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Hands behind your back: Effects of arm posture on tactile attention in the space behind the body

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Abstract

Previous research has shown that tactile-spatial information originating from the front of the body is remapped from an anatomical to an external-spatial coordinate system, guided by the availability of visual information early in development. Comparably little is known about regions of space for which visual information is not typically available, such as the space behind the body. This study tests for the first time the electrophysiological correlates of the effects of proprioceptive information on tactile-attentional mechanisms in the space behind the back. Observers were blindfolded and tactually cued to detect infrequent tactile targets on either their left or right hand and to respond to them either vocally or with index finger movements. We measured event-related potentials (ERPs) to tactile probes on the hands in order to explore tactile-spatial attention when the hands were either held close together or far apart behind the observer's back. Results show systematic effects of arm posture on tactile-spatial attention different from those previously found for front space. While attentional selection is typically more effective for hands placed far apart than close together in front space, we found that selection occurred more rapidly for close than far hands behind the back, during both covert attention and movement preparation tasks. This suggests that proprioceptive space may ‘wrap’ around the body, following the hands as they extend horizontally from the front body midline to the centre of the back.

Keywords: tactile; spatial attention; somatosensory; ERPs; body representation

1. Introduction

In order to respond to the sources of tactile sensations quickly and appropriately, proprioceptive information (ie. position of body parts relative to each other and to objects) needs to be integrated early during tactile processing. It is now known that changes in body posture are taken into account automatically (e.g. Azañón and Soto-Faraco 2008; Azañón et al 2010a) because the representation of our body in space is constantly being updated by structures such as posterior parietal cortex (e.g. Bolognini and Maravita 2007; Azañón et al 2010b). In other words, as we move our body parts through the environment, the location of a tactile sensation is continuously remapped from an anatomically defined coordinate system (e.g. touch on the left hand) to one defined by coordinates in external space (e.g. touch near the left edge of the table).

While studies of congenitally and early blind individuals strongly suggest that the dominance of the external spatial reference frame in touch is determined by the availability of visual information early in development (Röder et al 2007, 2008), two recent studies on sighted individuals indicate that it is unlikely to be a purely visual coordinate system (Kóbor et al 2006; Heed and Röder in press). Both of these studies measured tactile temporal order judgments, which are typically affected by body posture: We are less able to determine which of two hands was touched first when the arms are crossed rather than uncrossed (e.g. Yamamoto and Kitazawa 2001), and when they are near rather than far apart (Shore et al 2005). Kóbor et al (2006) showed that the detrimental effects of crossing the arms were still present, although smaller in size, when the arms were crossed in the back compared to in front of the body. Heed and Röder (in press) report equivalent effects on performance when the arms were crossed in front of the body and in the back, suggesting that external spatial information is taken into account to the same extent in both front and rear spatial regions. As there is limited availability of visual information about the regions behind our body, interactions between body parts and the environment in this space will not give rise to the kinds of visual-tactile experiences (e.g. visually-guided manipulation of objects in front of our body) that contribute to the development of the visually-dominated spatial representations of front space. Therefore, effects of arm posture in the space behind the back are testament to an external spatial coordinate system that guides tactile localisation without visual references.

The present study used event-related potentials (ERPs) to test and further describe the effects of external spatial (proprioceptive) information on the processing of touch on the hands when the hands are positioned behind the back. Kóbor et al's (2006) and Heed and Röder's (in press) findings indicate that, despite the absence of visual references in back space, the integration of information about the location our body parts does not simply end at our sides, just as object manipulation does not simply end at our sides. Whenever we need to niftily pass a basketball behind our back, button up a dress, or just hold onto something behind us, the position of our arms is likely to affect how we represent tactile information we receive on our hands when performing these actions. To test this we manipulated hand distance (near vs. far) and measured ERPs in response to touch at cued locations (attended hands) and uncued locations (unattended hands). Observers were asked to respond to infrequent targets at cued and uncued locations either vocally (covert attention) or manually by flexing the touched index finger (movement preparation). This manipulation of attentional mode tested whether the functional similarities between the mechanisms engaged in covert attention to the hands and the preparation of hand movements shown for front space (Gherri and Eimer 2008; Gherri et al 2008) extends into the space behind the back. To eliminate any additional effects of visual-spatial processing on tactile-spatial attention, attentional cues were delivered tactually to a central location at the nape of the neck and observers were blindfolded and asked to close their eyes throughout the task.

An externally defined spatial framework is well known to mediate the mechanisms underlying exogenous and endogenous tactile and crossmodal (involving touch) spatial attention in studies investigating body posture effects on selection between touch on the hands in front space (e.g. Driver and Grossenbacher 1996; Eimer et al 2001, 2003, 2004; Gillmeister et al 2010a; Heed and Röder 2010; Kennett et al 2001; Spence et al 2000; Soto-Faraco et al 2004). Previous ERP studies using hand distance to manipulate external spatial influences have shown that the closeness of tactile event locations interferes with tactile-spatial selection. Eimer et al (2004) showed that attentional modulations over somatosensory N140 component were smaller when the hands were near together than when they were far apart. Gillmeister et al (2010a) found that attentional effects were present later when the hands were near (N200) than when they were far (P100-N140 component range). If external spatial information is integrated into tactile processing in both front and rear space, we should thus expect to see similar effects of hand distance on attentional modulations in somatosensory ERPs. Specifically, if the representation of space behind our back exactly mirrors that in front of the body, attentional effects should be smaller or present later for hands close together behind the body than further apart. In addition, this pattern of attentional effects should be observable during both covert attention to the hands and during the preparation of hand movements.

2. Materials and methods

2.1. Participants

Twenty participants gave informed consent to participate. Six participants were excluded due to poor eye fixation control (see section 2.4), so that 14 participants (seven men; 12 right-handed; mean age = 25.5 years) remained in the sample. The study was approved by the local ethics committee and conducted in accordance with the 1964 Declaration of Helsinki.

2.2. Stimuli and Apparatus

Tactile stimuli were presented using two 12-volt solenoids, masked by white noise (65 dB SPL). Attentional cues were presented centrally to the nape of the neck. There were two cues types, indicating the left hand or the right hand as likely target locations, counterbalanced across participants: ‘taps’, where the rod of the solenoid contacted the skin continuously for 200 ms, and ‘buzzes’, where contact was made twenty times for 5 ms, followed by 5-ms pauses, resulting in a total cue duration of 200 ms. Tactile target and non-target stimuli were presented unilaterally to the left or right index fingertip. To present tactile non-targets the rod of the solenoid contacted the fingertip for 200 ms (‘single taps’), and to present tactile targets the 200-ms contact was interrupted for 4 ms half-way through presentation (‘double tap’).

Participants were seated in an adapted chair (see Figure 1), with their backs leaning against a pillow attached to the edge of a table, their arms placed behind their back, and the dorsal aspect of their hands loosely placed against a board attached to the back of the chair, held in place by wooden guides.

Figure 1 about here

Participants’ eyes were covered with one soft and one more rigid light-excluding blindfold (www.mindfold.com) throughout the experimental session. Vocal response times were measured with a free-standing microphone. Index finger movement response times were registered when infrared light beams between transmitter and receiver LEDs were interrupted by flexing the index finger (see Figure 1).

2.3. Procedure

Each participant completed eight blocks of 100 trials, consisting of two successive blocks of each combination of attentional mode (covert attention vs. movement preparation) and hand distance (near vs. far). Half of all participants completed all four covert attention blocks first, and the other half completed all four movement preparation blocks first. One half placed their hands near together for the first two blocks of each attentional mode condition, and far apart for the remaining two blocks. This was reversed for the other half of participants. Each block began with a 300-ms warning sound (1000 Hz), followed by a 1000-ms pause. Each trial started with a 500-ms pause, followed by the presentation of the 200-ms cue. Attention was cued to the left hand in half of all trials, and to the right hand in the other half. 800 ms after cue offset, the 200-ms tactile target or non-target stimulus was presented to the left or right index finger, followed by a 1000-ms pause. Target stimuli were more likely to occur on the cued than on the uncued hand (3:1 ratio), that is, there were 24 target stimuli on the cued hand and 8 target stimuli on the uncued hand in each block. Of the 68 non-target stimuli per block, half were presented to the cued hand, and the other half to the uncued hand. In covert attention blocks participants were instructed to respond vocally (“pa”) whenever a target stimulus was detected at cued and uncued locations, and to ignore all non-target stimuli. In movement preparation blocks, they were instructed to flex the index finger on which the target stimulus was felt. The response interval was 1200 ms, measured from target onset. After each block, participants were given feedback about their accuracy.

2.4. EEG recording and ERP analysis

EEG was recorded with Ag/AgCl electrodes from Fp1, Fp2, F3, Fz, F4, FC5, FC1, FCz, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, O1 and O2 (subset of the international 10-10 system), referenced offline to the average earlobes. Horizontal EOG was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 2 kΩ for reference and ground electrodes, and below 5 kΩ for all other electrodes, and the impedances of the earlobe electrodes were kept as equal as possible. A BrainAmps amplifier and Brain Vision Recorder (version 1.02) and Analyzer (version 1.05) software (BrainProducts GmbH) were used for recording and offline analysis of the EEG data. EEG was amplified, band-pass filtered at 0.01 – 100 Hz, digitised at 500 Hz, and filtered off-line with a low pass filter of 30 Hz and a notch filter of 50 Hz. EEG and HEOG were epoched for a period from 200 ms before to 400 ms after the onset of the non-target stimulus. To check for eye movements in the interval between cue and non-target, epochs were also extracted for the 1000-ms period between the onset of the cue and the onset of the non-target stimulus. Averaged HEOG waveforms obtained in this interval were scored for systematic deviations of eye position, relative to a 200-ms pre-cue baseline, indicating a tendency to move the eyes toward the cued side. Two participants were disqualified due to residual HEOG deflections exceeding ±3 μV in this interval. Trials with horizontal eye movements (HEOG exceeding ±30 μV relative to baseline), eye blinks or other artefacts (a voltage exceeding ±70 μV at any electrode relative to baseline) measured in the interval starting 200 ms before cue onset and ending 400 ms after the onset of the non-target stimulus were excluded from further analysis. Four participants were disqualified due to HEOG exceeding this criterion in more than 70% of trials. ERPs to non-targets were averaged relative to a 200-ms pre-stimulus baseline for all combinations of attentional mode (covert attention or movement preparation), hand distance (near or far), cue validity (validly or invalidly cued locations), and stimulated hand (left or right). ERP mean amplitudes were computed within separate measurement windows centred on somatosensory components N80 (70-90 ms post-stimulus onset), P100 (90-130 ms), N140 (130-170 ms), and N200 (170-270 ms). Within each measurement window statistical analyses of ERP mean amplitudes were conducted for lateral electrodes F3, F4, FC5, FC1, FC2, FC6, C3, C4, CP5, CP1, CP2, CP6, P3, and P4, and for midline electrodes Fz, FCz, Cz, and Pz. Repeated-measures ANOVAs were conducted for the factors attentional mode (covert attention vs. movement preparation), hand distance (near vs. far), cue validity (validly cued vs. invalidly cued locations), hemisphere (electrodes ipsi- and contralateral to the stimulated hand), and electrode (see above). Follow-up ANOVAs were conducted for each time window in which effects of attentional mode and/or hand distance on cue validity were found. When appropriate, Greenhouse-Geisser adjustments to the degrees of freedom were applied.

3. Results

3.1. Behavioural performance

Observers missed 4.6% of responses on average (1.4% of vocal and 7.8% of finger movement responses; the higher number of missed finger movements was due to apparatus rather than inattention). Responses were faster to targets in validly cued than in invalidly cued trials (cue validity: $F_{1,13} = 31.6$, $p < .001$), showing that observers allocated their attention to the cued hand in line with task instructions. Effects of spatial-selective attention were not significantly larger when hands were near (80 ms) than far apart (71 ms) (cue validity * hand distance: $F_{1,13} = 1.4$, $p = .267$). Cue validity did not vary across attentional mode (cue validity * attentional mode: $F_{1,13} < 1$, $p = .594$, cue validity * attentional mode * hand distance: $F_{1,13} = 2.2$, $p = .165$).

3.2. Somatosensory event-related potentials

Figures 2A and 2B shows ERP waveforms in response to tactile non-targets at validly and invalidly cued locations in covert attention (Figure 2A) and movement preparation (Figure 2B) tasks when observers' hands were near or far apart; Figure 3 shows effects of cue validity and difference waveforms across conditions of attentional mode and hand distance enlarged for one electrode.

Figures 2A and 2B about here

Figure 3 about here

For somatosensory component N80, there was a significant effect of hand distance on spatial-selective attention (cue validity * hand distance: all $F_{1,13} \geq 4.7$, all $p \leq .049$, for lateral and midline electrodes), which did not differ across attentional mode (cue validity * attentional mode * hand distance: all $F<1$, all $p \geq .633$, for lateral and midline electrodes). Separate follow-up analyses for each hand distance showed that, for both attentional modes, there were effects of attention in the N80 time range when hands were near (cue validity: all $F_{1,13} \geq 11.9$, all $p \leq .004$, cue validity * attentional mode: all $F<1$, all $p \geq .787$, for lateral and midline electrodes), but not when they were far apart (cue validity: all $F<1$, all $p \geq .876$, cue validity * attentional mode: all $F<1$, all $p \geq .643$, for lateral and midline electrodes). This suggests that, in the N80 time range, selection between the hands for covert attention and movement preparation takes place only when hands are placed close together behind the body.

For somatosensory component P100, effects of attention were only present as an interaction with electrode (cue validity * electrode: all $F_{1,13} \geq 4.3$, all $p \leq .035$, for lateral and midline electrodes), but this did not differ across attentional mode or hand distance (cue validity * attentional mode * electrode: all $F<1$, all $p \geq .472$, cue validity * hand distance * electrode: all $F<1$, all $p \geq .597$, cue validity * attentional mode * hand distance * electrode: all $F<1$, all $p \geq .755$, for lateral and midline electrodes). Pairwise comparisons showed that there were overall effects of cue validity for frontal electrodes F3/4, Fz, FC1/2, and FCz (all $p \leq .034$), marginal effects for FC5/6 ($p=.051$), but no effects for any other electrode (all $p \geq .126$). This suggests that, in the P100 time range, selection between the hands for covert attention and movement preparation takes place irrespective of proprioceptive distance between the hands, but for some frontal electrodes only.

For somatosensory component N140, effects of attention (cue validity: all $F_{1,13} \geq 20.4$, all $p \leq .001$, for lateral and midline electrodes) were not affected by attentional mode or hand distance (cue validity * attentional mode: all $F<1$, all $p \geq .513$, cue validity * hand distance: all $F_{1,13} \leq 1.8$, all $p \geq .194$, cue validity * attentional mode * hand distance: all $F<1$, all $p \geq .429$, for lateral and midline electrodes), except in an interaction between cue validity, hand distance, and hemisphere (cue validity * hand distance * hemisphere: $F_{1,13}=18.3$, $p=.001$, for lateral electrodes). Pairwise comparisons showed that while effects of cue validity were present for all conditions of hand distance and hemisphere (all $p \leq .028$), they were somewhat larger for contralateral than ipsilateral electrodes when hands were placed far apart, while the reverse was the case when hands were near. This suggests that, similar to the P100, in the N140 time range selection between the hands for covert attention and movement preparation takes place irrespective of proprioceptive distance between the hands.

For latencies following the descending flank of the N140, which we have called N200 here, effects of attention (cue validity: all $F_{1,13} \geq 16.1$, all $p \leq .001$, for lateral and midline electrodes) were also not affected by attentional mode or hand distance (cue validity * attentional mode: all $F<1$, all $p \geq .406$, cue validity * hand distance: all $F<1$, all $p \geq .454$, cue validity * attentional mode * hand distance: all $F<1$, all $p \geq .812$, for lateral and midline electrodes), except in an interaction between cue validity, hand distance, and hemisphere (cue validity * hand distance * hemisphere: $F_{1,13}=10.0$, $p=.008$, for lateral electrodes). Similar to the patterns found for N140, pairwise comparisons showed that effects of cue validity were present for all conditions of hand distance and hemisphere (all $p \leq .014$), but that they were somewhat larger for contralateral than ipsilateral electrodes when hands were placed far apart, while the reverse was the case when hands were near. This suggests that, similar to P100 and N140 time ranges, at longer latencies (post-N140) selection between the hands for covert attention and movement preparation takes place irrespective of proprioceptive distance between the hands.

4. Discussion

Using ERPs in a spatial-attentional paradigm, we show that body posture (proprioceptive distance between the hands) systematically affects attentional selection of touch on the hands, when the hands are held behind the back. We found attentional modulations at earlier stages of processing (N80) when the hands were positioned near one another than when they were further apart (P100-N140), both during covert attention (vocal response upon target detection) and during movement preparation (left or right finger movement upon target detection). This suggests that, similar to front space, proprioceptive information about the relative location of body parts in the space behind the body is integrated with tactile information prior to attentional selection. In other words, and in line with the findings from two previous behavioural studies (Kóbor et al 2006; Heed and Röder in press), remapping of tactile locations from anatomical into external spatial coordinates may take place, not only when the touched hands are positioned in front space, but also when they are behind the body, despite limited visual representations of this region of space. Our results also suggest that the functional overlap between the mechanisms engaged in covert attention to the hands and in the preparation of hand movements that is well documented for the space in front of the body (e.g. Gherri and Eimer 2008; Gherri et al 2008; see also Praamstra et al 2005) extends into the space behind the back.

There is one striking difference between the present findings and those of previous ERP studies investigating tactile-spatial representations in front space, however. When proprioceptive distance between the hands is manipulated in front space, attentional effects are larger for far compared to near hands over N140 (Eimer et al 2004), or they occur earlier in processing for far (P100-N140) compared to near (N200) hands (Gillmeister et al 2010a), showing that attentional selection between the hands is more effective with greater hand distances. The reverse was found in the present study: attentional effects occurred earlier in processing for near (N80) compared to far (P100-N140) hands when the hands were held behind the back. This indicates that tactile-spatial selection in rear space takes place more rapidly the closer together the hands are behind the body[1].

Taken together, these findings suggest that the reference frame used for tactile processing in the space behind our back does not mirror that used for tactile information arising in front of the body. Instead, they suggest that the representation of external (proprioceptive) space may ‘wrap’ around the body, following the hands as they extend horizontally along the dorsoventral axis from the front body midline to the centre of the back. Although speculative, a representational continuum where the hands can be treated as increasingly separate sources of information the further they are from each other, not linearly, but in relative distance around the body, would

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[1] It is possible that cueing modality affects precisely how ERP modulations express tactile-spatial selection and its modulation by body posture: Eimer et al found that the size of the N140 attentional modulation reflected effects of hand distance when attention was cued visually, while Gillmeister et al and the present study both showed that the latency of attentional modulations reflected hand distance effects when attention was cued tactually.

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explain our findings, and those of similar ERP studies, well. A representational continuum like this would give rise to a gradient of proprioceptive effects on attentional selection in touch, such that selection takes place more rapidly (ie. attentional modulations occur earlier in processing) the greater the distance between the hands from the front body midline. Specifically, for hands close together in front of the body, attention may “spill over” from one hand to the other as tactile locations are more likely to overlap in an external spatial coordinate system (see Heed and Röder 2010). Such overlap is less likely (and therefore attentional selection can occur more rapidly) when hands are placed further away from each other and outward to the side, and least likely when the hands are positioned even further away from the front body midline, that is, close together behind the body. This would explain why the earliest effects of attentional selection between touch on the hands were found when the hands were placed close together behind the back (N80, the present study), followed by hands far apart behind the back (P100-N140, the present study) or in front (P100-N140, Gillmeister et al 2010; N140, Eimer et al 2004), and why later effects were found for hands close together in front of the body (N140, Eimer et al 2004; N200, Gillmeister et al 2010).

Our study is the first to show effects of transient spatial attention in the relatively early time range of the N80 when the hands were close together behind the body, but only over mid-latency components P100 (for some frontal electrodes) and N140 when the hands were further apart. As it is thought that the N80 component of the somatosensory event-related potential is most probably generated in primary somatosensory cortex (SI, e.g. Hari et al 1984; Mima et al 1998), our findings suggest that spatial attention modulates tactile processing in SI, but only when the hands are held close together behind the body. Some previous studies have shown effects of spatial attention overlapping with N80 when the hands were positioned in front space or by the side of the body (e.g. Desmedt and Robertson 1977; Eimer and Forster 2003; Hötting et al 2003; Michie et al 1987; Schubert et al 2008). In these studies attention to the hands was sustained, however, which is thought to give rise to earlier ERP modulations than cueing attention on a trial-by-trial basis like in the present study because attention may be focused more efficiently when it is maintained on one location (e.g. Eimer and Forster 2003). We propose that tactile attentional effects at latencies as early as N80 are evoked, and modulated by hand posture, because hands close together (but not touching) behind the body are most likely to be represented as distinct sources of information in the 'wrapped' space we hypothesise, thus enabling more rapid attentional shifts to the cued hand than would be the case for any other hand configuration. A similar selection advantage has been shown to give rise to N80 effects of transient attention in a hand movement task. Forster & Eimer (2007) found that attention shifted to the hand that was to be moved more rapidly when the hand to be moved was cued (N80) than when the movement goal (the other hand) was cued (N140), presumably because hand cues stressed hand selection while goal cues did not. Alternatively, it may be argued that N80 effects in our study are the result of observers closing their eyes throughout the present task, which was not the case in previous hand distance studies. However, this is unlikely to be the sole reason for early latency modulations, as N80 effects have been shown when observers' eyes were open during transient attention tasks (Forster & Eimer 2007; Gillmeister et al 2010b).

We further found effects of tactile-spatial attention overlapping with mid- and long-latency components P100 (for some frontal electrodes only), N140 and N200, where they are more typically found also for front space. These components are thought to be associated with processing in numerous areas including secondary somatosensory cortex and bilateral frontal and parietal regions (e.g. Allison et al 1989; De Santis et al 2007; Desmedt and Robertson 1977; Hari et al 1984; Mima et al 1998). Previous studies have shown effects of hand distance (Eimer et al 2004; Gillmeister et al 2010a) and of vision of the hands (Sambo et al 2009) on modulations reflecting transient attentional selection between the hands in the P100-N140 time range. In the present study, attentional effects at P100 and beyond were found irrespective of whether hands were close or further apart, however. The presence of N80 rather than P100-N140 modulations by hand distance suggests that the external spatial components of attention are linked to different stages of processing in rear (N80) compared to front space (P100-N140). Specifically, transient spatial selection of the hands may take place in SI when they are near together behind the body, while such selection only takes place in SII and/or regions beyond somatosensory cortex when they are further apart in back or front space, or close together in front of the body. Spatial-attentional effects at later stages (N200) are thought to reflect greater in-depth processing of task-relevant features of attended stimuli (Michie 1984), irrespective of differences in front or back space (the present study), body posture (the present study; Eimer et al 2004; Gillmeister et al 2010a), vision of the body (Sambo et al 2009; Gillmeister et al 2010b), and body parts selected (Gillmeister et al 2010b)[2].

Future studies should directly compare hand posture effects on attentional selection in front, side, and rear space to investigate whether the representation of external proprioceptive space wraps around the body in a continuous fashion (as suggested above) and with diminishing visual dominance as it extends outward along

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[2] The only indication that hand distance may affect attention over N140 and N200 were larger effects of attention contralaterally than ipsilaterally when hands were far, while the reverse was the case when hands were near. As N140 and N200 are bilateral components with multiple generators, the reason for this laterality bias for attentional effects as a function of body posture is presently unclear.

the dorsoventral axis and around the body, or is instead warped at the transitory zones from front to rear space (ie. at the edges of our visual field). Another interesting question concerns the point at which the hands are proprioceptively closest (ie. the location at which attentional spill-over is greatest). We have suggested above that this may be the front body midline, as our and previous studies have typically aligned head position, eye gaze direction, and retinal location with trunk position rather than test the independent contributions of these anchors (although see Driver and Grossenbacher 1996, for some effects of gaze direction), but there is no reason to presume that the point of greatest proprioceptive closeness could not be, for example, centred on head or gaze direction. Interestingly, it has recently been suggested that the external reference frame utilised for tactile information processing may be action-based rather than purely visual, that is, anchored to the eyes for those regions of space currently accessible to the eyes (e.g. a touched object in front space), but additionally using head, trunk or whole body coordinates to enable the directing of the eyes (and one's attention) toward currently inaccessible locations (e.g. a touched object in rear space) (Heed and Röder in press). Further research related to these questions would therefore seem both interesting and timely.

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Figure legends

Figure 1. Experimental setup showing a participant seated in a purpose-built chair with hands held near (left panel) or far (right panel) behind their back, palms facing away. Hands were held in place by adjustable guides (white rectangles) and positioned between transmitter and receiver LEDs of two infrared devices (black boxes). Tactile stimulators (grey circles) were attached to the nape of the neck and to the left and right index fingertips.

Figure 2. Grand-averaged ERP waveforms to tactile stimuli at validly (black lines) and invalidly (grey lines) cued locations in covert attention (Figure 2A) and movement preparation (Figure 2B) tasks when hands were near (top panel) or far apart (bottom panel) at a selection of electrodes ipsilateral (left cluster) and contralateral (right cluster) to the stimulated hand. Highlighted electrodes are shown in Figure 3.

Figure 3. Somatosensory ERPs at electrode C3/4c across cue validity in covert attention (A) and movement preparation (B) tasks when hands were near (left panel) or far (right panel). Difference waveforms (far right panel) were obtained by subtracting ERPs in invalidly cued trials from those in validly cued trials. Shaded areas indicate measurement windows. Asterisks indicate significant main effects of cue validity (left and right panels), or interactions between cue validity and hand distance (far right panel).