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Effects of hand posture on preparatory control processes and sensory modulations in tactile-spatial attention

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Abstract

Objective: Event-related brain potentials (ERPs) were measured to investigate spatial coordinate systems involved in the control of preparatory tactile-spatial orienting, and in subsequent attentional modulations of somatosensory processing.

Methods: On each trial, a visual precue directed attention to the left or right hand, where infrequent tactile targets had to be detected. Hands were positioned either close together or wide apart. ERPs were recorded in the cue-target interval and in response to attended and unattended tactile non-targets.

Results: A frontal anterior directing attention negativity (ADAN) and a posterior late directing attention positivity (LDAP) were elicited in the cue-target interval contralateral to the direction of an attentional shift. The ADAN was unaffected by hand posture, but the LDAP was attenuated when hands were close together. N140 amplitudes were enhanced in response to tactile stimuli presented to the attended hand, and this effect was more pronounced when hands were wide apart.

Conclusions: ADAN and LDAP are linked to separable anterior and posterior attentional control systems, which use coordinate systems based on somatotopic and external space, respectively. Effects of spatial attention on somatosensory stimulus processing are affected by variations in body posture.

Significance: Our results demonstrate that representations of body locations in external space play a central role in the control of tactile attention.

Keywords: Selective attention; Somatosensory; Event related brain potential; Spatial cognition

1. Introduction

Selective attention is crucial for the detection, analysis, and identification of objects and events, as well as for the selection of appropriate actions based on such stimuli. Without attention, "the consciousness of every creature would be a gray chaotic indiscriminateness, impossible for us even to conceive" (James, 1901). While mechanisms underlying processes of selective attention in the visual and auditory domain have been studied intensively, the principles underlying attentional selectivity in somatosensation are still poorly understood. In one pioneering study investigating selective spatial attention in touch, Posner (1978) failed to find attentional effects on response latencies. However, more recent experiments have now demonstrated that, similar to vision and audition, spatial attention directed to the location of tactile events can improve the accuracy (Sathian and Burton, 1991) as well as the speed (Spence et al., 2000) of responses to tactile stimulation.

A number of electrophysiological experiments have measured event-related brain potentials (ERPs) in order to uncover which stages in the processing of somatosensory information are modulated by spatial attention. In these studies, electrical or mechanical stimuli were delivered to the left or right hand, with attention focused on one designated hand (Michie, 1984; Michie et al., 1987; García-Larrea et al., 1995; Eimer and Driver, 2000; Eimer et al., 2001, 2002; Van Velzen et al., 2002; Eimer and Forster, 2003a,b; Hötting et al., 2003). These experiments have consistently found that tactile-spatial attention

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modulates the somatosensory N140 component, with increased N140 amplitudes in response to tactile stimuli delivered to the currently attended hand as compared to tactile stimuli presented to the unattended hand. These findings, together with the fact attentional effects on even earlier sensory-specific somatosensory ERP components such as P40 (Desmedt and Tomberg, 1989; García-Larrea et al., 1991), N80 and P100 (Michie et al., 1987; Eimer and Forster, 2003b) have also been reported, suggest that spatial attention affects early stages of sensory-perceptual processes in modality-specific somatosensory cortical areas. At longer latencies, a sustained negativity (‘Nd’) for tactile stimuli at attended locations was observed (cf. Michie, 1984; Eimer and Forster, 2003a,b), which may reflect the in-depth processing of task-relevant features of attended stimuli.

In addition to investigating ERP correlates of the spatially selective processing of tactile stimuli at attended and unattended locations, recent ERP studies have now also begun to investigate preparatory attentional control processes, which are activated in anticipation of expected tactile stimuli at specific locations on the body surface, and are assumed to be responsible for subsequent attentional modulations of stimulus processing. In these experiments, ERPs were measured during the anticipatory orienting of tactile-spatial attention, which takes place in the interval between centrally presented symbolic visual or auditory cues directing attention to the left or right hand, and the subsequent tactile stimulation of one of these hands (Eimer et al., 2001, 2003a; Eimer and Van Velzen, 2002; Van Velzen et al., 2002). ERP components sensitive to the direction of a cued attentional shift were identified by examining systematic differences between ERP waveforms in response to cues directing tactile attention to the left side and ERPs in response to cues signalling an attention shift to the right side.

Using this approach, two successive lateralized components were uncovered. At frontal recording sites, ERPs were more negative over the hemisphere contralateral to the cued attentional shift relative to ERPs elicited over the ipsilateral hemisphere (‘Anterior Directing Attention Negativity’, ADAN). This effect had an onset latency of about 350 ms after cue onset, and was followed at about 500 ms post-stimulus by an enhanced posterior positivity at contralateral as compared to ipsilateral electrode sites (‘Late Directing Attention Positivity’, LDAP).[1] These effects were similar to the results found in earlier studies which have measured ERPs elicited during covert shifts of visual attention. For example, Harter et al. (1989) measured ERPs triggered by a central arrow cue indicating the side of an upcoming visual event. An early negative deflection at posterior electrodes contralateral to the direction of the induced attentional shift (‘Early Directing Attention Negativity’, EDAN) was followed by a contralateral positivity at posterior electrodes (LDAP; see also Yamaguchi et al., 1994; Hopf and Mangun, 2000; Nobre et al., 2000). In addition, an enhanced negativity at frontal electrodes contralateral to the direction of an attentional shift (ADAN) has also been observed during shifts of visual attention (Hopf and Mangun, 2000; Nobre et al., 2000).

These lateralized components have previously been interpreted as reflecting successive phases in the control of visual-spatial orienting, such as the decoding of the attentional cue (EDAN), the initiation of an attention shift (ADAN), and the preparatory activation of sensory-specific visual areas (LDAP). However, recent findings have cast doubt on some of these interpretations. First, we have shown that the posterior EDAN component reported in several earlier studies (cf. Harter et al., 1989; Hopf and Mangun, 2000) is not directly linked to the control of attentional shifts, but appears to reflect a lateralized visual response triggered by non-symmetrical visual cue stimulus (such as left-pointing and right-pointing arrows; see Van Velzen and Eimer, 2003, for more details). This component is absent in response to auditory attention cues (Eimer and Van Velzen, 2002), and when symmetrical visual cues are used (Eimer et al., 2002, and the present experiment). Second, the fact that LDAP components can be observed during shifts attention towards the expected location of tactile and auditory events (Eimer et al., 2002; Eimer and Van Velzen, 2002) calls into question the hypothesis that this component reflects the anticipatory preparation of sensory-specific extrastriate visual areas (Harter et al., 1989). Based on these findings, we have previously argued that both ADAN and LDAP components reflect sensory-unspecific preparatory processes operating within a multimodal attentional control system (see Eimer et al., 2002; Eimer and Driver, 2002; for more detailed discussion).

In order to gain further insights into the principles underlying the operation of selective spatial attention in the somatosensory modality, it is important to understand which spatial coordinate frames are used to guide attention to specific locations on the body surface. Shifts of attention towards expected tactile stimuli delivered to the left or right hand could be exclusively controlled by representations of external space (i.e. the representation of hand locations relative to other external objects, or representations coding hand position in external space relative to each other or relative to the body midline). Alternatively, shifts of attention could be mediated by anatomically defined spatial representations of relevant locations on the body surface (i.e. representations of the left and right hand as provided by somatotopic maps in somatosensory cortex).

In order to dissociate the roles of external and anatomical spatial codes in the control of tactile-spatial orienting,

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[1] It should be noted that characterizing these effects as an enhanced negativity (or positivity) contralateral to the direction of an attentional shift is logically equivalent to describing them as an enhanced positivity (or negativity) ipsilateral to an attentional shift. Since all previous studies in this field (starting with Harter et al., 1989) have described the polarity of these effects with reference to the contralateral hemisphere, this convention is also adopted here.

we have recently measured ERPs in response to cues directing attention to the left versus right hand under conditions where hands were either crossed or uncrossed (Eimer et al., 2003b). External and anatomical codes specifying task-relevant locations were congruent with uncrossed hands, but incongruent when hands were crossed (as the anatomically left hand was located on the right side of external space, and vice versa). Results revealed a striking dissociation in the effects of hand posture on the frontal ADAN and the posterior LDAP component. When attention shifts were considered in terms of their direction in external space, the LDAP was unaffected by the hand posture manipulation, suggesting that attentional control processes reflected by this component operate primarily on the basis of representations of external space, and are not sensitive to the anatomical identity of the attended hand. In contrast, the ADAN component was strongly affected by hand posture. When hands were uncrossed, an enhanced anterior negativity was elicited contralateral to the cued side of external space (that is, over the hemisphere receiving sensory input from the attended hand). With crossed hands, however, this negativity was now elicited *ipsilateral* to the cued side of external space (but, importantly, still over the hemisphere receiving input from the attended hand). This result indicates that, in contrast to the posterior LDAP, the ADAN component is sensitive to the anatomical identity of the cued hand (and not to the direction of an attentional shift in external space), and thus is likely to reflect attentional control processes based on somatotopically defined coordinates.

In our previous study (Eimer et al., 2003b), the hand posture manipulation (crossed versus uncrossed hands) affected the ADAN component, but had no effect on the LDAP. The aim of the current experiment was to provide positive evidence for the claim that the posterior LDAP component reflects attentional control mechanisms based on coordinates of external space. To achieve this aim, we used a different manipulation of hand posture, which was expected to have a systematic effect on the LDAP, but not on the ADAN component, that is, to yield a pattern of results exactly opposite to what was found by Eimer et al. (2003b). As in this earlier experiment, ERP correlates of anticipatory tactile-spatial orienting were measured while participants directed attention to the left or right side, as indicated by a central visual precue at the start of each trial, in order to detect infrequent tactile target stimuli when these were delivered to the cued hand. Thus, participants were required to make a target/non-target discrimination for stimuli presented to the cued (attended) hand, while stimuli delivered to the uncued hand were always task-irrelevant and therefore could be entirely ignored. Hands were always uncrossed in the present study, and the crucial hand posture manipulation concerned the distance between both hands in external space. In different blocks, hands were either located close together (Hands Near condition), or were wide apart (Hands Far condition), and hand posture was changed from Near to Far, or vice versa, between each successive block. To exclude any visual information about the current hand and arm posture, hands and arms were completely covered and hidden from view throughout the experiment.[2]

While manipulating the distance between hands in external space will affect the representation of task-relevant locations within an external spatial coordinate frame, their representation in a purely anatomically defined coordinate system should be unaffected by this manipulation. If the posterior LDAP and the frontal ADAN components elicited during preparatory shifts of tactile-spatial attention were linked to functionally separable attentional control processes, which operate on the basis of external and anatomical spatial codes, respectively, varying hand posture should have no effect on the ADAN, but might systematically affect the LDAP component. More specifically, if the attentional control processes reflected by the LDAP were sensitive to the horizontal position of the left and right hand in external space (that is, to the amplitude of cued attentional shifts, as represented within an external spatial coordinate system), the amplitude of this component should be smaller in blocks where hands are positioned close together, and larger in blocks where hands are located wide apart.

Another aim of the present experiment was to investigate the impact of hand posture on attentional modulations of the processing of tactile stimuli delivered to attended versus unattended locations. To achieve this aim, ERPs in response to tactile non-target stimuli at cued (attended) versus uncued (unattended) locations were compared separately for the Hands Far and Hands Near condition. If effects of spatial attention on somatosensory processing were affected by the distance between attended and unattended stimulus locations, one might expect to find attentional modulations effects of somatosensory ERP components (such as the N140) to be more pronounced in the Hands Far condition. Preliminary evidence for such a relationship was found in one recent study (Eimer and Forster, 2003a), where tactile attention was directed to one out of 4 possible stimulation locations on the right hand (middle or bottom phalanx of the index or middle finger). Here, attentional ERP modulations decreased as a function of the distance of a tactile stimulus from the current focus of attention, thus suggesting the presence of ‘attentional gradients’ in touch. One obvious shortcoming of this experiment was that the representation of the distance between attended and unattended locations in terms of external and somatotopic spatial codes was confounded. In contrast, the present manipulation of the distance between hands in external space should affect representations of attended versus unattended locations only

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[2] In our previous experiment investigating ERP correlates of tactile attention shifts with uncrossed and crossed hands (Eimer et al., 2003b), hands and arms were continuously visible. Thus, visual information could in principle have contributed to the differential effects observed in this study.

as far as they are based on external spatial coordinates. Thus, any impact of hand posture on attentional modulations of somatosensory ERPs would indicate that effects of spatial attention on somatosensory processing are not exclusively mediated by anatomically defined representations of attended locations on the body surface.

2. Methods

2.1. Participants

Sixteen paid volunteers participated in the experiment. Four participants were excluded due to poor eye fixation control (see below), so that 12 participants (7 females, 5 males, aged 20–32 years, with a mean of 26 years) remained in the sample. All participants were right-handed and had normal or corrected-to-normal vision by self-report.

2.2. Stimuli and apparatus

Participants sat in a dimly lit experimental chamber, wearing a head-mounted microphone. Two adjacent triangles, presented centrally on a computer screen at a viewing distance of 55 cm (total visual angle covered: $3.5° \times 2.5°$; visual angle of each triangle: $1.2° \times 2.5°$), served as cue stimuli. One triangle was red (luminance: 14 cd/m^2), the other blue (luminance: 19 cd/m^2), and they always pointed in opposite directions. A fixation cross, located between both triangles, was continuously present.

Tactile stimuli were presented using two 6 V solenoids, driving a metal rod with a blunt conical tip to the radial side of the middle phalanx of the left and right index fingers, making contact with a finger whenever a current was passed through the solenoid. The solenoids were attached to the fingers with white medical tape. White noise (65 dB SPL, measured from the position of the participants' head) was continuously present to mask any sounds made by the tactile stimulators. Tactile stimuli were vibrations, and these were generated by presenting a sequence of 20 rapidly delivered brief pulses. The stimulus onset asynchrony between successive pulses was 17 ms, corresponding to a rectangular stimulation frequency of 58.8 Hz. Tactile vibrations differed with respect to their intensity. To present 'weak' vibrations (which served as target stimuli), the contact time between rod and skin was set to 2 ms, followed by a 15 ms interpulse interval. To present 'strong' vibrations (which were non-target stimuli), contact time was set to 3 ms, followed by a 14 ms interpulse interval. Subjectively, these manipulations resulted in perceived vibrations with identical frequencies, but different intensities. The duration of each vibratory stimulus (measured as the interval between the onset of the first pulse and the offset of the last pulse) was 325 ms (for weak vibrations) or 326 ms (for strong vibrations).

2.3. Procedure

The experiment consisted of 12 blocks, each consisting of 74 trials. Each trial started with a 100 ms presentation of the cue. Six hundred milliseconds after cue offset, a tactile stimulus was presented unilaterally to the left or right hand. Intertrial interval was 1000 ms. Participants were instructed to keep their gaze focused on the central fixation cross, to respond vocally ('yes') whenever a target stimulus (a weak vibration) was detected at the cued hand, and to ignore all tactile stimuli (regardless of their intensity) presented to the uncued hand. Thus, participants had to direct their attention to the cued hand, as stimuli presented to this hand required a target/non-target discrimination. In contrast, stimuli delivered to the uncued hand were completely task-irrelevant. Vocal response latencies were measured with a voice key. The relevant hand for the current trial was signalled by the direction of one of the triangles. For 6 participants, the direction of blue triangles indicated the task-relevant hand. For the other 6 participants, the task-relevant hand was indicated by the direction of red triangles. Relevant left-pointing or right-pointing triangles were presented with equal probability to the left or right of fixation. In 60 trials, non-target stimuli (strong vibrations) were presented with equal probability to the left or right hand. These were preceded with equal probability by a left or right cue, resulting in 15 trials for each of the 4 combination of cued location and stimulus location. The remaining 14 trials contained target stimuli (weak vibrations). In 10 trials per block, target stimuli were delivered to the cued hand, and thus required a vocal response. In the remaining four trials, targets were delivered on the uncued hand, and no response was to be given to these stimuli.

Participants were instructed to place their hands on a table, with hand posture varied between blocks. In 6 blocks, hands were positioned close to each other (Near position), with a horizontal distance between the left and right index finger of 6 cm. In the other 6 blocks, hands were positioned wide apart (Far position), with a horizontal distance of 56 cm between the index fingers. Hand position was changed in each successive block, and both hands were always equidistant from the body midline. Half of the participants started the experiment with a Near position block, and the other half started with a Far position block. The position to be adopted in any given block was specified in advance of each block on the computer screen. To eliminate any visual information about the current hand and arm posture, the participants' hands and forearms were placed under a second table top. Additionally, the upper arms were covered by a piece of cloth that was attached to the second table top. Near and Far positions on the left and right side were marked by small plastic cones attached to the table surface, and these markers were used by the participants when changing their posture from Far to Near, or vice versa, in the interval between each block. Participants were monitored continuously with a video camera, to ensure that they adopted and maintained the instructed hand position.

2.4. Recording and data analysis

EEG was recorded with Ag-AgCl electrodes and linked-earlobe reference from FPz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, and Oz (according to the 10–20 system), and from OL and OR (located halfway between O1 and P7, and O2 and P8, respectively). Horizontal EOG was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 5 kΩ, and the impedances of the earlobe electrodes were kept as equal as possible. Amplifier bandpass was 0.1–40 Hz, and digitization rate was 200 Hz. Trials with eye blinks, horizontal eye movements, or muscle artefacts were excluded. Averaged HEOG waveforms obtained in the interval between cue onset and 400 ms after the onset of the peripheral tactile stimulus were scored for systematic deviations of eye position, indicating a tendency to move the eyes towards the cued side. Three participants were disqualified due to residual HEOG deflections exceeding ± 3 μV in the cue-target interval, and one participant was excluded because of HEOG deflections after tactile stimulus onset, which exceeded this criterion.

Separate analyses were conducted for ERPs obtained in the cue-target interval, and for ERPs in response to tactile non-target stimuli. ERPs in response to cue stimuli were averaged relative to a 100 ms pre-cue baseline for the time interval between cue onset and 700 ms after cue onset (corresponding to the onset of the subsequent tactile stimulus), for all combinations of hand position (Near vs. Far) and cue direction (left vs. right). ERP mean amplitudes were analysed with repeated measures analyses of variance (ANOVAs), and separate analyses were conducted for lateral anterior sites and for lateral posterior sites. These analyses included the factors electrode site (F7/8 vs. F3/4 vs. FC5/6, for the anterior analysis, and OL/R vs. P3/4 vs. P7/8, for the posterior analysis), hand position, cue direction, and hemisphere (left vs. right). Importantly, the presence of ERP liberalizations sensitive to the direction of an attentional shift will be revealed in these analyses by significant hemisphere × cue direction interactions. As in our previous studies of tactile-spatial orienting (cf. Eimer et al., 2002; Van Velzen et al., 2002), these analyses were based on mean amplitudes obtained between 150 and 350 ms, 350 and 500 ms, and 500 and 700 ms after cue onset.

ERPs to tactile non-targets (strong vibrations) were averaged relative to a 100 ms pre-stimulus baseline for all combinations of hand position, cue direction, and stimulated hand (left vs. right). ERP mean amplitudes were computed within successive measurement windows centred on the latencies (in ms post-stimulus) of early SEP components: P50 (40–60 ms), N80 (70–90 ms), P100 (90–120 ms), N140 (130–170 ms). To investigate longer-latency effects of attention, mean amplitudes were also computed between 200 and 300 ms post-stimulus. Statistical analyses of ERP mean amplitudes were conducted for lateral recording sites where the amplitudes of early ERP somatosensory components are maximal (F3/4, FC5/6, C3/4, CP5/6, and P3/4), as well as for midline electrodes Fz, Cz, and Pz. Separate analyses were conducted for midline electrodes, and for electrodes contralateral and ipsilateral to the anatomical side of the stimulated hand. Mean amplitude values were analysed with repeated measures ANOVAs for the factors hand position (Near vs. Far), attention (stimulus delivered to cued/attended vs. uncued/unattended hand), stimulated hand (left vs. right), and electrode site (frontal vs. frontocentral vs. central vs. centroparietal vs. parietal, for contralateral and ipsilateral electrodes; Fz vs. Cz vs. Pz, for midline sites). When appropriate, Greenhouse-Geisser adjustments to the degrees of freedom were applied. For vocal response times (RTs; recorded with a voice key), repeated measures ANOVAs were performed for the factors hand position and stimulated hand.

3. Results

3.1. Behavioural performance

Mean vocal RT to correctly detected infrequent weak target stimuli at attended locations was 620 ms. No main effects of hand position or stimulated hand, and no interaction between these factors was obtained. Participants missed less than 1% of all tactile targets at cued locations. False alarms to targets presented to the unattended hand and to non-target stimuli were very rare (less than 0.2% of all trials).

3.2. ERPs elicited in the cue-target interval during covert shifts of tactile-spatial attention

Fig. 1 shows grand-averaged ERPs elicited at lateral anterior electrode pairs (F7/8; F3/4) and lateral posterior electrode pairs (P7/8; OL/R) in the interval between the onset of the central visual cue and the onset of the subsequent peripheral tactile stimulus in blocks where hands were wide apart (top) and in blocks where hands were positioned close together (bottom). Waveforms are shown separately for cues directing attention to the left hand (solid lines) and for cues eliciting shifts of attention to the right hand (dashed lines). Fig. 2 shows ERP waveforms for one individual representative participant at lateral anterior (F7/8) and posterior (P7/8) electrodes for the Far (top) and Near (bottom) hand posture. As can be seen from these Figures, systematic ERP modulations sensitive to the direction of an attentional shift were obtained for both hand positions. At lateral anterior sites, ERPs were more negative at electrodes contralateral to the direction of an attentional shift than at ipsilateral electrodes (anterior

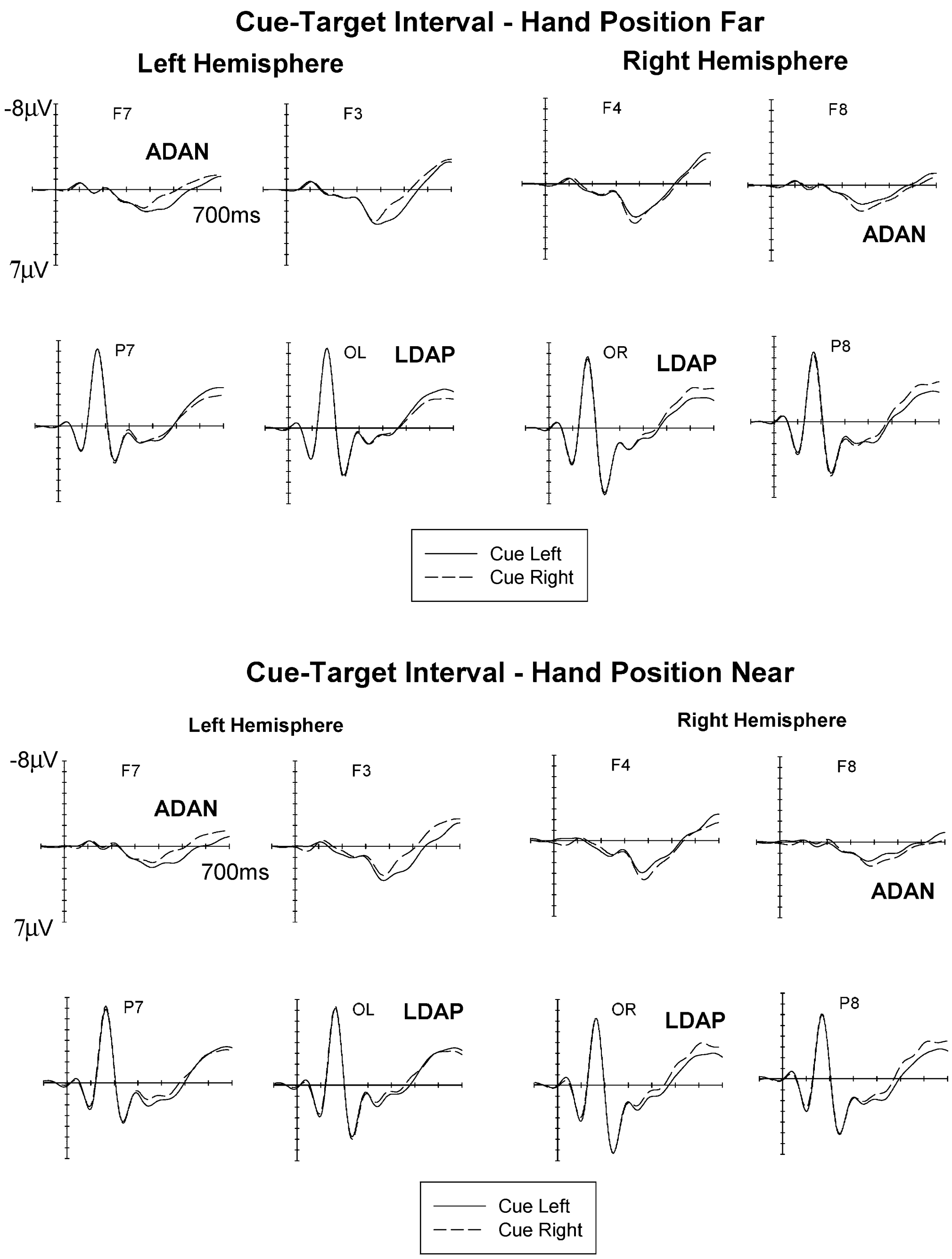

Fig. 1. Grand-averaged ERPs elicited at anterior (F3/4; F7/8) and at posterior electrodes (P7/8; OL/R) over the left and right hemisphere in the interval between cue onset and the onset of the subsequent peripheral tactile stimulus in response to visual cues directing attention to the left side (solid lines), or cues directing attention to the right side (dashed lines). Waveforms reveal a bilateral anterior directing attention negativity (ADAN) and a bilateral posterior late directing attention positivity (LDAP) contralateral to the direction of an attentional shift. Top panel: Hands Far condition. Bottom panel: Hands Near condition.

directing attention negativity; ADAN). At lateral posterior sites, ERPs were more positive contralateral as compared to ipsilateral to the cued attentional shift (late directing attention positivity; LDAP). The anterior ADAN component appears largely unaffected by hand position, as it was elicited bilaterally in the Hands Far condition as well as in the Hands Near condition. In contrast, the posterior LDAP appears to be attenuated in the Hands Near condition relative to the Hands Far condition, especially over the left hemisphere (P7, OL; Fig. 1, bottom). This pattern of ERP modulations was present in the grand-averaged waveforms (Fig. 1) as well as in the ERPs shown for one representative participant (Fig. 2), thus demonstrating that these lateralized components could be reliably observed for individual subjects.

These informal observations were confirmed by statistical analyses. No main effects or interactions involving cue direction were found between 150 ms and 350 ms following

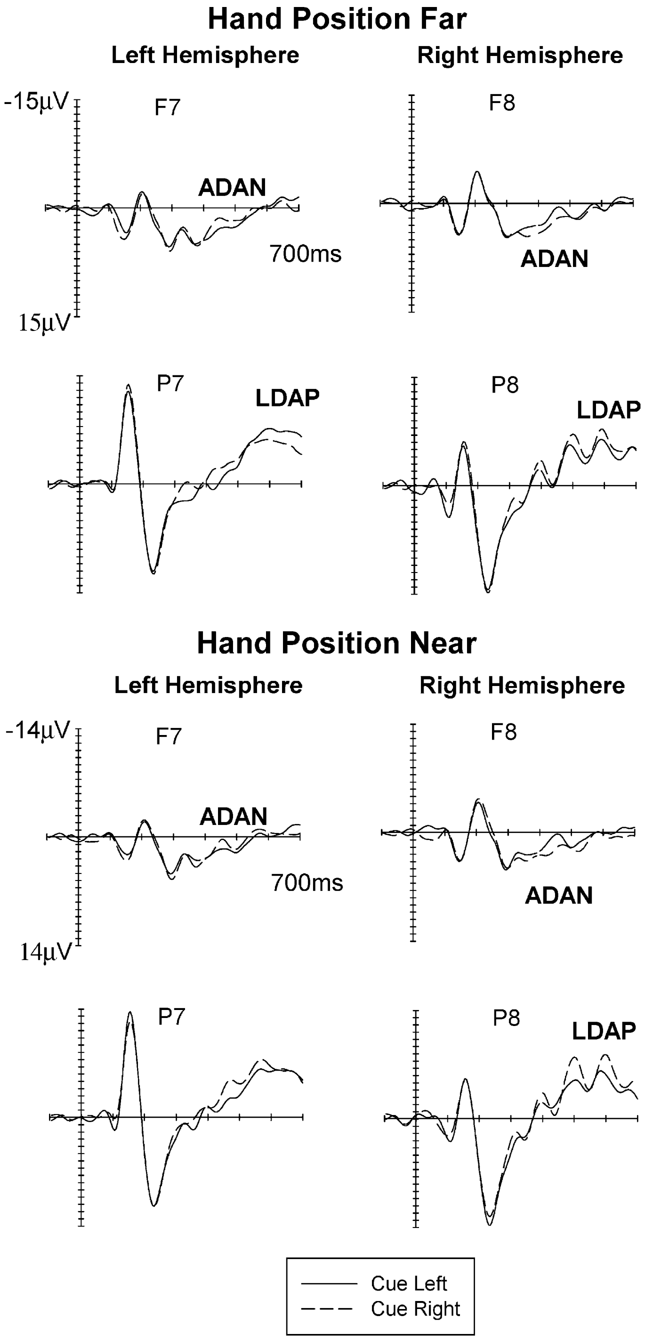

Fig. 2. ERPs elicited for one representative individual participant at anterior (F7/8) and at posterior electrodes (P7/8) over the left and right hemisphere in the interval between cue onset and the onset of the subsequent peripheral tactile stimulus in response to visual cues directing attention to the left side (solid lines), or cues directing attention to the right side (dashed lines). Top panel: Hands Far condition. Bottom panel: Hands Near condition.

cue onset. In the 350–500 ms measurement window, a main effect of electrode site was obtained for lateral anterior electrode pairs ($F(2,22) = 5.6$; $P < 0.02$; $\varepsilon = 0.854$), indicating that ERP amplitudes varied across the three electrode sites (F7/8, F3/4, FC5/6) included in this analysis. More importantly, significant hemisphere × cue direction interaction was present at these lateral anterior electrode pairs ($F(1,11) = 27.4$; $P < 0.001$), reflecting the presence of the ADAN component. No electrode site × hemisphere × cue direction interaction was obtained ($F(2,22) < 1$). When ERPs obtained at anterior electrodes over the left and right hemisphere were analysed separately, significant main effects of cue direction were obtained for the left hemisphere ($F(1,11) = 29.1$; $P < 0.001$), as well as for the right hemisphere ($F(1,11) = 4.9$; $P < 0.05$), thus demonstrating that the ADAN component was elicited bilaterally. Importantly, there were no higher-order interactions involving hand position (hand position × hemisphere × cue direction: $F(1,11) < 1$; electrode site × hand position × hemisphere × cue direction: $F(2,22) < 2.7$), suggesting that the ADAN component was not affected by the manipulation of the distance between the left and right hand. Accordingly, highly significant hemisphere × cue direction interactions were obtained in additional analyses conducted separately for the Hands Near condition ($F(1,11) = 31.7$; $P < 0.001$) and for the Hands Far condition ($F(1,11) = 16.8$; $P < 0.002$). No hemisphere × cue direction interaction was present between 350 and 500 ms at lateral posterior electrodes ($F(1,11) < 1$), thus confirming earlier observations that the frontal ADAN component precedes the posterior LDAP component.

In the subsequent 500–700 ms measurement window (corresponding to the final 200 ms of the cue-target interval), a main effect of electrode site was again obtained for lateral anterior electrode pairs ($F(2,22) = 8.3$; $P < 0.01$; $\varepsilon = 0.807$), as ERP amplitudes varied across the three electrode sites included (F7/8, F3/4, FC5/6). Again, and more importantly, significant hemisphere × cue direction interaction was again present for lateral anterior electrode pairs ($F(1,11) = 30.7$; $P < 0.001$), reflecting the later portion of the ADAN component. No electrode site × hemisphere × cue direction interaction was obtained ($F(2,22) < 1$). As before, higher-order interactions involving hand position were absent (hand position × hemisphere × cue direction: $F(1,11) < 2.3$; electrode site × hand position × hemisphere × cue direction: $F(2,22) < 1$), indicate that the later portion of the ADAN was unaffected by hand posture. Accordingly, subsequent analyses found significant hemisphere × cue direction interactions for the Hands Near condition ($F(1,11) = 27.4$; $P < 0.001$) as well as for the Hands Far condition ($F(1,11) = 18.7$; $P < 0.001$).[3]

At lateral posterior electrodes, no main effect of electrode site (OL/R vs. P3/4 vs. P7/8) was obtained in the 500–700 ms measurement window ($F(2,22) < 2.5$). More importantly, the presence of the posterior LDAP

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[3] When ERPs obtained in the 500–700 ms interval at anterior electrodes over the left and right hemisphere were analysed separately, a significant main effect of cue direction was obtained over the left hemisphere ($F(1,11) = 19.3$; $P < 0.001$). This effect only approached significance over the right hemisphere ($F(1,11) = 3.9$; $P < 0.08$), thus indicating that the ADAN component was more pronounced over the left hemisphere (see also Eimer et al., 2002, 2003b, for analogous findings).

component was reflected by a hemisphere × cue direction interaction obtained at these electrodes in the final 200 ms of the cue-target interval ($F(1,11) = 8.6$; $P < 0.02$). No electrode site × hemisphere × cue direction interaction was obtained ($F(2,22) < 2.7$). Importantly, a significant three-way interaction (hand position × hemisphere × cue direction) was obtained ($F(1,11) = 6.3$; $P < 0.03$), reflecting the fact that the LDAP component was larger when hands were far apart than when they were located close together. No electrode site × hand position × hemisphere × cue direction interaction was present ($F(2,22) < 1$). In analyses conducted separately for both hand positions, a highly significant hemisphere × cue direction interaction was obtained for the Hands Far condition ($F(1,11) = 13.0$; $P < 0.004$). In contrast, this interaction marginally failed to reach significance for the Hands Near condition ($F(1,11) = 4.5$; $P < 0.06$). To further investigate this differential effect of hand position on the posterior LDAP component, additional planned comparisons were conducted for ERPs elicited during leftward and rightward attentional shifts at occipital electrodes OL and OR, where this component is maximal. In the Hands Far condition, ERPs triggered during leftward and rightward shifts differed significantly at both OL ($t(11) = 2.5$; $P < 0.03$) and at OR ($t(11) = 2.7$; $P < 0.03$), demonstrating the presence of a bilateral LDAP component in this condition. In contrast, for the Hands Near condition, only a marginally significant difference between ERPs in response to left and right cues was obtained at OR ($t(11) = 2.1$; $P < 0.07$). No significant difference whatsoever was present at OL ($t(11) < 1$), thus confirming that the posterior LDAP component was attenuated in the Hands Near condition, in particular over the left hemisphere (see also Fig. 1, bottom).

The difference waveforms in Fig. 3 are shown to further visualize the amplitudes and the time course of these ERP liberalizations elicited during shifts of tactile-spatial attention, and to contrast the impact of different hand postures on these components. These waveforms are included exclusively to simplify graphical presentation, and to highlight the effects revealed by the statistical analyses reported above, but not for formal statistics. They were generated by first subtracting grand-averaged ERPs recorded during attentional shifts to the right side from grand-averaged ERPs elicited during leftward attentional shifts. To extract the lateralized portion of these differential responses, difference waveforms obtained for right-hemisphere electrodes were then subtracted from the difference waveforms emerging at homologous electrodes over the left hemisphere. In the resulting double subtraction waveforms, a negativity contralateral to the direction of an attentional

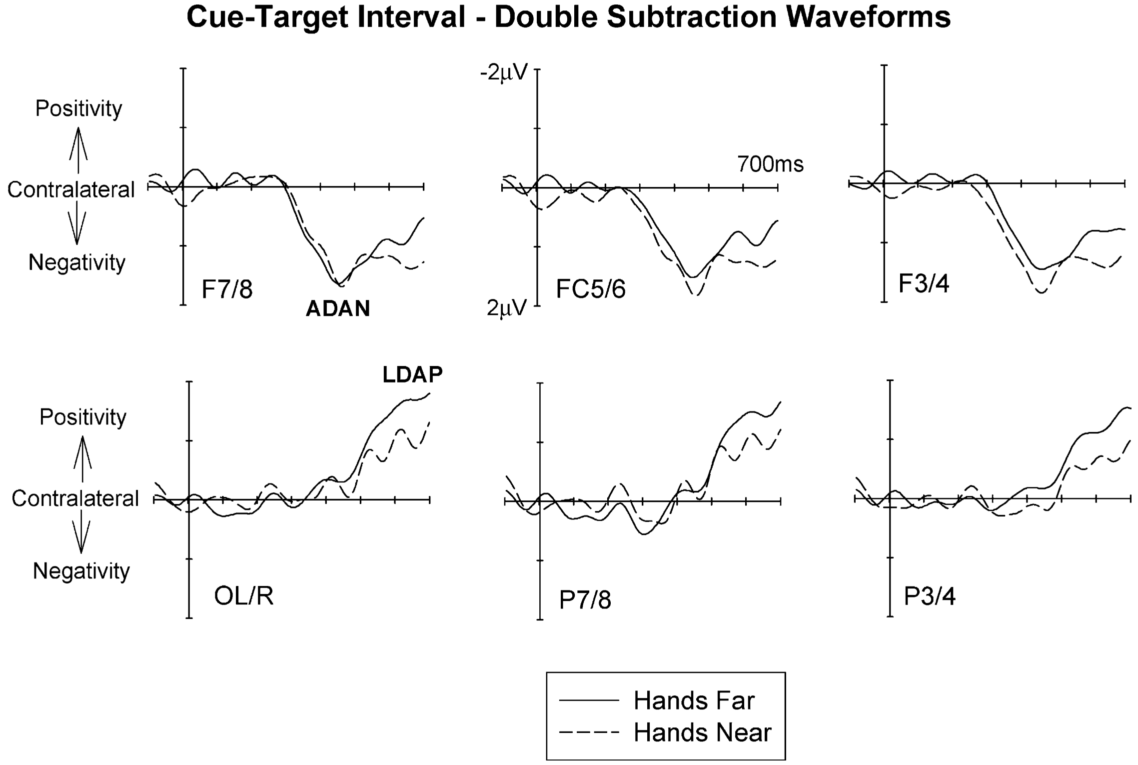

Fig. 3. Difference waveforms obtained at lateral anterior (top), and at lateral posterior (bottom) electrodes in the 700 ms cue-target interval in the Hands Far condition (solid lines) and in the Hands Near condition (dashed lines). Waveforms were generated by subtracting ERPs in response to cues directing attention to the right side of external space from ERPs in response to cues directing attention to the left side; and then subtracting the resulting difference waves at right electrodes from the difference waveform obtained for the corresponding left-hemisphere electrode. Enhanced negativities contralateral to the direction of attentional shifts are reflected by positive values (downward deflections), and enhanced positivities at contralateral sites are reflected by negative values (upward deflections).

shift is reflected by positive amplitude values (downward-going deflections), and a contralateral positivity is indicated by negative values (upward-going deflections). Fig. 3 shows difference waveforms obtained for anterior (top panel) and posterior (bottom panel) electrode pairs, displayed separately for the Hands Far condition (solid lines) and the Hands Near condition (dashed lines). In line with the statistical results, an anterior contralateral negativity (ADAN), which started about 350 ms after cue onset, was followed by a posterior contralateral positivity (LDAP) with an onset latency of about 500 ms after cue onset. While the ADAN component was largely unaffected by the variation of hand position, the posterior LDAP was clearly attenuated under conditions when hands were close together, as compared to blocks where hands were positioned wide apart.

3.3. Effects of spatial attention on somatosensory ERPs to tactile non-target stimuli

Fig. 4 shows ERPs elicited in response to tactile non-target stimuli (strong vibrations) at cued (attended) and uncued (unattended) locations. ERPs are shown for midline

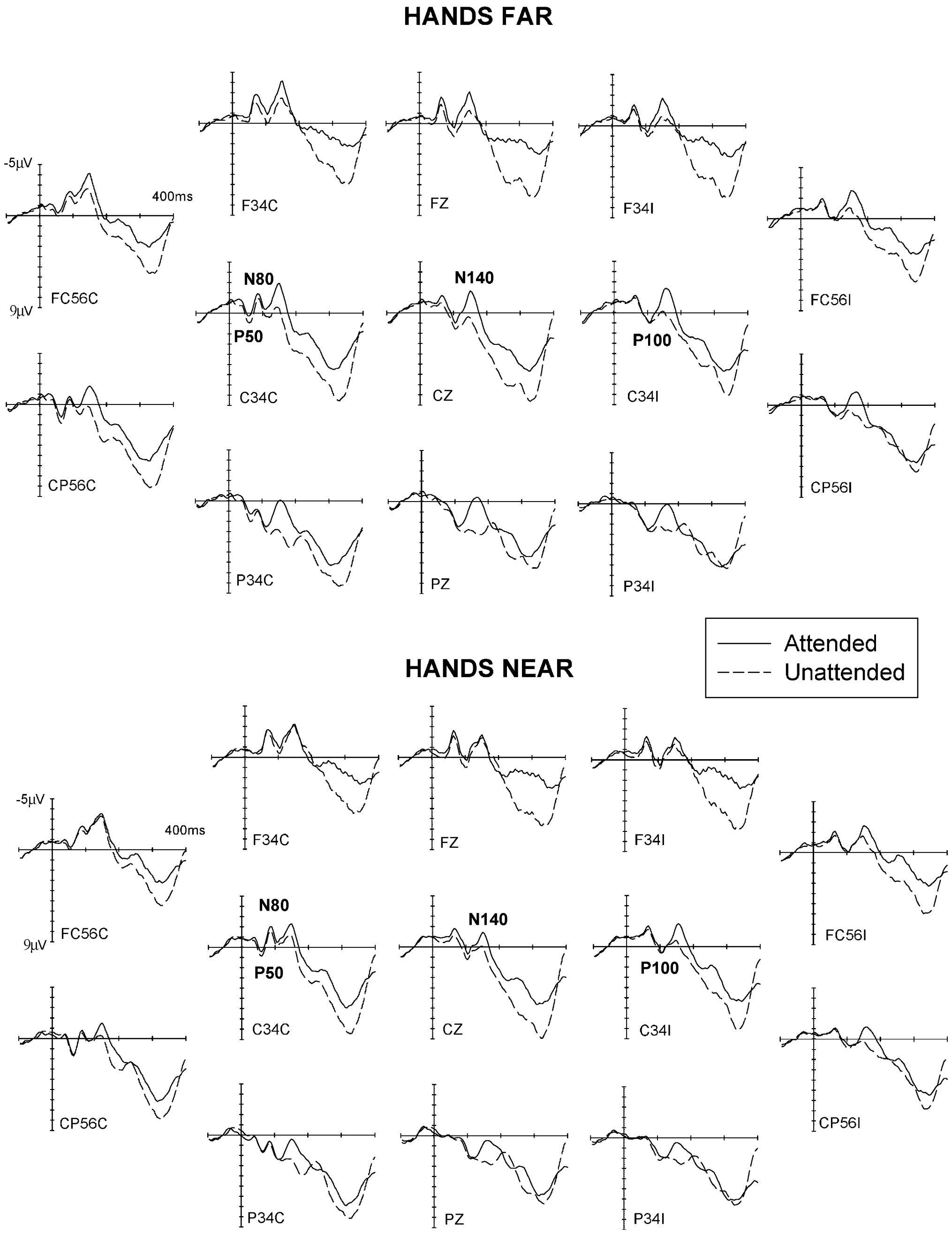

Fig. 4. Grand-averaged somatosensory ERPs elicited in the uncrossed hands condition at midline electrodes, and at sites contralateral (C) and ipsilateral (I) to the anatomical side of the stimulated hand, by tactile non-target stimuli at cued locations (solid lines) and uncued locations (dashed lines) in the 400 ms interval following stimulus onset. Top: Hands Far condition. Bottom: Hands Near condition.

electrodes and for electrodes contralateral (C) and ipsilateral (I) to the stimulated hand, and are displayed separately for the Hands Far condition (top) and the Hands Near condition (bottom). Spatial attention had systematic effects on somatosensory ERPs, with enhanced N140 components for tactile stimuli at attended as compared to unattended locations, followed by a sustained attentional negativity for cued versus uncued locations. These effects were present for both hand positions, although attentional N140 modulations appear considerably larger in the Hands Far condition (Fig. 4, top).

These observations were again confirmed by statistical analyses. No reliable effects of attention were found for the P50, N80, and P100 components. In contrast, significant main effects of attention were present in the N140 time range (130 -170 ms post-stimulus) at contralateral ($F(1,11) = 14.8$; $P < 0.003$), ipsilateral ($F(1,11) = 17.3$; $P < 0.002$), as well as at midline electrodes ($F(1,11) = 13.9$; $P < 0.003$). Importantly, reliable hand position × attention interactions were obtained contralaterally ($F(1,11) = 12.2$; $P < 0.005$) as well as at midline electrodes ($F(1,11) = 5.7$; $P < 0.04$), reflecting the fact that attentional N140 enhancements were more pronounced in the Hands Far condition than in the Hands Near condition. No significant hand position × attention interaction was found at ipsilateral electrodes ($F(1,11) < 2.3$). Follow-up analyses conducted separately for the Hands Far and Hands Near conditions revealed reliable attentional modulations of N140 amplitudes in the Hands Far condition at contralateral ($F(1,11) = 20.8$; $P < 0.001$), midline ($F(1,11) = 23.8$; $P < 0.001$), and ipsilateral electrodes ($F(1,11) > 23.4$; $P < 0.001$). In the Hands Near condition, significant main effects of attention were observed at contralateral ($F(1,11) = 6.1$; $P < 0.04$). and ipsilateral sites ($F(1,11) = 7.9$; $P < 0.02$), and this effect only narrowly failed to reach statistical significance at midline electrodes ($F(1,11) = 4.4$; $P < 0.06$).

The impact of hand position on attentional modulations of the somatosensory N140 component, as reflected by the hand position × attention interactions reported above, is further illustrated in Fig. 5, which shows the size of the N140 attention effect, measured by subtracting ERPs to tactile stimuli at unattended locations from ERPs to tactile stimuli at attended locations in the N140 time range (130–170 ms post-stimulus), displayed separately for the Hands Far and Hands Near condition. Attentional modulations of N140 amplitudes were consistently, and considerably larger for blocks where hands were wide apart, as compared to blocks where hands were positioned closely together.

In the 200–300 ms time interval, main effects of attention were present contralaterally ($F(1,11) = 14.0$; $P < 0.003$), ipsilaterally ($F(1,11) = 18.5$; $P < 0.001$), as well as at midline electrodes ($F(1,11) = 19.5$; $P < 0.001$), reflecting a sustained enhanced negativity for tactile stimuli at attended locations (see Fig. 4). In contrast to the results obtained for the N140 component, no reliable hand position × attention interactions were obtained in this measurement window (all $F(1,11) < 2.7$; all $P > 0.13$), thus suggesting that this later sustained attentional negativity was not affected by the manipulation of hand position. Separate subsequent analyses revealed reliable attention effects for the Hands Far condition ($F(1,11) = 14.1$, 18.9, and 25.5; $P < 0.003$, 0.001, and 0.001, for contralateral, ipsilateral, and midline sites) as well as for the Hands Near condition ($F(1,11) = 9.1$, 11.1, and 9.2; $P < 0.02$, 0.01, and 0.02, for contralateral, ipsilateral, and midline sites).

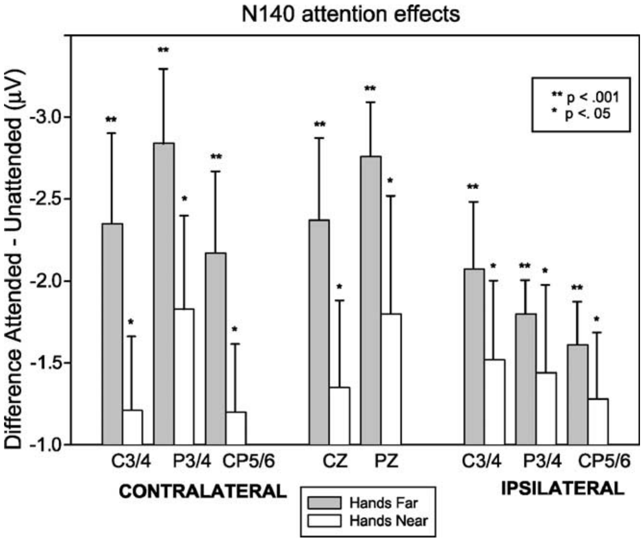

Fig. 5. Size of the attentional modulation of the N140 component (mean attended-unattended difference amplitudes between 130 and 170 ms post-stimulus) at midline electrodes, and at electrodes contralateral and ipsilateral to the anatomical side of the stimulated hand. Line bars indicate SE of mean for individual difference amplitudes. Dark bars: Hands Far condition. White bars: Hands Near condition. $^{**}P < 0.001$; $^{*}P < 0.05$.

4. Discussion

The primary aim of the present ERP study was to investigate spatial coordinates involved in the control of anticipatory shifts of attention towards expected locations of tactile events on the body surface, and to test the hypothesis that ERP components elicited during covert shifts of tactile attention (ADAN, LDAP) reflect separable attentional control processes which are sensitive to anatomical and external spatial codes, respectively. In a previous study (Eimer et al., 2003b), we have shown that the ADAN, but not the LDAP component is affected when hand posture is changed from an uncrossed to a crossed position. The present experiment investigated whether the opposite pattern of results (effects of hand posture on the LDAP, but not the ADAN component) will be observed when the horizontal distance between uncrossed hands is manipulated.

ERPs were recorded in response to visual symbolic cues signalling anticipatory shifts of tactile attention to the left or right hand. In different blocks, both hands were either located close together (Hands Near condition), or wide apart (Hands Far condition). Hands and arms were covered and thus hidden from view, in order to ensure that any effects of hand posture would be mediated exclusively by proprioceptive, and not by visual information. Our prediction was that this manipulation of hand position in external space would influence the posterior LDAP component (which was linked to preparatory processes sensitive to coordinates of external space), but not the ADAN component (which was linked to control processes sensitive to anatomically defined spatial coordinates). The results obtained for ERPs measured during the cue-target interval were fully in line with these predictions. A frontal ADAN component was elicited contralateral to the direction of a cued shift of tactile attention, thereby confirming earlier observations (Eimer et al., 2001, 2003a; Eimer and Van Velzen, 2002; Van Velzen et al., 2002). Importantly, hand posture had no effect on this component (see Figs. 1 and 3). This is exactly what is to be expected if the ADAN is linked to preparatory attentional control processes which are sensitive to representations of anatomical space. Somatotopically defined representation of task-relevant locations on the left versus right hand should not be affected by the distance between hands in external space.

In contrast, manipulating the horizontal separation between hands (and thus the amplitudes of attentional shifts as represented within coordinates of external space) had a clear effect on the posterior LDAP component. As predicted, this component was attenuated in the Hands Near condition as compared to the Hands Far condition, and this was reflected in significant hand position × hemisphere × cue direction interactions. When hands were located far apart, a bilaterally enhanced positivity was elicited in the final 200 ms of the cue-target interval contralateral to the direction of a cued attentional shift (similar to results from earlier studies investigating ERP correlates of tactile-spatial orienting; Eimer et al., 2001, 2003a; Eimer and Van Velzen, 2002; Van Velzen et al., 2002). In contrast, with hands positioned close together, this effect was only marginally significant over the right hemisphere, and completely absent over the left hemisphere. The fact that the LDAP was modulated by the amplitude of a cued attentional shift of tactile attention to the left versus right side of external space provides further evidence for the hypothesis that this component is linked to attentional control processes which are sensitive to representations of externally defined locations.

Overall, the results of the present experiment and of our previous study (Eimer et al., 2003b) demonstrate close interactions between representations of external space and representations of somatotopic space in the control of tactile spatial attention, and suggest that different mechanisms are involved in the coordination of somatotopic organization and external space. The scalp distribution of the anterior ADAN and the posterior LDAP suggests that these components may reflect activity within anterior and posterior attentional control networks, respectively, which have been identified in recent functional imaging studies of spatial attention (see Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002, for reviews). The observation that the LDAP, but not the ADAN component was affected by the distance between hands in external space provides further evidence for the assumption that these two lateralized components are linked to functionally separable attentional control systems. The anterior system (as reflected by the ADAN) appears to operate on the basis of anatomically defined spatial coordinates, while the posterior system (indicated by the LDAP) seems to be based on coordinates of external space. The sensitivity of the LDAP component to the present manipulation of hand posture is also in line with recent findings from single-cell recordings in monkeys, which demonstrated that neurons in posterior parietal cortex encode the direction of planned reaching movements in eye-centred coordinates, but not with respect to a limb-centred reference frame (see Andersen and Buneo, 2002, for review).

Another aim of the present study was to investigate whether spatially selective modulations in the processing of tactile events at attended versus unattended locations are affected by the horizontal separation between hands. Similar to earlier ERP studies of tactile-spatial attention (Michie, 1984; Michie et al., 1987; García-Larrea et al., 1995; Eimer et al., 2001, 2002; Eimer and Forster, 2003b), tactile events at attended locations elicited enhanced N140 components, which were followed by a sustained attentional negativity.[4] The N140 is assumed to be generated by multiple cortical sources, with generators located in SII, but also in frontal or cingulate cortex (García-Larrea et al., 1995). Attentional N140 modulations were present in the Hands Far as well as in the Hands Near condition. However, and more importantly, effects of tactile attention on N140 amplitudes were smaller when hands were located close together, as compared to blocks where hands were positioned far apart (see Figs. 3 and 4). This observation strongly suggests that the spatially selective processing of tactile stimuli in modality-specific somatosensory brain areas is not exclusively determined by somatotopic representations of the body surface, but is at least partially mediated by the representation of task-relevant locations in external space. The fact that no visual information about hand position was available in the current

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[4] Using a trial-by-trial cueing paradigm similar to the procedure used here, Eimer and Forster (2003b) also observed a bilateral attentional modulation of the somatosensory P100 component, which was absent in the present experiment. This discrepancy may be due to differences in the nature of the tactile stimuli used and in the attentional demands of the tactile discrimination tasks. In the Eimer and Forster (2003b) study, tactile targets were double pulses presented among single-pulse stimuli, whereas the task used in the present experiment required participants to discriminate intensities of vibratory tactile stimuli.

study further indicates that such representations can be based primarily on proprioceptive signals.

The present ERP results suggest that the efficiency of spatial attention in somatosensation is at least in part determined by the separation between attended and unattended locations on the body surface in external space. This is in line with observations from earlier studies demonstrating reliable effects of hand posture on behavioural performance (Nicoletti et al., 1982, 1984). Choice reaction times (RTs) were delayed when hands were crossed relative to uncrossed hands, and this 'hand posture effect' was assumed to result from a conflict between external and anatomical spatial codes during response selection. Importantly, behavioural effects of hand posture on somatosensory processing have previously been demonstrated by Driver and Grossenbacher (1996). These authors found impairments in the discrimination of vibrations delivered to the fingertip under conditions when response-incongruent vibrations were simultaneously delivered to the opposite hand, indicating that tactile attention was not completely focused on the task-relevant hand. Most importantly, the size of this interference effect was determined by the spatial separation between hands, with reduced interference effects (reflecting more efficient attentional selectivity) when hands were positioned far apart. This pattern of results remained present even when participants were blindfolded, indicating (in line with the current ERP results) that these effects of hand posture were primarily mediated by proprioceptive signals.

In summary, the present results provide new electrophysiological evidence for the hypothesis that anterior and posterior attentional control systems which are activated during covert shifts of tactile-spatial attention towards specific locations on the body surface are functionally separable, as they appear to employ different spatial coordinates (anatomical/somatotopic codes for the anterior system; representations of locations in external space for the posterior system). Moreover, attentional modulations of tactile stimulus processing in somatosensory cortex are sensitive to variations in body posture, suggesting that representations of the location of body parts in external space play an important role for attentional selectivity in the somatosensory modality.

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