

# Common Anatomical and External Coding for Hands and Feet in Tactile Attention: Evidence from Event-related Potentials

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## Abstract

Recent studies have suggested that the location of tactile stimuli is automatically recoded from anatomical into external coordinates, independent of the task requirements. However, research has mainly involved the two hands, which may not be representative for the whole body because they are excessively used for the visually guided manipulation of objects and tools. We recorded event-related potentials (ERPs) while participants received tactile stimuli to the hands and feet, but attended only one limb. The hands were placed near the feet either in an uncrossed or a crossed posture, thus varying the spatial distance of each hand from each foot. Centro-parietal ERPs 100–140 msec poststimulus were more positive when stimulating

the anatomically same-side hand while attending a foot. They were also more positive when the Euclidean distance between the stimulated hand and the attended foot was small rather than large. When a foot was stimulated and a hand attended, a similar modulation of foot ERPs was observed for the right foot. To assess the spatial distance between two limbs in space, the external location of both must be known. The present ERP results therefore suggest that not only the hands but also other body parts are remapped into external coordinates. The use of both anatomical and external coordinates may facilitate the control of actions toward tactile events and the choice of the most suitable effector. ■

## INTRODUCTION

When a touch is felt somewhere on the body, one knows immediately where to look to identify the source of the touch, and where (and with which effector) to reach to interact with the object that caused the touch, for example, to brush it away or to grab it. This task is not trivial: The body is constantly in motion, and thus, both the visual location of a tactile event and the target location in relation to the effector depend on body posture. The brain must therefore take posture into account when calculating the location of a touch as it would be seen by the eyes (i.e., visual or external space) based on the anatomical coordinates of a tactile event as signaled by the sensors on the skin.

Evidence suggests that this kind of coordinate transformation may be routinely and automatically performed by the brain for every tactile stimulus. One example is the temporal order judgment task, in which participants judge which of two tactile stimuli, one to each hand, occurred first. Although hand location is theoretically irrelevant to solve the task, performance is impaired when the arms are held in a crossed rather than in an uncrossed posture (Röder, Rösler, & Spence, 2004; Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001). This has

been interpreted to indicate a conflict between two reference frames, one anatomical and one external, because with crossed hands a hand's visual location is opposite its anatomical side. Limb crossing effects also occur when the two feet, and even when a hand and a foot, are stimulated (Schicke & Röder, 2006), suggesting that posture effects do not arise primarily from a confusion of identical limbs (e.g., the two hands), but from a more general confusion of the location of tactile events. Congenitally blind people perform well when it is advantageous to use an anatomical reference frame (e.g., when it is beneficial to disregard posture, as in the temporal order judgment task), and, conversely, are impaired compared to sighted participants when the use of an external reference frame is beneficial for performance (Röder, Kusmierek, Spence, & Schicke, 2007; Röder et al., 2004). Therefore, the automated use of an external reference frame is probably induced by the visual system during child development.

It has been proposed that the brain contains a representation of the current configuration of the body in space, referred to as body schema (see Holmes & Spence, 2004; Gallagher, 1986). Such an entity might keep track of the current state of the body and may either enable or perform the kinds of transformations necessary to convert between different sensory and motor coordinates. Indeed, areas in the intraparietal sulcus (IPS) and frontal premotor cortex have frequently been suggested to form

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distinct fronto-parietal circuits, each of which subserves a specific function in target selection and motor planning for specific effectors. Evidence suggests circuits for arm reaching, hand grasping, eye movements, and defensive movements for the space around the upper body, termed the peripersonal space (Graziano & Cooke, 2006; Matelli & Luppino, 2001; Rizzolatti, Luppino, & Matelli, 1998). Homologous areas are thought to exist in the human brain (Medendorp, Goltz, & Vilis, 2005; Connolly, Andersen, & Goodale, 2003; Grefkes, Weiss, Zilles, & Fink, 2002; Bremmer et al., 2001). Such a parcellation according to function and/or body parts seems to contradict the notion of an all-encompassing body schema, and accordingly, it has been proposed that there is not one such representation of the body; rather, the body schema is thought to be an emergent property of the interaction of multiple, specialized areas (Holmes & Spence, 2004). Along the same lines, it has recently been speculated that, given their dense interconnections, areas in the IPS and in frontal cortex probably share a lot of information, and, despite their specialization, are “team players” (Graziano & Cooke, 2006). However, it is noteworthy that all these circuits are concerned with the eyes, hands, and the upper body. It is, in contrast, largely unknown how and where analogous functions for the feet and lower body are carried out in the brain.

One important property of the IPS and its connected frontal areas is that their neurons’ responsiveness is modulated by attention (Cook & Maunsell, 2002; Graziano & Gross, 1998). Similarly, patients with parietal or frontal lobe damage frequently suffer from hemispatial neglect, a disorder which impairs functions both related to reference frames and to attention in the contralesional hemifield (Halligan, Fink, Marshall, & Vallar, 2003; Vallar, 1998). Some hemineglect patients display dysfunctional behavior only in peripersonal space, suggesting that a fronto-parietal circuit for peripersonal space, homologous to the monkey brain, is affected in these patients (Ladavas, 2002).

In healthy humans, the use of anatomical and external reference frames in the context of attention has frequently been studied using event-related potentials (ERPs) derived from the EEG. Several studies have investigated the influence of body posture on the attentional modulation of somatosensory ERPs preceding and following tactile stimulation while participants directed attention to one hand. Orienting spatial attention to one hand in expectation of a stimulus was accompanied by frontal and parietal prestimulus ERP deflections. The parietal deflection was mainly determined by the external rather than the anatomical location of the to-be-attended hand (Eimer, Forster, & Van Velzen, 2003). In the same study, when the hands were in a normal, uncrossed posture, poststimulus ERPs were more positive after 100 msec (named P100) and more negative after 140 msec (named N140) for attended than unattended stimuli; these attention-related differences were no longer observed when the hands were crossed. A higher negativity

for attended stimuli (termed the negative difference, Nd) in the time interval of 200–300 msec was also reduced. In a second study, similar effects were reported after 80 msec (termed N80) and 140 msec; even more, a tendency for a reversal of the attention effect was evident in the 140-msec time range (Eimer, Cockburn, Smedley, & Driver, 2001). In both studies, the results were interpreted to indicate a disruption of attentional selection when anatomical and external coordinates are incongruent, as in the case of crossed hands.

In a third study, the difference between ERPs for attended and unattended stimuli was larger when the hands were held far apart rather than close to each other (Eimer, Forster, Fieger, & Harbich, 2004). Thus, ERP differed as an effect of external spatial distance because, in terms of an anatomical reference frame, both conditions were identical. Thus, if tactile attention used only an anatomical reference frame, no influence of hand crossing or hand distance on ERPs should have occurred in these studies.

However, as is true for most of the research discussed thus far, these ERP experiments involved only the fingers and hands. Only one behavioral study has provided evidence that external space may be relevant for tactile attention to all body parts by showing that body posture influences the time required to shift attention between different body sites on the arms and legs (Lakatos & Shepard, 1997). It is therefore largely unclear if tactile coordinates are indeed transformed for all body parts, or if this feature is specific for the eyes and hands, the two effectors that are ubiquitously used for actions and object manipulation and that need to be coordinated for most of our actions.

The ERP studies above have all directly compared ERPs to attended and unattended stimuli. Another experimental approach in attention research is the so-called spatial attentional gradient, which refers to a modulation of sensory ERPs by the distance of the ERP-eliciting stimulus from the current focus of attention; more specifically, the ERP attention effect is larger the closer a stimulus occurs to an attended location (e.g., Eimer & Forster, 2003b; Teder-Salejarvi & Hillyard, 1998; Mangun & Hillyard, 1988). Thus, rather than relying on the relatively crude distinction of attended versus unattended stimulation, the spatial gradient paradigm allows investigating unattended stimuli when they are at different distances to the attended location.

To investigate the use of anatomical and external reference frames in the context of body parts other than the hands, the present study combined the manipulation of posture and the use of the spatial attentional gradient. We recorded somatosensory ERPs to stimulation of both hands and both feet while participants placed their hands near their feet in either an uncrossed or crossed hand posture. In each block, participants monitored one of the four stimulated limbs for the occurrence of infrequent target stimuli. Note that, theoretically, this task would not require participants to take their body posture into account; they were required only to monitor one limb for infrequent targets and ignore all other tactile stimuli.

The strength of this experimental paradigm is the possibility to exploit the spatial attentional gradient to disentangle the spatial reference frames used by the brain during the monitoring of tactile events both at the hands and at the feet. If the brain uses an anatomical reference frame to code for tactile events, the gradient in the ERPs should be determined by the anatomical distance of the tactile event from the attended location and should thus be independent of body posture. If, in contrast, the brain uses an external reference frame, the ERP gradients should be determined by the spatial distance of the tactile event from the attended location in external space, and thus, be influenced by body posture. In other words, the ERP enhancement should be larger if a tactile stimulus occurs at an unattended limb that is currently located near another, attended limb, whereas it should be smaller if the unattended limb is located far away from that limb.

## METHODS

### Participants

Sixteen participants were recruited from the University of Hamburg and from the Hamburg community. The data of two participants were excluded from all analyses (see below). The remaining 14 participants (10 women, 4 men) were aged 21 to 31 years (mean = 25.2 years). All of them were right-handed, had normal or corrected-to-normal vision, normal hearing, and reported neither any deficits in the tactile domain nor any neurological disorders. The experiment was conducted according to the guidelines laid down in the Declaration of Helsinki (World Medical Association, 2004) and participants gave their informed consent to take part. Participants received monetary compensation (€7 per hour, €28–35 total) for participation.

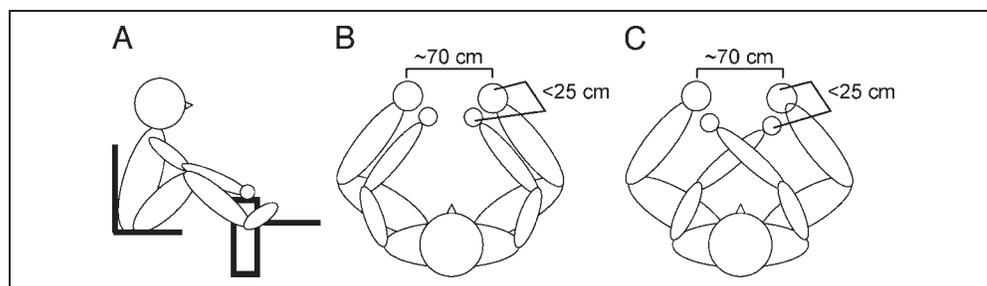
### Experimental Apparatus

Participants sat on a chair and rested their feet ~70 cm apart on a wooden sideboard placed in front of them. The hands rested on a foam block placed between the lower legs and were placed to be as near to the feet

as possible (see Figure 1A). The distance between the finger and the toe of one side was kept below 25 cm (see Figure 1B and C). To reduce artifacts in the EEG caused by muscle tension, participants' arms and legs were padded with pillows, and their legs were bound together at the knees with an elastic band so that they did not have to actively hold them upright during the experiment. Block length was 90 sec, and participants were encouraged to take breaks and stretch their arms and legs between blocks. The hands were placed at the same locations near the feet in the uncrossed and crossed conditions, thus keeping the distance between a foot and the nearest hand identical at all times.

Tactile stimuli consisted of a metal rod (diameter: 1.5 mm), which was electronically lifted from its resting position by a relay (lift from resting position: 0.5 mm). Relay and rod were contained in small plastic cubes. At the feet, these were attached to a plate which was attached to the foot, which allowed precise placement of the stimulator to the toe and comfortable placement of the foot against the sideboard (see Schicke & Röder, 2006 for a detailed description of this device). At the hands, the stimulators were attached using medical tape. The relays were controlled by the software Presentation (Neurobehavioral Systems, Albany, CA). Stimulation was applied to the distal phalanges of the index fingers and halluces (i.e., big toes) opposite to the finger/toe nail (i.e., to that part of the finger that is used when exploring by touch, and to the equivalent site on the big toe). Because the experimental task required participants to ignore most stimuli from the different limbs, stimulus intensity was adjusted separately for hands and feet for each participant such that all stimuli were subjectively perceived as equally strong to make them all equally (ir)relevant. This was achieved by adjusting the voltage used to drive the stimulators' relays. Because foot stimuli were felt less strongly by all participants at equal physical stimulation, foot stimulation was always delivered with the maximum voltage (24 V), whereas the voltage used for the hand stimuli was regulated down until participants reported them to be subjectively as strong as the foot stimuli. Stimulus strength was then adjusted slightly up and down several times to assure

**Figure 1.** Experimental conditions. (A) Participants were seated with their feet rested on a sideboard placed in front of them. (B) Uncrossed conditions: The hands were placed each next to the foot of the same anatomical body side. (C) Crossed conditions: The hands were placed each next to the foot of the opposite anatomical body side. Distance between hand and foot was identical in both postures.



that the chosen intensity was, indeed, felt as being equal to that of the feet.

## Experimental Procedure

Participants attended to one hand or one foot for an entire block (“sustained attention task”). In each block, the hands were either placed in parallel or in a crossed posture, one hand near each foot (see Figure 1B and C), resulting in eight attention–posture combinations (4 attended limbs  $\times$  2 postures). Each of these was repeated eight times, resulting in 64 experimental blocks.

Instructions were always given with respect to the limb, independent of the crossing status (e.g., “attend to your right hand”). In addition, the to-be-attended limb was pointed to. There were two kinds of tactile stimuli: Standard stimuli consisted of the lifting of the metal rod for 50 msec. Deviant stimuli differed from the standards in that they consisted of two 30-msec lifts, separated by 100 msec. Each block comprised 80 standard and 12 deviant stimuli. Stimuli were presented with a stimulus onset asynchrony of 800–1000 msec (uniform distribution) in a random sequence to all four limbs with equal probability. Thus, over the course of the experiment, 160 trials were acquired for standard stimuli in each attention–posture condition for each stimulated limb. The participants’ task was to say “ta” whenever they detected a deviant stimulus at the attended location. All other stimuli, especially all standard stimuli (including those at the attended location), did not require a response. With this paradigm, the ERP to standard stimuli could be recorded at both attended and unattended locations without the confound of a motor response. Participants’ responses were recorded with a voice key (SV-1; Cedrus, San Pedro, CA, USA). The room was dark, and participants fixated a green LED mounted straight ahead of their eyes during the duration of the block. Prior to the experiment, participants performed one to two practice blocks.

## Electroencephalographic Recording

The EEG and EOG were recorded continuously from 125 Ag/AgCl scalp electrodes which were each preamplified at the recording site (EasyCap Fast ‘n Easy active electrodes; EasyCap GmbH, Herrsching, Germany), referenced to the left earlobe and re-referenced off-line to a linked earlobe reference. Electrodes were mounted according to the 10–5 system (Oostenveld & Praamstra, 2001), an extension of the 10–20 system, using an elastic cap (EasyCap GmbH). Electrode positions were Fp1/2, AFz, AFF1/2h, AF3/4, AFF5/6h, AF7/8, Fz, F1/2, F3/4, F5/6, F7/8, F9/10, FFC1/2h, FFC3/4h, FFC5/6h, FFT7/8h, FFT9/10h, FCz, FC1/2, FC3/4, FC5/6, FT7/8, FT9/10, FCC1/2h, FCC3/4h, FCC5/6h, FTT7/8h, FTT9/10h, Cz, C1/2, C3/4, C5/6, T7/8, CCP1/2h, CCP3/4h, CCP5/6h, TTP7/8h, CPz, CP1/2, CP3/4, CP5/6, TP7/8, TP9/10, CPP1/2h, CPP3/4h, CPP5/6h, TPP7/8h, TPP9/10h, Pz, P1/2, P3/4, P5/6, P7/8,

P9/10, PPO1/2h, PPO5/6h, PPO9/10h, POz, PO3/4, PO7/8, PO9/10, POO1/2, POO9/10h, Oz, O1/2, Iz, I1, and I2.

Vertical eye movements were recorded with an electrode placed under the left eye, with the same reference as all other electrodes. Horizontal eye movements were derived by subtracting the signal at F10 from that at F9 which are located near the outer canthi of the eyes.

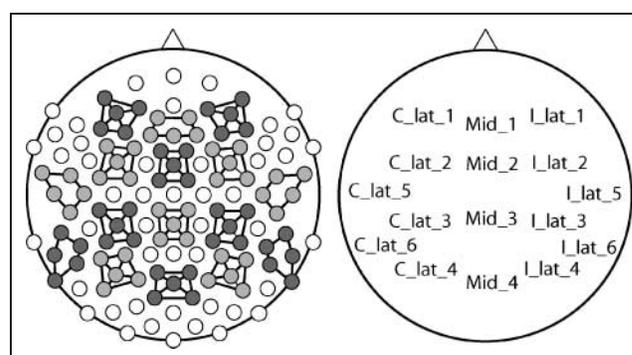
The electrode signals were amplified using three BrainAmp DC amplifiers and one BrainAmp MR DC amplifier with 32 channels each (Brain Products GmbH, Gilching, Germany) and digitally stored using the BrainVision Recorder software (Brain Products GmbH). The analog EEG signal was sampled at 5000 Hz, filtered on-line with a band pass of 0.1 to 250 Hz and then down sampled on-line to 500 Hz to be stored on disc. The signal was filtered off-line with a high cutoff at 20 Hz, 12 dB/oct.

## EEG Analysis

EEG data processing was conducted with VisionAnalyzer 1.05 (Brain Products GmbH) and included segmentation of the continuous signal into bins of 100 msec pre-, and 450 msec poststimulus, artifact rejection (eye artifacts and segments with absolute voltage differences of  $>100$ – $160$   $\mu$ V), averaging by condition, and baseline correction (100 msec prestimulus baseline). Data from a participant were not used if more than 30% of the trials were discarded in this manner (2 participants).

Only standard stimuli, which never required a response (see Experimental Procedure), were used in the analyses. Trials after which an erroneous response was given by the participant were discarded from the analyses.

Electrodes were clustered into groups of 5 for statistical analyses (see Figure 2) to increase the signal-to-noise ratio of the ERPs (see below). Clusters were chosen such that they covered most of the frontal, temporal, and parietal lobes; modulations in tactile ERPs in the time range of 80–300 msec have been reported in these areas (e.g., Eimer & Forster, 2003a). Furthermore, each clus-



**Figure 2.** Electrode positions and clusters for statistical analyses. Circles in the left figure denote electrode positions. Clusters are indicated by identical coloring and connecting lines (5 neighboring electrodes per cluster). The right figure indicates the names given to each cluster as used in the statistical results.



4. Finally, to allow a comparison of our experiment with previous findings, we analyzed the conditions in which the hands were both attended and stimulated. This analysis differs from the first three in that it does not analyze ERPs just to unattended stimuli; therefore, it does not assess an attentional gradient. We used a four-way ANOVA with factors hand crossing (uncrossed vs. crossed), attention (attended vs. unattended), hemisphere (ipsi- vs. contralateral to the stimulated hand), and electrode cluster (six clusters). Midline clusters were analyzed with a similar ANOVA without a hemisphere factor.

For repeated measures with more than two factor levels, ANOVA  $p$  values were corrected for violation of the sphericity assumption using the method suggested by Huynh and Feldt (1976). Voltage maps were created with the software EEGLAB, version 6.0b (Delorme & Makeig, 2004), using all 125 scalp electrodes.

Previous studies have reported effects of hand crossing in the time ranges of 80–160 and 200–300 msec (Eimer et al., 2001, 2003). Because our focus was on the analyses involving both hands and feet, we visually inspected ERPs in this time range for these analyses and found differences at 100–140 msec. In order to make all four conducted analyses comparable, we used this time interval for all analyses. However, ERP amplitudes are known to peak 20 to 30 msec later after foot than after hand stimulation (Kany & Treede, 1997), consistent with the prolonged neural transmission time from the foot to the brain as compared to the transmission time from the hand to the brain (Dowman & Schell, 1999; Nuwer et al., 1994; Macefield, Gandevia, & Burke, 1989; Treede, Kief, Holzer, & Bromm, 1988). We therefore adjusted the analyzed time window for our foot ERPs to 120–160 msec.

For the crossed hands analyses (Analysis 4), visual inspection suggested crossing effects also in the time interval of 190–300 msec, consistent with earlier reports (see Introduction). This time interval was therefore additionally analyzed for the crossed hand analysis.

## RESULTS

### Response Accuracy

Hit rates for targets were analyzed in an ANOVA with repeated measurement factors hand crossing (uncrossed vs. crossed), type of limb (hand vs. foot), and stimulated body side (right vs. left). Participants detected target stimuli at the hands better than at the feet [92.1% vs. 82.7%,  $SE = 1.3%$  and  $1.8%$ , main effect type of limb,  $F(1, 13) = 37.43$ ,  $p < .001$ ]. However, neither hand crossing (uncrossed: 87.7%,  $SE = 1.5%$ ; crossed: 87.1%,  $SE = 1.5%$ ), nor stimulated body side (right side: 88.7%,  $SE = 1.5%$ ; left side: 86.1%,  $SE = 1.5%$ ), nor any interaction were significant (all  $p > .17$ ). Participants hardly ever confused standard for deviant stimuli; the most common false alarm error was a response to a standard stimulus at the attended location (1.3%,  $SE = .3%$ ). The

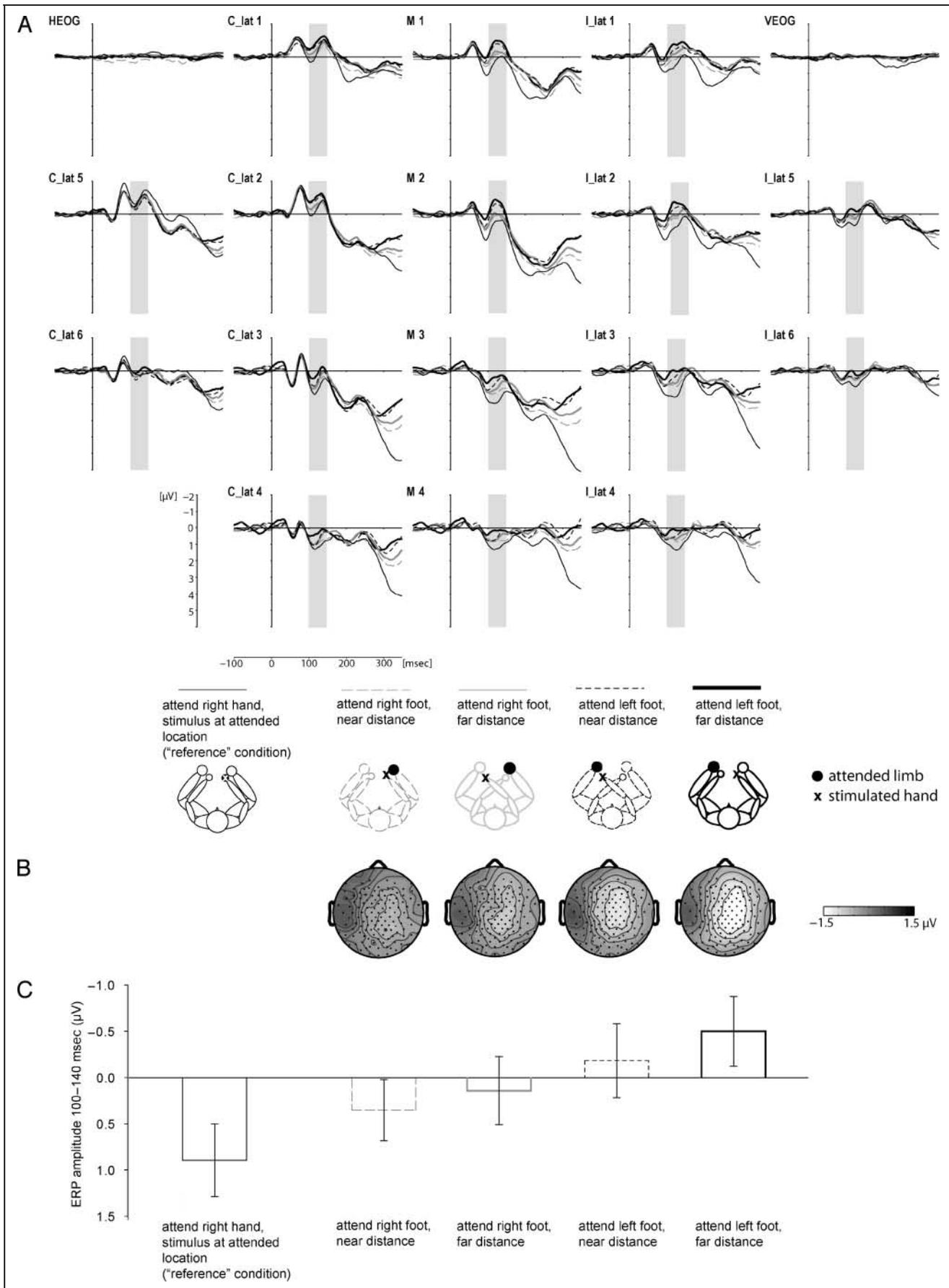
overall false alarm rate was 1.4%,  $SE = .3%$ . This low number of errors did not allow further analysis.

### Analysis 1: Influence of Body Posture on ERPs to Hand Stimulation

The aim of the first analysis was to assess whether somatosensory ERPs to unattended stimuli are modulated by posture not only when a homologous limb is attended (as evident in studies reporting hand crossing effects with hand stimulation) but also when a different limb is attended; more importantly, we wanted to know if such influences were modulated by either anatomical or (Euclidian) spatial distance of the tactile stimulus to the attended limb. We therefore compared ERPs to hand stimulation when participants attended one of the feet. The hands were placed near the feet either in an uncrossed manner (i.e., the right hand near the right foot, and the left hand near the left foot), or in a crossed manner (i.e., the right hand near the left foot, and vice versa). Therefore, in the different conditions, each hand could either be placed near or far from the attended foot. Because changes in posture lead to changes in the distance of the location of the unattended stimulus (here, the hand) to the attended location (here, the foot), it was possible to assess whether modulations of the ERP systematically changed with spatial distance between attended and unattended location. Note that physical stimulation was identical in all cases (tactile stimulation of a finger). Experimental manipulations were the direction of attention to the foot (either anatomically ipsi- or contralateral to the stimulated hand) and the posture of the stimulated hand in relation to the attended foot (spatially near to vs. far from the attended foot).

Results are shown in Figure 3A for all analyzed electrode clusters. The thin, continuous black trace shows the ERP of the condition in which the hand was both attended and stimulated; within the framework of the spatial attentional gradient, this condition is expected to elicit higher ERP amplitudes than all other conditions and is therefore shown as a reference condition, but was not included in the statistical analyses.

ERPs were influenced both by anatomical and external reference frames. At ipsilateral electrodes, ERPs were more positive in the 100–140 msec time interval when attention was directed to the foot ipsilateral to the stimulated hand (Figure 3A, gray traces) than when attention was directed to the foot opposite of the stimulated hand (Figure 3A, black traces), indicating an influence of an anatomical reference frame. At the same time, however, ERPs were more positive when the stimulated hand was placed near (Figure 3A, thin, dashed traces) rather than far from (Figure 3A, bold, continuous traces) the attended foot, indicating an influence of an external reference frame. Figure 3C shows the ERP mean amplitudes for the analyzed time interval for one electrode cluster at which the observed effects were most clear (Cluster I\_lat 2 depicted in Figure 3A).



Statistical analyses of the 100–140 msec time window confirmed the influence of both anatomical side of attention and external spatial distance: An ANOVA with factors spatial distance (stimulated hand positioned far vs. near to the attended foot, i.e., a spatial attentional gradient according to an external reference frame), attended body side (attended foot anatomically ipsilateral vs. contralateral to the stimulated hand, i.e., an attentional gradient according to an anatomical reference frame), hemisphere (ipsi- vs. contralateral to the stimulated hand), and electrode cluster revealed both a main effect of spatial distance [ $F(1, 13) = 12.38, p = .004$ ] and of attended body side [ $F(1, 13) = 12.08, p = .004$ ]. There was an interaction of Attended body side  $\times$  Electrode cluster [ $F(5, 65) = 6.15, p = .003$ ], a marginal interaction of Attended body side  $\times$  Hemisphere  $\times$  Electrode cluster [ $F(5, 65) = 2.49, p = .069$ ] and an interaction of Spatial distance  $\times$  Hemisphere  $\times$  Electrode cluster [ $F(5, 65) = 2.93, p = .032$ ]. In contrast, none of the interactions including both spatial distance and attended body side were significant. We therefore further analyzed each of these two factors separately for each hemisphere.

The main effect of spatial distance was significant both in the contralateral [ $F(1, 13) = 5.73, p = .032$ ] and in the ipsilateral hemispheres [ $F(1, 13) = 16.20, p = .001$ ], but the interactions with electrode cluster were not, indicating that the effect of distance was present at all clusters of both hemispheres. The main effect of attended body side was also present in both hemispheres [contralateral:  $F(1, 13) = 7.66, p = .016$ ; ipsilateral:  $F(1, 13) = 13.24, p = .003$ ], and interacted with electrode cluster in both hemispheres [contralateral:  $F(5, 65) = 5.38, p = .004$ ; ipsilateral:  $F(5, 65) = 6.37, p = .003$ ].  $t$  Tests for the effect of attended body side at each cluster revealed significant differences ( $p < .05$ ) at Clusters C\_lat 3 and 4, and I\_lat 1–5, and marginal effects ( $p < .1$ ) at Clusters C\_lat 1 and 6.

An ANOVA for the midline clusters revealed a very similar result pattern. There was a main effect of spatial distance [ $F(1, 13) = 10.64, p = .006$ ] and a main effect of attended body side [ $F(1, 13) = 16.81, p = .001$ ], but no interaction involving both factors. There was an interaction of Attended body side  $\times$  Electrode cluster [ $F(3, 39) = 4.18, p = .030$ ]; the effect of attended body side,

assessed with  $t$  tests at each cluster, was, however, significant at all four clusters.

To better visualize the topography of the effects of attention and of spatial distance, we calculated the difference map of each respective condition minus the reference condition “stimulated limb = attended limb” and displayed these differences in voltage maps (Figure 3B). The difference maps thus show the scalp distribution of the effects of our attentional manipulations on unattended stimuli with respect to an attended stimulus. In all four voltage maps, these difference maps showed an ipsilateral negativity with a central–parietal focus which became stronger and more widespread both with anatomical distance (attention on the same side vs. other side of the body of the stimulated hand) and with external distance (stimulated hand held near vs. far from the attended foot).

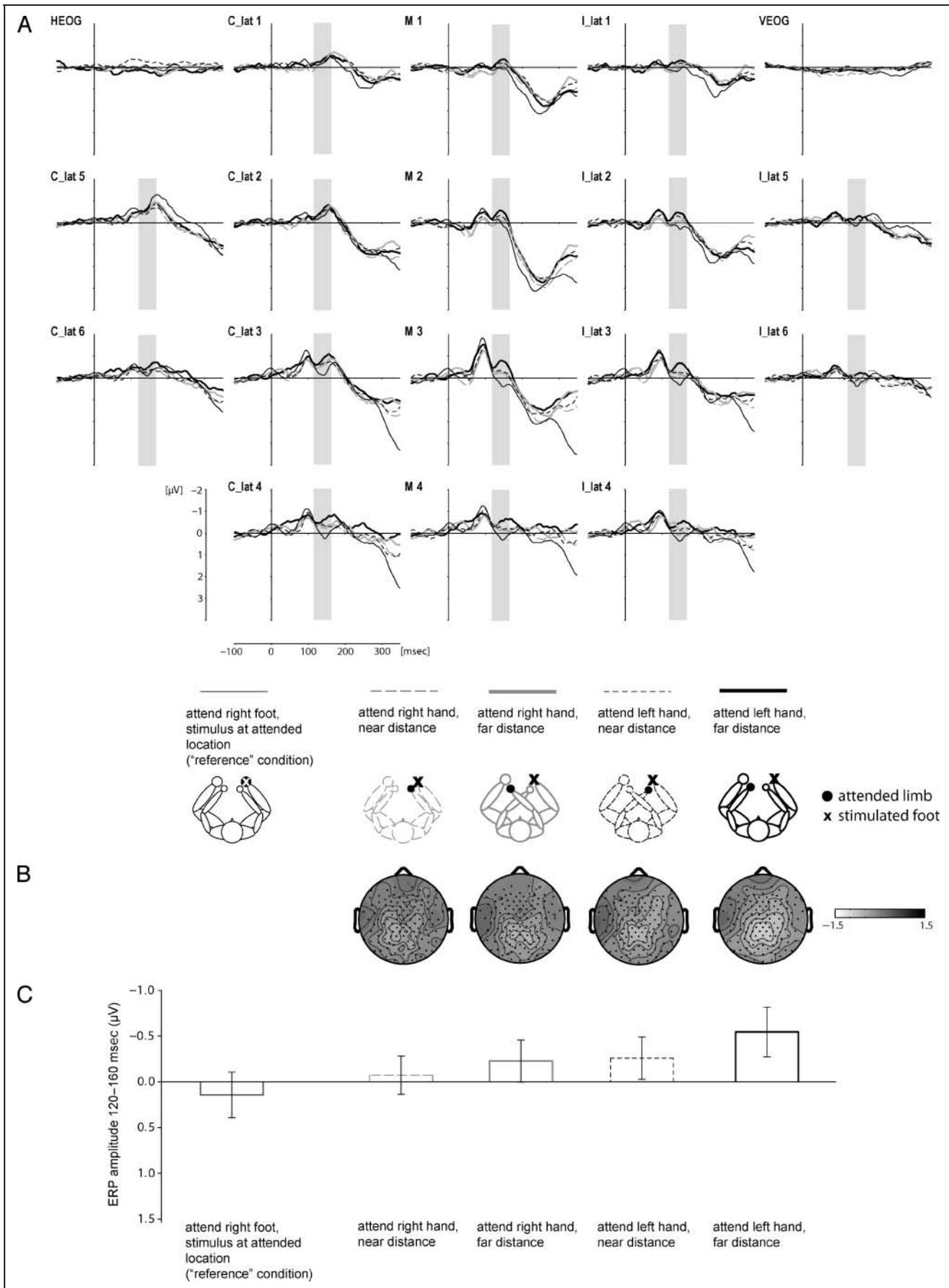
## Analysis 2: Influence of Body Posture on ERPs to Foot Stimulation

In analogy to the comparison of ERPs to hand stimulation, we compared ERPs to foot stimulation while participants attended their hands in a second analysis. This analysis assessed if the ERP to a stimulus to a foot, which is currently not attended, is modulated by the foot’s distance (either anatomical or external spatial) to an attended hand. Again, the hands were placed near the feet either in an uncrossed or a crossed fashion. The conditions of hand versus foot stimulation differ in that for hand stimulation, the stimulated limbs (the hands) but not the attended limbs (the feet) changed position, whereas for foot stimulation, the attended limbs (the hands) but not the stimulated limbs (the feet) changed position.

Somatosensory ERPs to foot stimulation differ from those of hand stimulation in latency (20–30 msec; see Methods), as well as in morphology and topography over the scalp (Dowman & Schell, 1999; Kany & Treede, 1997; Treede et al., 1988); the effects of our experimental modulations may therefore be most evident at different electrode clusters for foot than for hand stimulation.

Visually, both the variation of ERP amplitude between 120 and 160 msec (Figure 4A) as well as those of the corresponding voltage difference maps (Figure 4B) paralleled those found for hand stimulation (Figure 4A; e.g.,

**Figure 3.** Across-limbs ERP effects of tactile localization of hand stimulation. (A) Grand mean ERPs ( $\mu V$ ) to tactile stimulation at the hand while attention is directed to a foot for all clusters that were analyzed statistically. Colors and dashed of the schematic figures correspond to those of the ERP traces. Schematic figures are sorted according to their signal amplitude in the 100–140 msec time interval (shaded area). The filled circle on the schematic figures indicates the locus of attention, the cross (x) indicates the place of stimulation. Note that in all depicted conditions, physical stimulation was identical. The thin black trace represents the condition in which the hand was both attended and stimulated as a “reference” for the remaining traces. Negativity is plotted upward. (B) Voltage difference maps of each condition minus the reference condition (i.e., attention and stimulation at same hand, thin black trace in A) for the time interval 100–140 msec after hand stimulation. Each map in B is depicted underneath its schematic figure from A. Scale bar in microvolts ( $\mu V$ ). (C) ERP mean amplitudes for the time interval 100–140 msec (shaded area in A) for hand stimulation at Cluster I\_lat 2, which most clearly showed the reported effects of spatial and anatomical distance between attended and unattended locations. The leftmost black bar depicts the amplitude of the “reference” condition, in which the attended hand was stimulated. Each bar is depicted underneath its schematic figure from A. Error bars are *SEM*. Scaling is reversed (negativity up) to comply with the ERP figures.



Cluster I\_lat 3). Parietal ERPs at and near the midline were more positive when the hand on the same anatomical side (Figure 4A, gray vs. black traces) as the stimulated foot was attended. At the same time, ERPs were more positive when the attended hand was placed near (Figure 4A, thin, dashed traces) rather than far (Figure 4A, bold, continuous traces) from the stimulated foot. Figure 4C shows the ERP mean amplitudes for an electrode cluster at which these effects were best observable (Cluster I\_lat 3 in Figure 4A).

However, the statistical analyses of the 120–160 msec time window, using an ANOVA with factors attended body side (ipsi- vs. contralateral to the stimulated hand), type of attended limb (hand vs. foot), hemisphere (ipsi- vs. contralateral to the stimulated hand), and electrode cluster did not confirm an effect of spatial distance [main effect of spatial distance:  $F(1, 13) = 1.06, p = .32$ ; all interactions involving this factor  $F < 2.2, p > .16$ ]. In contrast, although the main effect of attended body side was also not significant [ $F(1, 13) = 1.80, p = .20$ ], there was a significant interaction of Attended body side  $\times$  Hemisphere  $\times$  Electrode cluster [ $F(5, 65) = 7.64, p < .001$ ]. Separate analyses in the two hemispheres revealed a marginal main effect of attended body side in the ipsilateral [ $F(1, 13) = 3.26, p = .094$ ], but not in the contralateral, hemisphere. An interaction of Attended body side  $\times$  Electrode cluster was not present in either hemisphere.

For the midline clusters, there were also no significant effects [all  $F < 1$ , except for attended body side;  $F(1, 13) = 2.24, p = .16$ ].

Because visual inspection had suggested that both an effect of spatial distance and of attended body side might be present (see also Figure 4C), we investigated possible differences between stimulation to the right versus the left foot. Because these tests were not planned and followed up on nonsignificant results, we note the explorative character of these additional analyses. For the left foot, neither the main effect of spatial distance nor any of the interactions with this factor were significant. The main effect of attended body side was also nonsignificant, but there was an interaction of Attended body side  $\times$  Hemisphere  $\times$  Electrode cluster [ $F(5, 65) = 6.06, p < .001$ ]. However, in separate analyses for the two hemispheres, neither the main effect of attended body side nor the interaction of Attended body side  $\times$

Electrode cluster was significant for either the ipsilateral or the contralateral hemisphere.

For the right foot, again there were no main effects of spatial distance or attended body side. However, there was an interaction of Spatial distance  $\times$  Hemisphere [ $F(1, 13) = 7.26, p = .018$ ], and an interaction of Attended body side  $\times$  Hemisphere  $\times$  Electrode cluster [ $F(5, 65) = 4.57, p = .005$ ]. Separate analyses for the two hemispheres for the two factors showed a main effect of spatial distance [ $F(1, 13) = 5.02, p = .043$ ] and a marginal main effect of attended body side [ $F(1, 13) = 3.40, p = .088$ ] in the ipsilateral hemisphere, but no such main effects in the contralateral hemisphere. The experimental modulations of spatial distance and attended body side were thus observed for the right, but not for the left, foot in the present study.

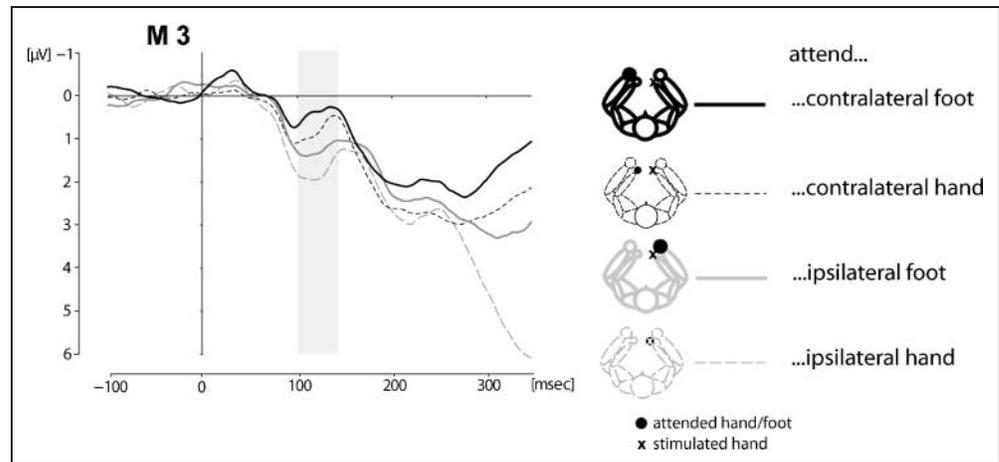
### Analysis 3: Attending a Hemifield vs. Attending a Limb

So far, we have implicitly assumed that participants indeed attended the body part specified in each condition. However, because within each analysis (hand stimulation while a foot was attended; foot stimulation while a hand was attended) attention was always directed to the same type of limb, it is possible that participants did not attend the specified limb, but simply attended one hemifield or one side of the body. To exclude this confound, we conducted a third analysis in which we compared ERPs to hand stimulation both when a foot and when a hand were attended. If participants just attended one side of the body, the type of attended limb (hand vs. foot) should not influence ERPs as long as both limbs are on the same side of the body. If, however, participants attended a specific limb, ERPs are expected to differ according to both the attended body side and the type of limb.

We compared ERPs to hand stimulation under manipulation of attended body side (ipsilateral vs. contralateral) and type of attended limb (hand vs. foot). In none of the conditions of this analysis were the hands crossed. Results are illustrated for a cluster with very clear main effects in Figure 5. An ANOVA with factors attended body side (ipsi- vs. contralateral to the stimulated limb), type of attended limb (hand vs. foot), hemisphere (ipsi- vs. contralateral to the stimulated limb), and electrode

**Figure 4.** Across-limbs ERP effects of tactile localization of foot stimulation. (A) Grand mean ERPs ( $\mu\text{V}$ ) to tactile stimulation at the foot while attention is directed to a hand for all clusters that were analyzed statistically. Colors and dashing of the schematic figures correspond to those of the ERP traces. Schematic figures are sorted according to their signal amplitude in the 120–160 msec time interval (shaded area). The filled circle on the schematic figures indicates the locus of attention, the cross (x) indicates the place of stimulation. The thin black trace represents the condition in which the foot was both attended and stimulated as a “reference” for the remaining traces. Negativity is plotted upward. (B) Voltage difference maps of each condition minus the reference condition (attention and stimulation at same hand, thin black trace in A) for the time interval 100–140 msec after hand stimulation. Each map in B is depicted underneath its schematic figure from A. Scale bar in microvolts ( $\mu\text{V}$ ). (C) ERP mean amplitudes for the time interval 120–160 msec (shaded area in A) for foot stimulation at Cluster I\_lat 3. The leftmost black bar depicts the amplitude of the “reference” condition, in which the attended foot was stimulated. Each bar is depicted underneath its schematic figure from A. Details as in Figure 3C.

**Figure 5.** Attention to specific limbs and sides. Grand mean ERPs ( $\mu\text{V}$ ) to tactile stimulation at the hand while attention is directed to a hand or foot (thin, dashed vs. thick, continuous traces) of the same or opposite anatomical side (gray vs. black traces) for Cluster M 3. Schematic figures are sorted according to their signal amplitude in the 100–140 msec time interval (shaded area). Note that the hands are not crossed in any of the compared conditions.



cluster for the 100–140 msec time range revealed a main effect of attended body side [ $F(1, 13) = 49.77, p < .001$ ], as evident in more positive traces for stimulation of the hand ipsilateral to the attended limb (Figure 6, gray traces vs. black traces). At the same time, ERPs were more positive when a hand than when a foot was attended [main effect of type of attended limb:  $F(1, 13) = 8.83, p = .039$ ; see Figure 6, thin, dashed vs. bold, continuous traces]. In contrast, the interaction of these two factors was not significant (interaction Attended body side  $\times$  Type of attended limb:  $F < 1$ ). The two effects did, however, interact with both factors electrode cluster and hemisphere [interaction Attended body side  $\times$  Hemisphere:  $F(1, 13) = 15.59, p = .002$ ; interaction Attended body side  $\times$  Electrode cluster:  $F(5, 65) = 13.97, p < .001$ ; interaction Attended body side  $\times$  Hemisphere  $\times$  Electrode cluster:  $F(5, 65) = 3.50, p = .018$ ; interaction Type of attended limb  $\times$  Hemisphere:  $F(1, 13) = 9.49, p = .009$ ; marginally significant interaction Type of attended limb  $\times$  Electrode cluster:  $F(5, 65) = 2.54, p = .099$ ; interaction Type of attended limb  $\times$  Hemisphere  $\times$  Electrode cluster:  $F(5, 65) = 5.07, p = .001$ ; marginally significant interaction Attended body side  $\times$  Type of attended limb  $\times$  Hemisphere:  $F(1, 13) = 4.52, p = .053$ ]. We therefore analyzed the two hemispheres separately. Whereas the main effect of attended body side was present in both hemispheres [contralateral:  $F(1, 13) = 11.88, p = .003$ ; ipsilateral:  $F(1, 13) = 42.65, p < .001$ ], the main effect of type of attended limb was evident in the ipsilateral hemisphere only [contralateral:  $F(1, 13) = 1.28, p = .28$ ; ipsilateral:  $F(1, 13) = 8.66, p = .011$ ]. The interactions of the two factors were not significant in either hemisphere. In the contralateral hemisphere, both attended body side [ $F(5, 65) = 11.83, p < .001$ ] and attended type of limb [ $F(5, 65) = 3.99, p = .022$ ] interacted with electrode cluster. Follow-up  $t$  tests at each cluster of the contralateral hemisphere revealed a significant effect of attended body side at Clusters C\_lat 1–4, but not at C\_lat 5 and 6; a significant effect of type of attended limb was evident at Clusters C\_lat 4 and 5,

and a marginally significant effect at C\_lat 3 ( $p = .050$ ). In the ipsilateral hemisphere, attended body side [ $F(5, 65) = 12.84, p < .001$ ], but not type of attended limb [ $F(5, 65) = 1.07, p = .35$ ] interacted with electrode cluster. Nonetheless, follow-up  $t$  tests at each cluster of the ipsilateral hemisphere revealed significant effects of attended body side at all six Clusters I\_lat 1–6.

Results for the midline clusters were comparable: There was a marginal effect of type of attended limb [ $F(1, 13) = 4.56, p = .052$ ] and a main effect of attention [ $F(1, 13) = 42.72, p < .001$ ], but no interactions between the two factors.

#### Analysis 4: Hand Crossing ERP Effects

So far, all analyses have investigated only unattended stimuli; the stimulated limb was never the attended one. Previous studies that have investigated posture effects on somatosensory ERPs, however, have used a paradigm in which the two hands were stimulated while one of the hands was attended; it was then tested if hand crossing changed the attentional modulation (i.e., the difference of attended vs. unattended conditions) of the ERPs. A subset of the conditions of our experiment can be directly compared to these studies; these are the conditions in which a hand (not a foot) was attended, and stimuli were also delivered to the hands. Previous studies have reported crossing effects in the time range between 80 and 160 msec; to allow a comparison to the first three analyses, we again analyzed the 100–140 msec time interval. However, as reported in previous studies (Eimer et al., 2001, 2003), modulations were evident also in the time range of 190–300 msec, which we therefore also analyzed.

#### Time Interval 100–140 msec

Figure 6A shows ERPs of the analyzed electrode clusters. We observed an attenuation of the attention effect in the 100–140 msec time range at ipsilateral electrodes

when the hands were crossed (Figure 6A, gray traces) compared to when the hands were uncrossed (black traces). This attenuation is evident also in the difference waves of attended minus unattended ERPs for the uncrossed versus the crossed conditions at the same clusters (Figure 6B). An ANOVA with factors hand crossing (uncrossed vs. crossed arm posture), attention (stimulus attended vs. unattended), hemisphere (ipsilateral vs. contralateral to the stimulus), and electrode cluster revealed a main effect of attention [ $F(1, 13) = 31.80, p = .001$ ], an interaction of Attention  $\times$  Electrode cluster [ $F(5, 65) = 13.92, p < .001$ ], of Attention  $\times$  Hemisphere [ $F(1, 13) = 4.15, p = .01$ ], and of Attention  $\times$  Hemisphere  $\times$  Electrode cluster [ $F(5, 65) = 2.78, p = .046$ ]. The most relevant result for the current question, however, was an interaction of Hand crossing  $\times$  Attention  $\times$  Hemisphere [ $F(1, 13) = 8.15, p = .014$ ], indicating that hand crossing modulated the attention effect, but differently in the two hemispheres. Consequently, separate analyses of hand crossing, attention, and electrode cluster for each hemisphere showed that a main effect of attention was present in both hemispheres, albeit stronger in the ipsilateral one [contralateral:  $F(1, 13) = 5.31, p = .038$ ; ipsilateral:  $F(1, 13) = 31.02, p < .001$ ]. This attention effect was modulated (though only marginally significantly) by hand crossing only in the ipsilateral hemisphere [interaction Hand crossing  $\times$  Attention:  $F(1, 13) = 3.86, p = .071$ ], but not in the contralateral hemisphere (interactions of Hand crossing  $\times$  Attention and Hand crossing  $\times$  Attention  $\times$  Electrode cluster,  $F < 1$ ). The ipsilateral Hand crossing  $\times$  Attention interaction was further analyzed by testing the effect of attention for both the uncrossed and the crossed conditions, as well as testing the influence of hand crossing for each attention condition separately. ERPs differed between attended and unattended stimuli for both hand postures [uncrossed:  $t(13) = 4.74, p < .001$ ; crossed:  $t(13) = 2.72, p = .017$ ]. However, ERPs were marginally modulated by hand crossing for unattended stimuli [ $t(13) = 2.13, p = .053$ ], but not for attended stimuli [ $t(13) = 0.92, p = .37$ ] (see, e.g., electrode I\_lat 2 in Figure 3A).

Midline clusters showed only a significant main effect of attention [ $F(1, 13) = 24.83, p < .001$ ], which interacted also with electrode cluster [ $F(5, 65) = 11.65, p = .001$ ]; follow-up  $t$  tests showed that attention affected only Clusters M 1–3 (all  $F > 15, p < .002$ ).

#### Time Interval 190–300 msec

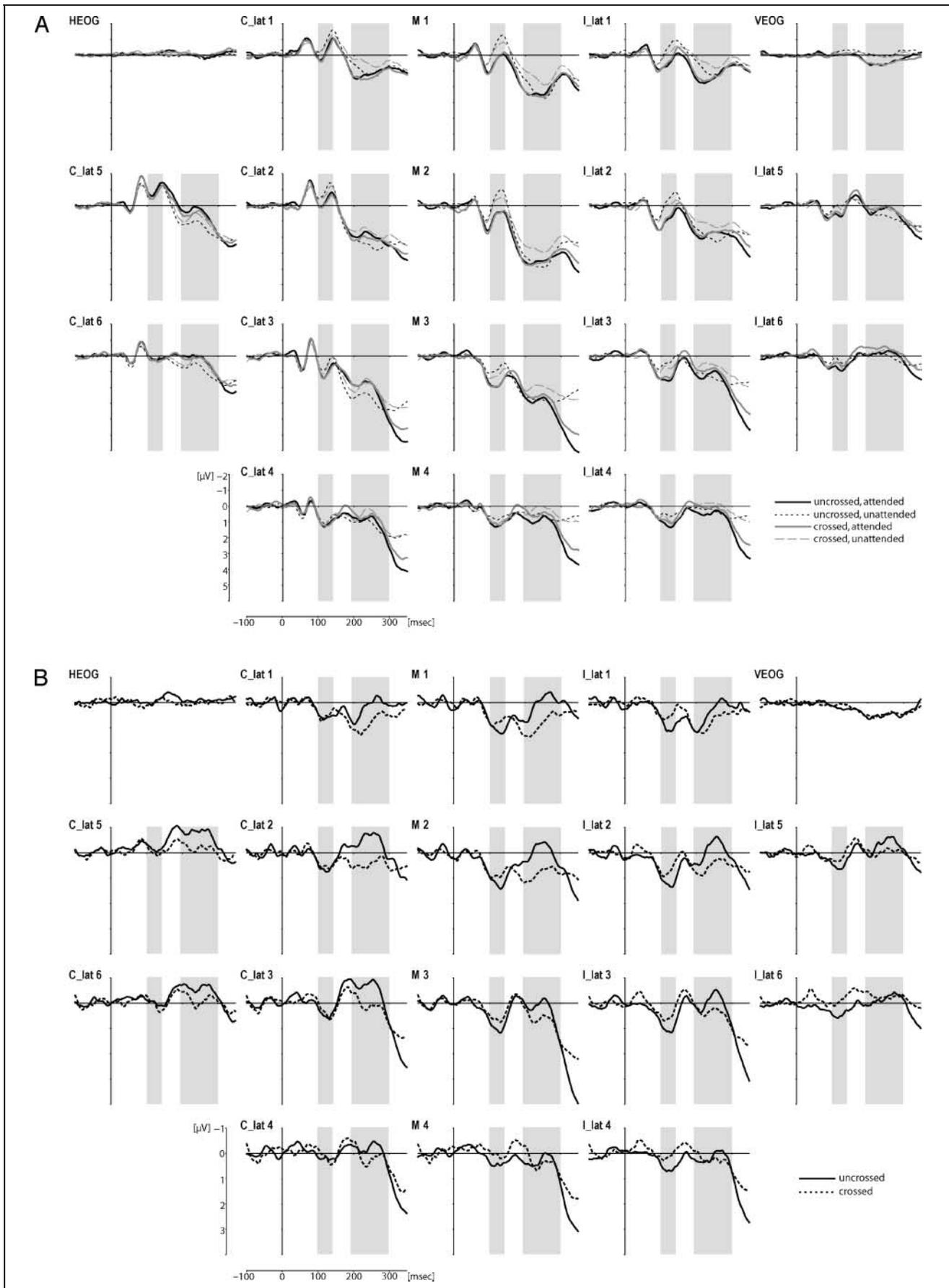
A modulation of the attentional effect was also evident in the time range of 190–300 msec. An ANOVA with factors hand crossing, attention, hemisphere, and electrode cluster revealed an interaction of Attention  $\times$  Electrode cluster [ $F(5, 65) = 11.21, p < .001$ ], Attention  $\times$  Hemisphere [ $F(1, 13) = 19.94, p = .001$ ], and of Attention  $\times$  Hemisphere  $\times$  Electrode cluster [ $F(5, 65) = 3.89, p = .006$ ]. Moreover, there was a main effect of hand cross-

ing [ $F(1, 13) = 7.70, p = .016$ ] and an interaction of Hand crossing  $\times$  Electrode cluster [ $F(5, 65) = 3.56, p = .039$ ]. There were two marginal interactions involving hand crossing and attention: Hand crossing  $\times$  Attention [ $F(1, 13) = 3.73, p = .076$ ] and Hand crossing  $\times$  Attention  $\times$  Hemisphere [ $F(5, 65) = 4.08, p = .065$ ]. We therefore analyzed the two hemispheres separately to further investigate the relationship between these two factors.

In the contralateral hemisphere, there was no main effect of attention, but an interaction of Attention  $\times$  Electrode cluster [ $F(5, 65) = 13.58, p < .001$ ]. There was, however, a main effect of hand crossing [ $F(1, 13) = 5.12, p = .041$ ], and a marginal interaction of Hand crossing  $\times$  Electrode cluster [ $F(5, 65) = 2.99, p = .060$ ]. Crucially, the Hand crossing  $\times$  Attention interaction was significant [ $F(1, 13) = 7.12, p = .019$ ]; this interaction was due to a significant difference between the ERPs in the uncrossed and crossed postures for unattended [ $t(13) = 3.80, p = .002$ ], but not for attended stimuli [ $t(13) = 0.21, p = .83$ ]. Inspection of Figure 3B (e.g., Cluster C\_lat 2) suggests that the attention effect may even have reversed with the crossed hand posture; however, whereas the difference between attended and unattended ERPs was marginally significant in the uncrossed posture [ $t(13) = 1.83, p = .09$ ], this was not the case in the crossed posture [ $t(13) = 1.05, p = .30$ ], indicating that the attention effect was eliminated rather than reversed.

In the ipsilateral hemisphere, the ANOVA revealed a significant interaction of Attention  $\times$  Electrode cluster [ $F(5, 65) = 8.11, p < .001$ ]. Moreover, there was a main effect of hand crossing [ $F(1, 13) = 8.54, p = .012$ ] and an interaction of Hand crossing  $\times$  Electrode cluster [ $F(5, 65) = 3.32, p = .027$ ]. The interaction between Hand crossing  $\times$  Attention was not significant, but there was a marginal interaction of Hand crossing  $\times$  Attention  $\times$  Electrode cluster. We therefore tested the interaction at each cluster separately, finding it significant only at Cluster I\_lat 2 [ $F(1, 13) = 5.38, p = .037$ ]. Interestingly, at this cluster, the difference between attended and unattended ERPs was marginally significant for the crossed [ $t(13) = 2.05, p = .061$ ], but not for the uncrossed posture [ $t(13) = -0.328, p = .75$ ]. As in the contralateral hemisphere, the interaction at I\_lat 2 was due to ERP changes due to crossing for the unattended [ $t(13) = 3.83, p = .002$ ], and not for the attended stimuli [ $t(13) = 0.59, p = .57$ ].

For the midline clusters, there was a significant main effect of hand crossing [ $F(1, 13) = 8.73, p = .011$ ], a marginal effect of attention [ $F(1, 13) = 4.51, p = .053$ ], a marginally significant interaction of Hand crossing  $\times$  Attention [ $F(1, 13) = 4.64, p = .050$ ] and an interaction of Hand crossing  $\times$  Attention  $\times$  Electrode cluster [ $F(3, 39) = 3.99, p = .049$ ]. ANOVAs at each midline cluster revealed a significant main effect of hand crossing at Clusters M 2–4 [all  $F(1, 13) > 5.9$ , all  $p < .031$ ], and a marginal one at Cluster M 1 [ $F(1, 13) = 4.55, p = .053$ ]. The main effect of attention was significant at Cluster M 1 only [ $F(1, 13) = 5.96, p = .030$ ]. The interaction of



Hand crossing  $\times$  Attention was significant at Clusters M 1 and 2 (both  $F \geq 6.00$ ,  $p < .024$ ). At these two clusters, M 1 and 2, the effect of attention was significant only for the crossed [M 1:  $t(13) = 3.12$ ,  $p = .008$ ; M 2:  $t(13) = 2.60$ ,  $p = .022$ ], but not the uncrossed hand posture [both  $t(13) < 1$ ,  $p > .68$ ].

## DISCUSSION

### Reference Frames for Tactile Localization

We recorded ERPs to hand and foot stimulation while participants attended one of the hands or feet. The spatial (Euclidean) distance between attended and unattended limbs was manipulated by placing the hands near the feet in either an uncrossed or a crossed arm posture such that each hand was placed either near the foot of the same or the opposite body side. We exploited the attentional gradient as indicated by ERPs, that is, the amplitude modulation of sensory ERPs by the distance between the attended location and the location of a stimulus. This approach allowed us to disentangle if the brain determines the distance of tactile events to different body parts according to an anatomical or according to an external reference frame. If spatial distance was determined solely by an anatomical reference frame, the distance of the attended and the stimulated limb on the skin or their common location on the same body side should lead to differences in ERPs, whereas the Euclidean distance between them (and thus, posture) should not modulate ERPs. Conversely, if solely an external reference frame was used, only the Euclidean distance between the attended and the stimulated limb should cause variations in the ERP, whereas their locations on the body (e.g., whether the two locations are on the same or opposite side of the body) should not influence ERPs.

ERPs were modulated by both types of reference frames in the time range of 100–140 msec poststimulus for hand stimulation (Analysis 1), evident over the whole scalp but most pronounced at midline and ipsilateral central–parietal electrodes: ERPs were more positive when a stimulus occurred on the same anatomical side of the body as the attended foot (anatomical reference frame). However, ERPs were also more positive when the stimulated hand was located near rather than far from the attended foot, indicating that the brain transforms tactile location into external, spatial coordinates independent of the current task requirements (external reference frame). We confirmed that participants indeed followed the instruction to attend to a specific limb by showing that ERPs differed depending on the type of

attended limb (Analysis 3), and that therefore, participants did not only attend to one hemifield in general. The timing of the concurrent use of anatomical and external reference frames in our study (100–140 msec) is consistent with a recent behavioral study which indicated that remapping of tactile coordinates starts somewhere between 60 and 180 msec after stimulus presentation (Azanon & Soto-Faraco, 2008).

Importantly, to calculate the spatial distance from the stimulated hand to the attended foot, both the location of the hand and the location of the attended foot must be available in external coordinates. Our results therefore suggest that coordinate transformations are carried out by the brain not just for the hands but also for other body parts, for example, the feet. These conclusions are corroborated by a study in which participants had to report if a tactile stimulus had occurred at an attended location or not: The further the stimulus had been presented from the attended location, the slower participants responded. This effect was modulated more by external spatial than by anatomical distance (Lakatos & Shepard, 1997). An influence of the external coordinates of different body parts was also evident in a study in which participants reached to tactile targets on their body with a hand of their choice (Kim & Cruse, 2001). In this study, both hand choice and reaction times were influenced by an external reference frame as well as by the anatomical side of the tactile stimulus. Finally, the use of both anatomical and external reference frames for both hands and feet has been demonstrated using temporal order judgments; the order of two stimuli, one at each limb involved, is confused more frequently when the two limbs are crossed rather than uncrossed, presumably because of a conflict between anatomical and external reference frames in crossed postures (Schicke & Röder, 2006).

The results for foot stimulation of the present study (Analysis 2), however, were not as clear as those for hand stimulation. ERP differences between conditions were smaller by about a factor of 2 for foot stimulation than those for hand stimulation (note the identical scaling of the voltage difference maps in Figures 3B and 4B). When the two feet were analyzed together, ERPs in the range of 120–160 msec did not show an influence of spatial distance and only a marginally significant influence of anatomical distance in the ipsilateral hemisphere. When the two feet were analyzed separately, no influence of distance—either spatial or anatomical—was evident for the left foot. In contrast, both spatial and anatomical distance affected ERPs for right foot stimulation. Because of these mixed results, the foot data must be interpreted

**Figure 6.** Effects of hand crossing on attention effects of hand ERPs. (A) Grand mean ERPs ( $\mu\text{V}$ ) to hand stimulation with an uncrossed (black) and a crossed (gray) posture. Thin, dashed traces are the unattended conditions. Shaded areas depict time intervals which were analyzed statistically (see text for details). (B) Difference ERPs between attended minus unattended stimulation for the uncrossed (continuous line) and crossed (dashed line) hand postures.

with caution, and firm conclusions should await results from further experiments. It is important to understand, however, that these data do not indicate that tactile events at the feet are not recoded into external coordinates because the modulation of ERPs by spatial distance during hand stimulation (with attention directed to a foot) suggests otherwise. The observed asymmetry between the two feet in the present study is at odds with the results from the abovementioned temporal order judgment study, in which the use of external coordinates was found for both feet (Schicke & Röder, 2006).

A higher influence of both the spatial and anatomical location of a tactile stimulus at the hand may be related to the prominent role of the hands for action and object manipulation. The constant use of the hands may increase the salience of the spatial relations body parts for tactile events at the hands compared to events at other body parts, even when the hands are currently not needed for the task. In contrast, the location of a foot may not be represented as efficiently when the foot is not currently task-relevant. However, on a purely anecdotal level, several participants in our experiment reported that they found it harder to detect the foot than the hand target stimuli, although subjective stimulus intensity was explicitly matched. These subjective reports were paralleled by performance differences to detect deviant stimuli at the hands and feet. Importantly, because none of our analyses directly compared hand with foot stimulation, but rather compared identical stimulation while attention was directed to different limbs, our ERP results cannot be attributed to these behavioral differences for hands versus feet.

Yet, other factors may be responsible for, or at least contribute to the differences in hand and foot ERP effects as well. The reduced voltage differences for foot stimulation may partly be due to differences in their cortical origin; for example, representations of the feet in primary somatosensory cortex (SI) are located in the medial wall of the brain, whereas the hand representations are on the cortical surface of the postcentral gyrus. The amount of cortical tissue dedicated to the hands is also larger than that dedicated to the feet, as evident, for example, in the overrepresentation of the hands in the sensory and motor homunculi. The upper limbs are represented more extensively also in secondary SI (SSI) and neighboring somatosensory areas (Disbrow, Roberts, & Krubitzer, 2000; Burton, Fabri, & Alloway, 1995).

### Hand Crossing vs. Spatial Distance

ERPs were most positive in the 100–140 msec time range when the tactile stimulus occurred at the attended limb. When a different limb was attended, ERPs were more similar to this reference condition when the spatial distance between attended and stimulated limb was small rather than large. Importantly, spatial distance in our ex-

periment was not confounded with hand crossing: When attending the foot on the same anatomical side as the stimulated hand, hand crossing resulted in a large spatial distance between the stimulated hand and the attended foot; conversely, when attending the foot on the opposite body side, hand crossing resulted in a small spatial distance. ERPs, however, were more similar to the reference condition (attended limb = stimulated limb) when Euclidean distance was small, independent of whether this distance was due to an uncrossed or a crossed posture.

A number of behavioral studies have shown that hand crossing deteriorates performance, and ERP studies have shown that hand crossing attenuates ERP attention effects. These results have frequently been interpreted to reflect influences of external spatial reference frames on tactile localization (e.g., Azanon & Soto-Faraco, 2007; Röder et al., 2004; Eimer et al., 2001, 2003; Shore et al., 2002; Yamamoto & Kitazawa, 2001). However, studies that varied posture without hand crossing, but used identical behavioral and ERP paradigms, have shown much smaller performance and ERP modulations due to posture (Shore, Gray, Spry, & Spence, 2005; Eimer et al., 2004; Roberts, Wing, Durkin, & Humphreys, 2003), indicating that hand crossing might induce qualitatively different processing requirements rather than indicating a pure influence of nonaligned spatial reference frames. A subgroup of our experimental conditions replicated this crossed hands ERP paradigm (i.e., those conditions in which the hands were both attended and stimulated). Interestingly, for both analyzed time intervals, 100–140 and 190–300 msec, our results suggest that there was no effect of hand crossing on the ERP of attended stimuli; rather, hand crossing affected the ERP of unattended stimuli. This may imply that these ERP hand crossing effects do not indicate an inability to deploy attention; they may, in contrast, be related to influences of an external reference frame on the processing of unattended stimuli. More specifically, unattended stimuli may be assigned more attentional capacity because they are (externally) located in the hemifield to which (anatomically) the attended limb belongs. That hand crossing does not simply lead to an inability to efficiently direct attention is also suggested by the fact that, at some midline and ipsilateral electrodes in the 190–300 msec time interval, the difference of ERPs between attended and unattended stimuli was significant for the crossed (but not the uncrossed) hand posture, indicating that the brain does differentiate attended and unattended stimuli also in the crossed hands condition. Finally, a reversal of ERPs due to hand crossing, as has been reported as a nonsignificant tendency for the ERP around 140 msec (Eimer et al., 2001), was not evident in our data in the 100–140 msec time range, and was not significant in the later, 190–300 msec, time interval (Clusters C\_lat 2, I\_lat 2).

The crossed hand analysis therefore corroborates the findings of the other analyses, which compared ERPs when attention was directed to the feet during

hand stimulation. Here, ERP attention effects in the 100–140 msec time interval were not modulated by hand crossing *per se*, but rather by the spatial distance induced by the respective body posture.

### Hand and Foot Somatosensory ERPs

In our study, the attentional modulation of the ERP in the 100–140 msec time range was observed primarily as an ipsilateral positivity centered over parietal cortex. Studies stimulating different hands have, in contrast, often found a bilateral negativity due to attention in this time interval. Nevertheless, a positivity due to attention in the reported time interval has also been reported in a task involving different locations on two fingers (Forster, Eardley, & Eimer, 2007; Eimer & Forster, 2003b). A higher negativity for unattended versus attended nontarget tactile stimuli was also evident around 110 msec in the vertex electrode in a study by Michie (1984). Similarly, the same author reported a higher positivity for unattended nontarget stimuli at frontal and fronto-central ipsilateral and vertex electrodes for strong versus weak stimulation. Our study used very strong stimulation because preliminary testing had revealed that weak stimulation (as usually used for hands-only experiments) was not reliably detected at the feet.

ERPs to tactile stimulation as well as the difference ERPs between the attended and unattended conditions differed for the hand and foot stimulation conditions, even when accounting for the longer neural transmission times for foot stimuli. This is consistent with the presumed origin of the P100/N140 ERP complex in SII (Eimer & Forster, 2003a; Frot & Mauguier, 1999): SII is organized in a body map-like organization and is probably accompanied by at least one other body map of opposite orientation (Eickhoff, Grefkes, Zilles, & Fink, 2007; Disbrow et al., 2000; Burton et al., 1995; Krubitzer, Clarey, Tweedale, Elston, & Calford, 1995); thus, differences in ERPs resulting from hand versus foot stimulation would be expected.

### Body Schema and Coordinate Transformations

The assumption that the ERPs between 100 and 140 msec originate partially in SII is also in line with findings from neuroimaging studies in humans showing that attention increases the BOLD signal in SII more strongly than in SI (Burton, Sinclair, & McLaren, 2008; Burton et al., 1999). Moreover, neurophysiological studies in monkeys have demonstrated weaker attentional influences on neuronal firing rates in SI than SII (Burton & Sinclair, 2000).

The suggestion that early (100–140 msec poststimulus) attentional modulations of the ERP originate in SII raises the question how spatial modulations and body posture are relayed to SII in the brain. There is ample evidence of top-down attentional modulations from parietal and frontal areas to the sensory cortices. Posterior parietal

cortex, specifically the areas in the IPS, have been implicated both in attention and stimulus selection (Colby & Goldberg, 1999), for example in the lateral intraparietal area (LIP) as well as in the transformation of sensory coordinates into different reference frames, presumably for motor planning toward visual, tactile, and auditory stimuli (Graziano & Cooke, 2006; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005; Duhamel, Colby, & Goldberg, 1998; Duhamel, Bremmer, BenHamed, & Graf, 1997) for example in the ventral intraparietal area (VIP). Neurons in ventral premotor cortex have visual-tactile receptive fields around the hand; when the hand is moved, the visual receptive field moves with it and is thus anchored to the hand, indicating that body posture is accounted for by continuously adjusting the visual receptive field (Graziano, Yap, & Gross, 1994).

To our knowledge, it has not been systematically tested how somatosensory stimuli are spatially coded in the IPS. An fMRI study in humans has demonstrated a change in intraparietal activation in response to passive tactile stimulation when the hands were crossed over the midline, suggesting either that posture is represented in this area, or, alternatively, that tactile location is remapped here into external coordinates (Lloyd, Shore, Spence, & Calvert, 2003). Finally, it has been demonstrated that movement preparation enhanced the ERP to tactile stimuli at the to-be-moved hand in the 100–140 msec time window, demonstrating a backward link from a movement plan to tactile attention (Eimer, Forster, Van Velzen, & Prabhu, 2005). It therefore seems plausible to suggest that somatosensory cortex receives top-down attentional signals from those frontal-parietal circuits that comprise intraparietal and premotor areas and presumably mediate both attentional and motor planning functions. In fact, a tracer study revealed projections from VIP to SII, and it was therefore suggested that SII might be higher in the processing hierarchy of the tactile system than VIP (Lewis & Van Essen, 2000).

Although the IPS is thought to be divided according to effectors (e.g., LIP for eye movements and parietal reach region [PRR] for hand reaches), a foot-specific area has not yet been reported. Similarly, the polysensory zone in ventral premotor cortex, which presumably represents peripersonal space, apparently contains neurons responsive for the upper, but apparently not the lower, body (Graziano, Taylor, & Moore, 2002). However, in monkeys, neurons in parietal area PEc, adjacent and connected to the IPS, fire to very specific and complex body postures, partly involving several limbs (Breveglieri, Galletti, Gamberini, Passarelli, & Fattori, 2006). In humans, simple hand and foot movements have both been shown to activate areas in posterior parietal cortex, including the IPS (Christensen et al., 2007; Kollias, Alkadhi, Jaermann, Crelier, & Hepp-Reymond, 2001). Indirect evidence for the involvement of parietal cortex also in foot movement planning comes from an fMRI study investigating action observation for actions with different body parts (Buccino et al., 2001).

When observed actions were related to an object, posterior parietal cortex was activated in a somatotopic manner. These activations were suggested to reveal parietal cortex as a part of the mirror neuron system, which maps the actions of others onto one's own motor structures for their identification and understanding. In fact, the observation of hand movements activated the putative intraparietal area for hand grasping, and the authors specifically linked their results to a limb-specific organization of the IPS.

The question of the neural mechanisms of the observed effects notwithstanding, our data suggest that, when localizing a tactile stimulus, the brain—at least partly—abstracts from the original location on the skin into a location in external space. When attention is directed to one location on the body, this attention spreads to nearby locations which are defined in external coordinates: a task-irrelevant limb receives more attention when it is placed near the attended tactile location than when it is far away. This attentional effect spreads over different limbs, as demonstrated in our experiment in the observed influences from the attended foot onto the hands (and, possibly, vice versa). The location of a limb therefore seems to be coded in external spatial coordinates by the brain. However, at the same time, the coding of a tactile stimulus is not independent from its original location on the skin. In other words, although a recoding into external spatial coordinates seems to take place, the location of the tactile stimulus on the skin also influences the brain's representation of the stimulus. The preservation of the original skin site or body part at which a stimulus was perceived carries importance when choosing a limb for action. Often, when a stimulus is perceived on a certain limb, this same limb cannot be used to act toward the stimulus. For example, when one feels a sting on the left arm, one must use the right hand to slap the insect, independent of where the hand is currently located in space. Thus, for the choice of the acting effector, original skin location of the stimulus is of importance (see also Kim & Cruse, 2001). However, once the effector has been chosen, it would suffice to provide stimulus location in (external) coordinates that can be merged with visual information for movement planning. Perhaps not surprisingly, effector choice has been shown to involve the frontal-parietal areas responsible for motor planning, like LIP and PRR (Beurze, de Lange, Toni, & Medendorp, 2007; Cui & Andersen, 2007; Calton, Dickinson, & Snyder, 2002).

## Conclusions

Our study demonstrated that ERPs to tactile stimuli are systematically modulated by attention to different parts of the body. This attentional modulation was influenced by the distance of the stimulated body part from the attended one. Attention to one body part, therefore, “spills over” to other body parts located near the attended one, reminiscent of what has been called the body

schema—a representation of the body and the posture of its limbs. Importantly, this body schema seems to use both anatomical and external spatial coordinates in parallel. When a simple tactile stimulus is sensed on the skin, posture is therefore taken into account when the stimulus is localized.

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