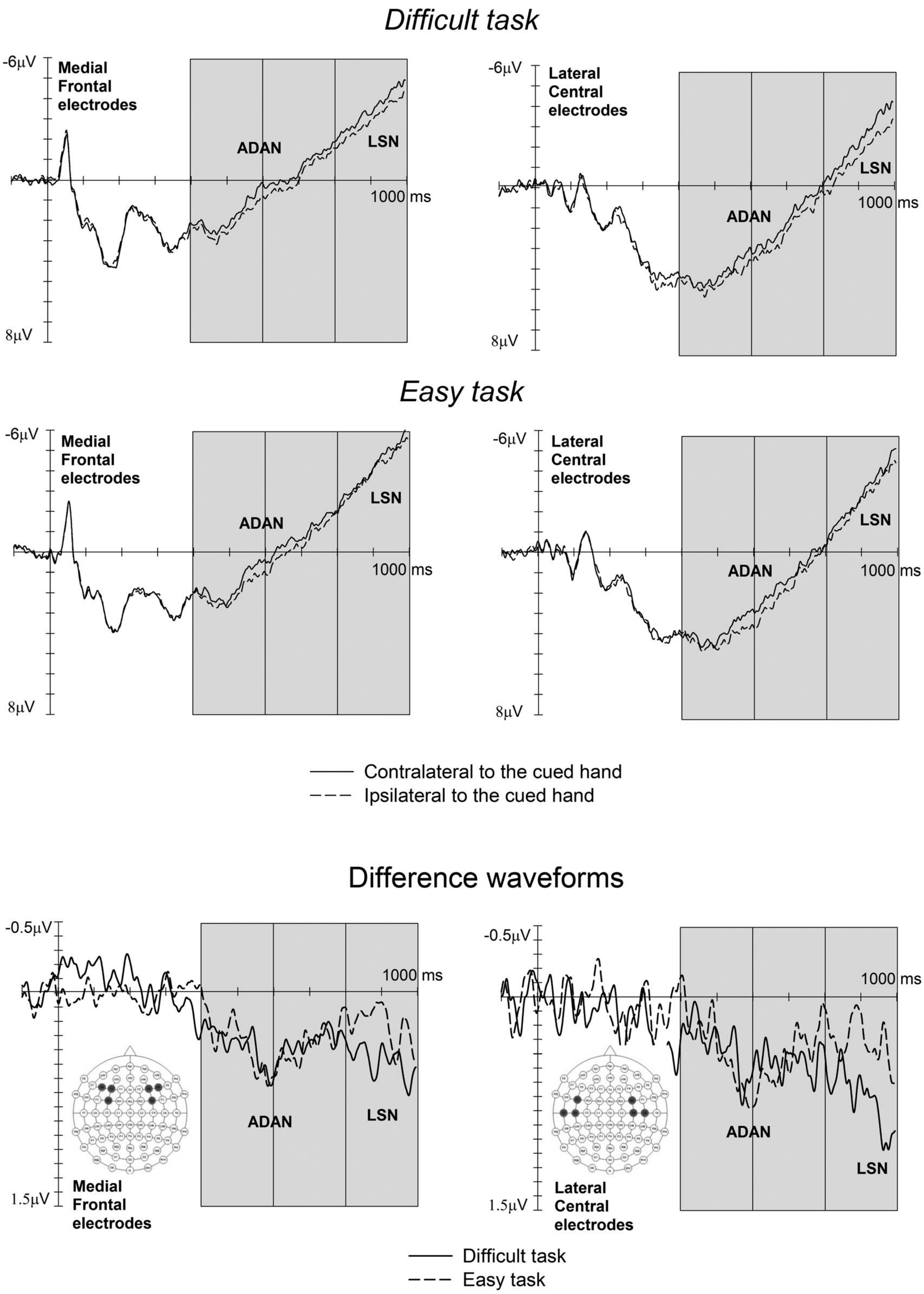

Figure 5. ERPs elicited in the 1000 ms following cue onset at pooled medial frontal (F3/4, F5/6 and FC5/6) and lateral central (C5/6, T7/8 and FC5/6) electrodes ipsilateral and contralateral to the cued hand, for the difficult and easy tasks (top and central panels, respectively). Relevant time intervals included in the analyses (400 - 600, 600 - 800, and 800 -

1000 ms) are highlighted in the gray boxes. The corresponding double subtraction waveforms are represented in the bottom panels separately for the difficult (solid line) and easy (dashed line) tasks. Here, enhanced negativities contralateral to the cued side are reflected by positive values (downward deflections).

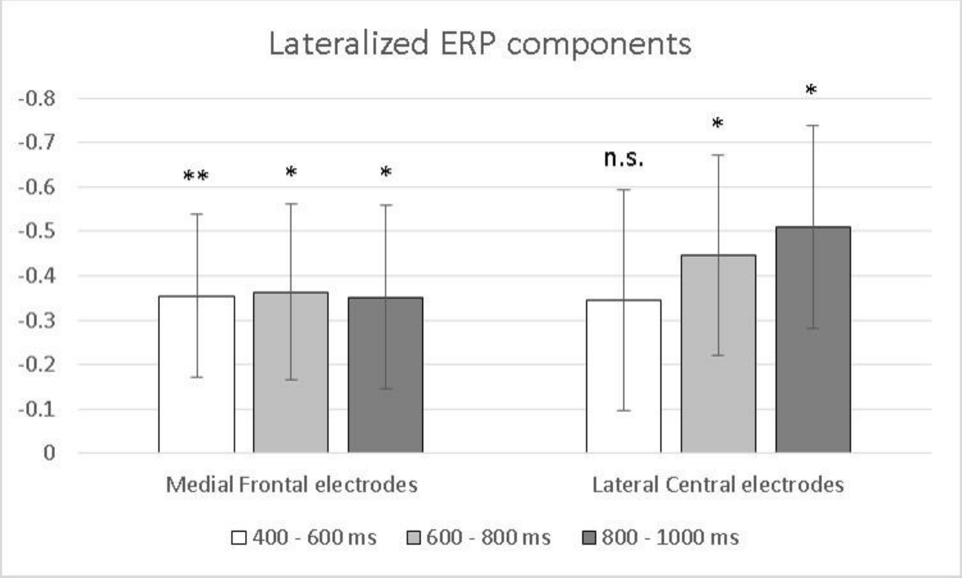

Figure 6. Average amplitude of the lateralized components elited in the time intervals 400-600 ms (white bars), 600–800 ms (light grey bars) and 800–1000 ms (dark grey bars) after cue onset shown separately for medial frontal (F3/4, F5/6 and FC5/6) and lateral central (C5/6, T7/8 and FC5/6) electrodes. These amplitude values were obtained by subtracting ERP mean amplitudes at electrodes ipsilateral to the cued side from mean amplitudes obtained at the corresponding contralateral electrodes and collapsing across the easy and difficult tasks.