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ERP investigation of transient attentional selection of single and multiple locations within touch

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Abstract

Mechanisms underlying pure tactile attentional selection were investigated. Tactile imperative stimuli were preceded by symbolic tactile cues directing attention to the left or right (directional cues), or to both hands (non-directional cues). Comparison of ERP waveforms on directional and non-directional cue trials showed that attentional modulations at N140 and P200 components reflect mainly enhancement of stimuli at the attended, while longer latency modulations reflect mainly suppression of processing of stimuli at the unattended location. This pattern of results differs from analogous studies involving other modalities suggesting that different mechanisms underlie pure tactile attention. Furthermore, ERP waveforms on non-directional cue trials were enhanced in comparison to directional cue trials at the P100 component and at longer latencies, indicating that tactile attentional mechanisms may differ when attending to one compared to multiple locations.

Descriptors: Transient attention, Somatosensation, ERP, Tactile cueing, Spatial selection

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We constantly receive an incoming stream of information from our senses. Through shifts of covert selective attention to objects or events, we are capable of selecting relevant information in our surrounding environment or on our body surface without having to change the orientation of our head or eyes. Directing attention to locations in our environment or on our body has been shown to speed reaction times and improve discrimination of events at that location (e.g., Posner, 1978; Posner, Snyder, & Davidson, 1980). Likewise, neurophysiological and functional neuroimaging studies have reported that attention can bias information processing in a top-down manner by increasing or decreasing the sensitivity of neurons responding to features that are task relevant or irrelevant, respectively (e.g., Moran & Desimone, 1985; Desimone & Duncan, 1995; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997).

A common task used to study transient covert shifts of visual-spatial attention on behavior and neuronal processes was introduced by Posner (1978). In this task, participants are first presented with a symbolic cue indicating the most likely target location at the start of each trial. Cue presentation is followed by the presentation of a target either to the right or left side of the cue. In the majority of trials, cue presentation is followed by a target at the previously indicated location, but on some trials the cue is misleading, that is, the cue indicates the location opposite to the actual target location. It has consistently been found that participants' responses to targets are faster and more accurate on validly compared to invalidly cued trials. This has been taken as an indication that participants shift their attention to the location indicated by the cue prior to target presentation. To further assess whether shifts of attention lead to enhancement or suppression of information processing, a 'neutral' cue condition is often introduced. In this condition the cue is non-directional, that is, the cue is non-informative with respect to the location of the subsequent target. It is generally assumed that, under such task conditions, attention is either focused on one location or divided between all possible target locations. Therefore, any enhancement of target processing due to attention shifts (also called attentional benefits) can be extracted by comparing responses on valid and neutral cue trials, while any suppression of target processing (also called attentional costs) can be extracted by comparing responses on neutral and invalid cue trials.

Effects of covert shifts of attention on behavior and its neuronal basis have been studied extensively in the visual modality. Behavioral effects are seen in speeded reaction times and improved discrimination of targets on validly cued trials as compared to targets on invalidly cued trials, while responses on neutral cue trials are intermediate (e.g., Luck et al., 1994; Posner et al., 1980). These behavioral findings suggest that in the visual modality shifts of covert spatial attention result in enhancement of information processing at attended locations (as benefits are present when comparing performance on valid cue trials compared to neutral cue trials) as well as suppression of processing at unattended locations (as costs are present when comparing performance on neutral compared to invalid cue trials). Moreover, electrophysiological studies (Luck et al., 1994; Talsma, Mulckhuyse, Slagter, & Theeuwes, 2007) have found a reduction

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of the P1 amplitude in response to visual targets on invalid compared to neutral cue trials, followed by an enhancement of the N1 component on valid compared to neutral cue trials. This pattern of results suggests that, in the visual modality, suppression of stimuli at unattended locations precedes enhancement of stimuli at attended locations, and that suppression and enhancement of stimulus processing are linked to different stages of visual processing. Therefore, it has been suggests that the visual P1 amplitude may reflect suppression of information processing from irrelevant locations, while the N1 amplitude specifically relates to gain control of relevant stimuli (Luck et al., 1994).

A similar pattern of behavioral and electrophysiological findings has also been reported for the auditory modality (Golob, Pratt, & Starr, 2002; Schröger & Eimer, 1997). That is, comparison of response times (RTs) on valid, invalid, and neutral cue trials shows evidence for both suppression and enhancement, while electrophysiological results suggest that shifts of attention initially lead to suppression of auditory processing at unattended locations in the time range of the N100/P200 complex, followed by enhancement of processing at attended locations at longer latencies. In contrast, a recent electrophysiological study investigating covert shifts of attention on tactile stimulus processing found a different pattern of results when comparing event-related potentials (ERPs) elicited by tactile stimuli on valid, invalid, and neutral cue trials (Forster & Eimer, 2005). We reported that attentional modulations, which emerged from the P100 component, reliably reflected both enhancement of tactile processing at attended locations (that is, a significant enhancement of ERPs on valid relative to neutral cue trials) and suppression at unattended locations (that is, a significant suppression of ERPs on invalid relative to neutral cue trials) for the N140 component. This was followed by attentional modulations that were largely due to suppression of unattended information at longer latencies (175–285 ms post-stimulus onset). Corresponding behavioral results on valid, invalid, and neutral cue trials suggested the presence of both suppression of tactile stimulus processing at unattended and, somewhat larger, enhancement at attended locations. This study was the first to suggest that the mechanisms of attentional selectivity in touch might be different from attentional processes in other modalities. While vision and audition deal with stimuli usually at a distance from our body, touch processes information directly impinging on our body surface. It is therefore conceivable that the mechanisms underlying selective spatial attention may differ when dealing with external information or information affecting us directly. Likewise, a close link between attention to touch on the body and motor activation has been shown, which is not present when dealing with external stimuli (Galazky et al. 2009).

In the study by Forster and Eimer (2005), attention was directed by visual arrow cues to either the right or left index finger, which were covered from sight. Therefore, in this study shifts of attention to touch were directed by engagement of the visual system. However, recent research suggests that the cue modality can affect behavioral (Chica, Sanabria, Lupianez, & Spence, 2007) and early sensory processing (Forster, Sambo, & Pavone, 2009; Foxe, Simpson, Ahlfors, & Saron, 2005; Talsma, Kok, Slagter, & Cipriani, 2008). Specifically, a recent study (Forster et al., 2009) directly compared the use of visual and tactile cues on somatosensory processing and found that attentional modulations are only present at later stages of sensory processing under conditions when any engagement of the visual system is excluded (i.e., by blindfolding), suggesting that in touch mechanisms of attentional selection differ in the absence of visual engagement (see also Sambo, Gillmeister, & Forster, 2009). Therefore, it is still not clear whether in touch shifts of attention lead to a pattern of suppression of information at unattended locations, followed by enhancement of information at attended locations, similar to the pattern reported for other modalities (Golob et al., 2002; Luck et al., 1994; Schröger & Eimer, 1997; Talsma et al. 2007), or whether the mechanisms underlying tactile attentional selection differ from attentional processes in other modalities, as suggested by our previous crossmodal tactile attention study (Forster & Eimer, 2005).

The present study was designed to expose the mechanisms underlying shifts of tactile attention to locations on the body by controlling for any crossmodal influences. We therefore employed symbolic tactile cues that were presented centrally to the nape of the neck and were either directional, indicating the most likely target location, or non-directional, giving no information with respect to the likely target location. To minimize any crossmodal influences, participants were blindfolded and white noise was presented throughout the experiment. Analogous to our previous study investigating the mechanisms underlying crossmodal shift of tactile attention (Forster & Eimer, 2005), we employed a short cue-target interval (CTI; 600 ms from cue offset to target onset). In addition, a long CTI (1200 ms from cue offset to target onset) was also used to elucidate the time course of attentional selection effects on somatosensory processing. In our previous study (Forster et al., 2009), which directly compared tactile attentional modulations following visual cues with those following tactile cues, we found that attentional modulations were already present in the time range of the P100 component when the visual system was engaged and visual cues were employed, while under pure tactile conditions attentional modulations only were present later, from the time range of the N140 component. We interpreted this finding as indication that the mechanisms underlying tactile-spatial attentional selection differ in the presence and absence of visual engagement. However, an alternative interpretation may be that tactile-spatial attentional selection is delayed under pure tactile conditions because complex tactile cues (vibrotactile frequencies) take longer to decode than the commonly used simple visual cues (arrows). For this reason, we also employed a long CTI (1200 ms) in the present study. If tactile spatial attention was delayed due to prolonged decoding of tactile cues (and not due to the absence of any visual information), we would expect earlier attentional modulations for tactile stimuli under long compared to short CTI conditions.

Finally, to assess whether shifts of tactile spatial attention in the absence of visual information lead to suppression of somatosensory processing at unattended locations, enhancement of somatosensory processing at attended locations, or a combination of both, we compared ERPs to tactile stimuli following attention-directing tactile cues on valid and invalid cue trials with those following non-directional cues on neutral cue trials in which participants were instructed to attend to both hands. If shifts of attention lead mainly to suppression of information processing at unattended locations, we would expect to find a significant difference between ERPs elicited on invalid compared to neutral cue trials; however, if shifts of attention lead mainly to enhancement of information processing at attended locations, we would expect a significant difference between ERPs elicited on valid cue trials compared to neutral cue trials. Alternatively, if both suppression and enhancement may play a role, then we would expect this to occur either at the same stage of processing,

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as previously reported for touch under crossmodal cueing conditions (i.e., visual cues followed by tactile targets; Forster & Eimer, 2005), or at different processing stages like the effects found in the visual and auditory modality (Golob et al., 2002; Luck et al., 1994; Talsma et al., 2007; Schröger & Eimer, 1997).

Methods

Participants

Eighteen participants (six males, aged 18–31 years, mean 23.7 years) gave informed written consent to take part in this experiment. All except two participants were right-handed and all had normal or corrected-to-normal vision by self-report. Five participants were excluded due to poor eye fixation control (residual horizontal electrooculogram (HEOG) deflections exceeding $\pm$ 5 μV in the interval between the onset of the cue and the onset of the tactile stimulus), and an additional participant was excluded due to an excess of alpha waves, so that twelve participants remained in the sample. The study was conducted in line with the 1964 Declaration of Helsinki.

Stimuli and Apparatus

Participants sat in a dark experimental chamber, and wore a blindfold (www.mindfold.com) throughout the experimental session. They were instructed to keep their eyes open and their gaze straight ahead. A tabletop microphone was placed in front of them to record vocal response latencies. Participants were monitored via an infrared camera throughout the experimental session. Participants placed their left and right hands on the tabletop in front of them, about 60 cm apart, and rested their left and right index and middle fingers on tactile stimulators. Tactile stimuli were presented using three 12-Volt solenoids (www.me-solve.co.uk) driving a metal rod with a blunt conical tip to the fingertips of the left and right index fingers and the nape of the neck, making contact with the skin whenever a current was passed through the solenoid. The software E-Prime (www.pstnet.com) was used for sending trigger signals to the tactile stimulators, for recording response accuracy and latency, and for sending markers to the electroencephalogram (EEG) recording system (below). White noise (65 dB SPL, measured from the position of the participants' head) was continuously present to mask any sounds made by the tactile stimulators.

Tactile attentional cues were presented centrally to the nape of the neck. There were three different cues types, indicating the left hand or the right hand as likely target locations on directional cue trials, or instructing participants to attend to both hands on non-directional cue trials. Non-directional cues were 'taps,' where the rod of the solenoid contacted the skin continuously for 300 ms. On directional cue trials, cue characteristics and assignment were counterbalanced across participants: 'flutter' vibrations, where the stimulus onset asynchrony (SOA) between successive 6-ms pulses was 54 ms (corresponding to a rectangular stimulation frequency of about 16.7 Hz), and 'continuous' vibrations, where the SOA between successive 3-ms pulses was 17 ms (corresponding to a frequency of 50 Hz). As the duration of each tactile cue (measured as the interval between the onset of the first pulse and the offset of the last pulse) would be different for the different types of cue, a 2-ms pulse was presented at 300 ms following cue onset, rendering the cue duration 302 ms for 'taps,' 'flutter,' and 'continuous' vibrations alike.

Tactile target and non-target stimuli, which were presented unilaterally to the left or the right index finger, consisted of single and double taps. For single taps (non-targets), the rod of the solenoid contacted the finger continuously for 200 ms. For double taps (targets), continuous contact was made for two periods of 85 ms, separated by a 30 ms-pause, resulting in a total stimulus duration of 200 ms.

Procedure

The experiment consisted of twenty blocks, each consisting of 76 trials (see Table 1 for trial types and their frequency). Each trial started with a 302-ms presentation of the tactile cue. At an interval of 600 ms (short CTI) or 1200 ms (long CTI) after cue offset, a tactile target or non-target stimulus was presented to the left or right index finger, followed by a 1000-ms inter-trial interval. Participants were instructed to respond vocally (''pa'') whenever a target stimulus (a double tap) was detected at cued and uncued locations, and to ignore all tactile non-target stimuli (single taps). Target stimuli were more likely to occur on the attended hand when one hand was attended (4:1 ratio), but they were equally likely to occur on the left or the right hand when both hands were attended. The response interval was 1200 ms, as measured from target onset.

EEG Recording

EEG was recorded using a Brain Product recoding system (www.brainproducts.com) 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) and referenced to the earlobes. HEOG was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 2 kΩ for reference and

Table 1. *Main Statistical Results for Analyses Comparing ERP Mean Amplitude Values on the Different Cue Type Trials for Each Component Analyzed*

Component	P100		N140		N200		Longer latencies			
CTI	Short & Long		Short		Short		Short		Long	
Electrodes	Midline	Lateral	Midline	Lateral	Midline	Lateral	Midline	Lateral	Midline	Lateral
Valid vs. Invalid	n.s.	n.s.	.05	.05	.02	.02	.001	.001	.009	.02
Valid vs. Neutral	n.s.	.02	.001 (PZ)	$<$.05 (P3/4,CP5/6, CP1/2)	.02	n.s.	n.s.	n.s	.04	.02
Invalid vs. Neutral	.01	.01	n.s.	n.s.	n.s.	n.s.	.01	.01	.001	.001

Note: Main statistical results (p-values) are stated for the overall analysis (short and long CTI) when no attention by CTI interaction was present; otherwise, only significant follow-up analyses are stated. Electrode names stated in brackets indicate that significance was only reached at the indicated sites. n.s.: not significant.

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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, Gilching, Germany) were used for recording and offline analysis of the EEG data. Amplifier band-pass was 0.01–100 Hz, and digitization rate was 500 Hz. EEG was filtered offline with a digital low pass filter of 40 Hz and a notch filter of 50 Hz. EEG and HEOG were epoched in separate offline analysis and were extracted for a period from 100 before to 900 ms (short cue-target interval) or to 1500 ms (long cue-target interval) after cue onset to check for eye movements in the interval between cue and tactile stimulus onsets, and epochs were also extracted from 100 ms before to 400 ms after the onset of the tactile stimulus. Trials with horizontal eye movements (HEOG exceeding $\pm$ 40 μV relative to baseline), eye blinks, or other artifacts (a voltage exceeding $\pm$ 70 μV at any electrode relative to baseline) measured in the interval starting 100 ms before cue onset and ending 400 ms after the onset of the non-target stimulus were excluded from analysis.

Averaged HEOG waveforms obtained in this interval were scored for systematic deviations of eye position, indicating a tendency to move the eyes toward the cued side. Five participants were disqualified due to residual HEOG deflections exceeding $\pm$ 5 μV in this interval. Analyses were only conducted for ERPs obtained in response to tactile non-target stimuli.

ERP Analysis

ERPs to tactile non-targets were averaged relative to a 100-ms pre-stimulus baseline for all combinations of attention (unattended vs. one hand attended vs. both hands attended), stimulated hand (left vs. right), and CTI (short vs. long). ERP mean amplitudes were computed within measurement windows centred on the latencies of successive somatosensory ERP components, that is, the N80 (64–92 ms post-stimulus), P100 (94–122 ms post-stimulus), N140 (124–174 ms post-stimulus) and P200 component (174–244 ms post-stimulus), as well as at longer latencies (244–374 ms post-stimulus). For each of these time windows, statistical analyses of ERP mean amplitudes were conducted to test for effects of attention and CTI. These analyses were conducted separately for lateral recording sites F3/4, FC1/2, FC5/6, C3/4, CP1/2, CP5/6, and P3/4 and for midline electrodes Fz, FCz, Cz, and Pz. For lateral recording sites, repeated measures analyses of variance (ANOVAs) were conducted for the within-subject factors attention (invalid vs. valid vs. neutral cue trials), CTI (short vs. long), hemisphere (contralateral vs. ipsilateral electrode sites), and electrode. For recording sites along the midline, repeated measures ANOVAs were conducted for the within-subject factors attention (invalid vs. valid vs. neutral cue trials), CTI (short vs. long), and electrode. When appropriate, Greenhouse-Geisser adjustments to the degrees of freedom were applied.

Results

Behavioral Performance

Mean vocal RTs were submitted to a repeated measurements ANOVA with the factors cue target interval (short versus long) and attention (valid versus invalid versus neutral cue trial). Responses were no faster following short than following the long cue target intervals (see Figure 1). Overall effects of attention ($F(2,22) = 10.0$, $p < .01$) differed as a function of CTI

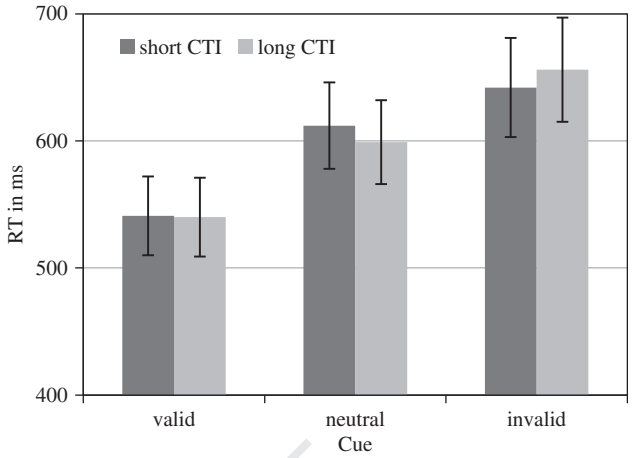

Figure 1. Mean response times (in ms) and standard errors to tactile targets on valid, neutral, and invalid cue trials for short and long cue target intervals.

($F(2,22) = 5.7$, $p < .02$). For both short and long CTI, responses were slowest for targets on invalid cue trials (642 and 656 ms, respectively), faster for targets on neutral cue trials when both hands were attended (612 and 599 ms, respectively), and fastest for targets on valid cue trials (541 and 540 ms, respectively). Pairwise comparisons showed that RTs for targets on neutral cue trials when both hands were attended were not significantly faster than those for targets on invalid cue trials, both when the CTI was short and when it was long. All other comparisons were significant ($p \leq .012$). Taken together, behavioral responses were faster to stimuli at currently attended compared to unattended locations and, importantly, comparison of RTs on these directional cue trials with neutral cue trials suggests that in touch shifts of attention lead mainly to enhancement of response times to tactile stimuli at the attended location.

Somatosensory Event-Related Potentials

Figures 2 and 3 show somatosensory ERPs in response to tactile non-target stimuli on invalid (gray lines), valid (dashed lines), and neutral (black lines) cue trials after short and long CTIs, respectively. Figure 4 contrasts short and long cue target ERP waveforms at one representative electrode (C3/4) and the corresponding difference waveforms generated by subtracting ERPs on valid from neutral and ERPs on invalid from neutral cue trials. Figures 2 and 4 show that, for the short CTI, attentional modulations were present in non-directional compared to directional cue trials at latencies overlapping with the N80 and P100 components with an enhanced positivity when attention was allocated to both hands. Spatial-attentional modulations on directional cue trials were present for the N140 and P200 components, as well as at longer latencies, with an enhanced negativity when stimuli were presented at attended compared to unattended locations. Comparing attentional modulations on directional cue trials (invalid and valid) to non-directional cue trials (neutral) shows that for the N140 and P200 components ERPs on neutral cue trials primarily differ from those on valid cue trials. This suggests that attentional modulations on directional cue trials are mainly due to enhancement of processing at the attended location. At longer latencies, ERPs on neutral cue trials differ from those on invalid cue trials, suggesting that at these latencies there is mainly suppression of information processing at the unattended location on directional cue trials. In

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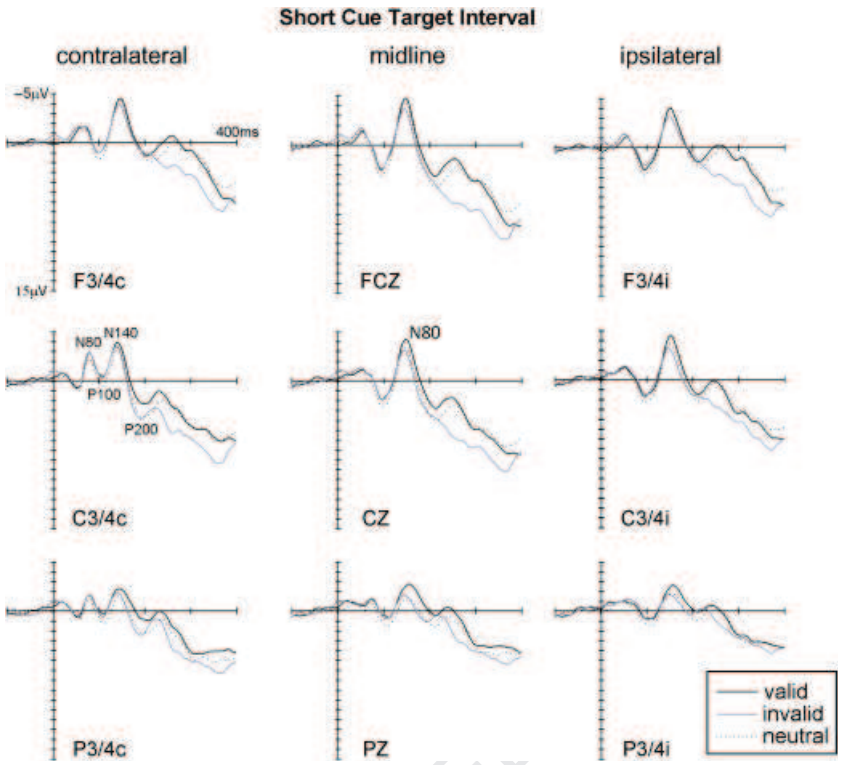

Figure 2. Grand-averaged ERP waveforms over and close to somatosensory cortex elicited by tactile stimuli following a short cue target interval (600 ms) shown separately for trials when the cue indicated the correct stimulus location (valid cue; dashed lines), when it was misleading and indicated the incorrect location (invalid cue; gray lines), and when it was non-informative with regard to the upcoming stimulus location (neutral cue; black lines) at midline electrodes and electrodes over the hemisphere contra- and ipsilateral to the stimulated hand.

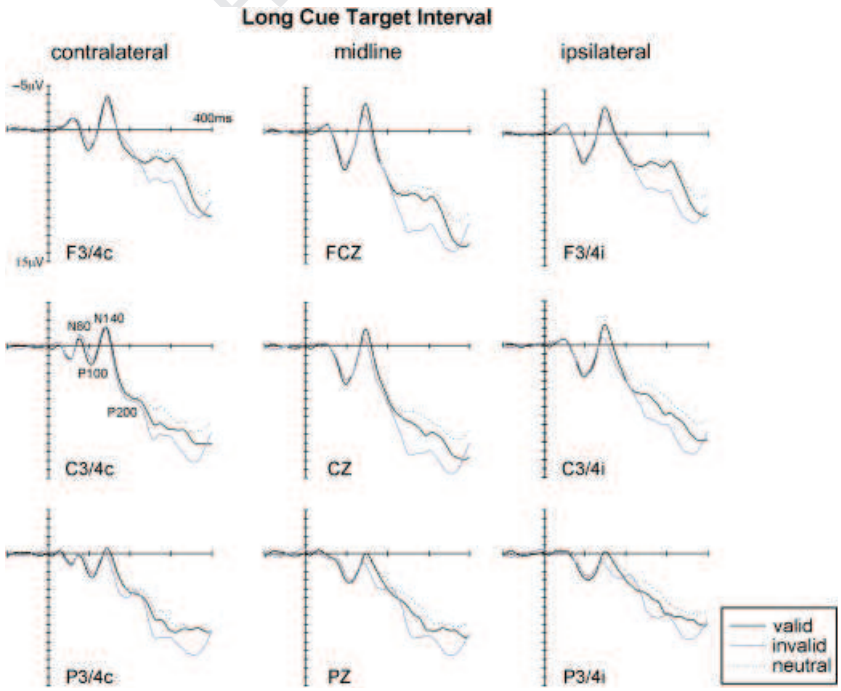

Figure 3. Grand-averaged ERP waveforms over and close to somatosensory cortex elicited by tactile non-target stimuli following a long cue target interval (1200 ms) shown separately for trials when the cue indicated the correct stimulus location (valid cue; dashed lines), when it was misleading and indicated the incorrect location (invalid cue; gray lines), and when it was non-informative with regard to the upcoming stimulus location (neutral cue; black lines) at midline electrodes and electrodes over the hemisphere contra- and ipsilateral to the stimulated hand.

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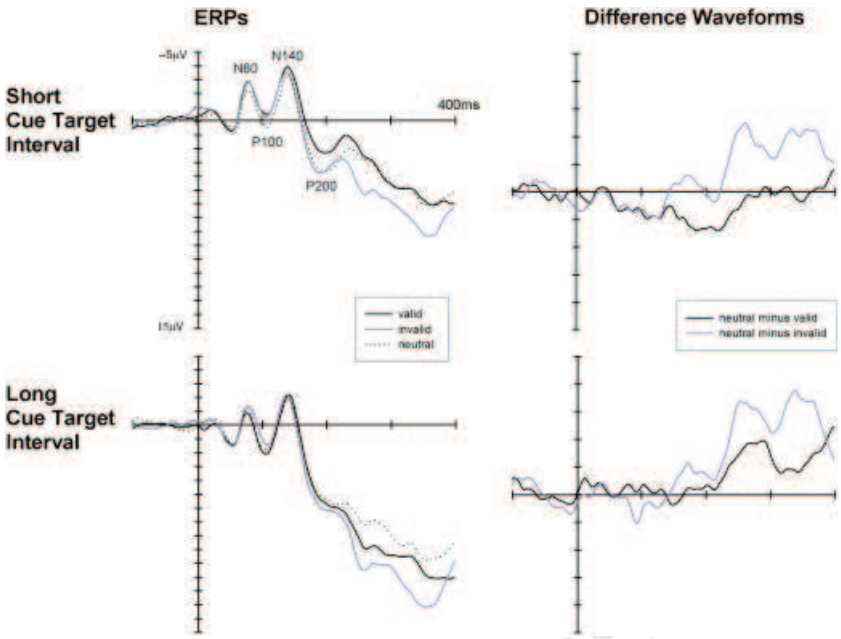

Figure 4. Grand-averaged ERP waveforms (left panels) on valid (black lines), invalid (gray lines), and neutral (dotted lines) cue trials and corresponding difference waveforms (right panels) for neutral minus valid cue trial ERPs (black lines) and for neutral minus invalid cue trial ERPs (gray lines) at one representative electrode (C3/4) contralateral to the stimulated hand shown for short (top panels) and long (bottom panels) cue target intervals.

contrast to this pattern of results, for the long CTI, attentional modulations were only present at longer latencies (Figures 3 and 4). ERP traces were more negative for valid compared to invalid cue trials, as well as more negative for neutral compared to valid cue trials, suggesting that attentional modulations on directional cue trials are based on suppression of information processing at the unattended location, as well as at the attended location. To formally test these observations, ERP amplitude averages for the N80, P100, N140, and P200 components and longer latencies were subjected to repeated measures ANOVAs to test for the effects of attention (invalid vs. valid vs. neutral cue trials) and CTI (short vs. long). If this analysis showed an interaction between attention and CTI at lateral or midline electrodes, follow-up analyses were conducted separately for the short and long CTI comparing the three attention conditions to each other (i.e., invalid vs. valid; invalid vs. neutral; valid vs. neutral) (see Table 1 for summary of main statistical results).

For the time window of the N80 component, there was no main effect of attention or interaction involving attention. For the following time window of the P100 component for lateral electrodes, only a main effect of attention ($F(2/22) = 11.10$, $p < .001$) was present. Bonferroni-corrected pairwise comparisons showed that ERPs on valid cue trials did not differ from invalid cue trials; however, neutral cue trials differed from invalid ($p < .01$) and valid ($p < .03$) cue trials. For midline electrodes also, only a main effect of attention was present ($F(2/22) = 6.25$, $p < .01$). Bonferroni-corrected pairwise comparisons showed that ERPs on valid cued trials did not differ from invalid or neutral cue trials, but neutral differed from invalid cue trials ($p < .02$). Taken together, these statistical results confirm the presence of attentional modulations of the somatosensory P100 component, with an enhanced positivity elicited by tactile stimuli following non-directional cues that instructed the allocation of attention to both hands compared to those following directional cue conditions when only one hand was attended.

For the time window of the N140 component for lateral electrodes, no main effect of attention was present, but there was an attention × hemisphere × electrode interaction ($F(12/132) = 2.90$, $p < .04$). Follow-up analyses showed that, only for the short CTI, ERPs on invalid cue trials were marginally different from those on valid cue trials ($F(1/11) = 4.77$, $p = .05$), and ERPs on neutral cue trials differed from those on valid cue trials at posterior electrodes P3/4, CP5/6, and CP1/2 ipsilateral and contralateral to the tactile stimulus ($p \leq .05$). For midline electrodes, an attention × electrode ($F(6/66) = 2.99$, $p < .05$) and an attention × CTI × electrode ($F(6/66) = 3.95$, $p < .03$) interaction was present. Follow-up analyses also showed only for the short CTI a marginally significant difference between ERPs on invalid and valid cue trials ($F(1/11) = 4.86$, $p = .05$), while neutral cue trials differed from valid cue trials at posterior electrode Pz ($p < .01$). This confirms that, in the time range of the N140 component, attentional modulations on directional cue trials were present for the short CTI only, with an enhanced negativity to stimuli at attended compared to unattended locations. Comparison of directional and non-directional cue trials further showed a difference between valid and neutral cue trials at posterior electrodes, suggesting that spatial-attentional modulations on directional cue trials were mainly due to enhancement of tactile processing at the attended location.

For the time window of the N200 component (174–244 ms post-stimulus onset) for lateral electrodes, there was no main effect of attention, but there was an attention × CTI × electrode interaction ($F(12/132) = 4.41$, $p < .02$). Follow-up analyses showed that only for the short CTI there was a significant difference between ERPs on invalid and valid cue trials ($F(1/11) = 7.06$, $p < .03$). For midline electrodes, there was also no main effect of attention, but there were attention × electrode ($F(6/66) = 5.07$, $p < .001$) and attention × CTI × electrode ($F(6/66) = 4.62$, $p < .01$) interactions. Follow-up analyses showed that also only for the short CTI there was a significant difference

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between ERPs on invalid and valid cue trials ($F(1/11) = 7.98$, $p < .02$) and a significant difference between ERPs on valid and neutral cue trials at Pz ($p < .03$). Taken together, in this later analysis time window attentional modulations were again present for directional cue conditions for the short CTI only, with an enhanced negativity for stimuli presented at attended compared to unattended locations. In addition, comparison of modulations on directional and non-directional cue trials only showed a difference between valid and neutral cue conditions, suggesting that attentional modulations on directional cue trials were mainly due to enhancement of processing at the currently attended location.

For ERP waveforms at longer latencies (244–374 ms post-stimulus onset) for lateral electrodes, there was a main effect of attention ($F(2/22) = 13.85$, $p < .0001$), as well as an attention × CTI × electrode ($F(12/132) = 2.99$, $p < .04$) and an attention × hemisphere × CTI ($F(2/22) = 5.25$, $p < .02$) interaction. Follow-up analyses separate for each CTI showed a significant effect of attention for both CTIs when comparing ERPs on valid and invalid cue trials (short CTI: $F(1/11) = 19.95$, $p < .01$; long CTI: $F(1/11) = 8.15$, $p < .02$) and neutral and invalid cue trials (short CTI: $F(1/11) = 8.43$, $p < .02$; long CTI: $F(1/11) = 21.74$, $p < .01$). For the neutral versus valid cue comparison, a significant difference was only present for the long CTI ($F(1/11) = 6.83$, $p < .03$). For midline electrodes, there was a main effect of attention ($F(1/11) = 16.45$, $p < .001$) and a significant attention × CTI × electrode interaction ($F(6/66) = 3.75$, $p < .02$). Follow-up analyses also showed significant differences when comparing ERPs on valid versus invalid (short CTI: $F(1/11) = 25.04$, $p < .001$; long CTI: $F(1/11) = 9.86$, $p < .01$) and neutral versus invalid (short CTI: $F(1/11) = 9.49$, $p < .01$; long CTI: $F(1/11) = 24.37$, $p < .001$) cue trials. For the neutral versus valid comparison, a significant difference was also only present for the long CTI ($F(1/11) = 5.80$, $p < .04$). Taken together, attentional modulations on directional cue trials were present for both CTIs, with an enhanced negativity to stimuli at the currently attended compared to unattended location. Comparing ERPs on non-directional cue trials when both hands were attended with ERPs on directional cue trials when only one hand was attended showed an enhanced negativity for ERPs when both hands were attended compared to ERPs on trials when the tactile stimulus was presented to the unattended location on directional cue trials for both CTIs. This suggests that information processing was mainly suppressed for stimuli at the currently unattended location. However, for the long CTI an enhanced negativity for stimuli presented on non-directional cue trials when both hands were attended was present compared to stimuli at the unattended as well as the attended location on directional cue trials. This suggests that information processing was suppressed, not only for stimuli at unattended locations, but also for stimuli at attended locations on directional cue trials when the CTI was long.

Discussion

The aim of the present study was to elucidate whether allocation of transient tactile-spatial attention leads to suppression or enhancement of information at attended and unattended locations on the body. Analogous to previous studies (e.g., Luck et al., 1994) we compared early somatosensory ERPs and RTs on directional (valid and invalid) cue trials with ERPs and RTs on non-directional (neutral) cue trials when participants were instructed to attend to both hands. Typically ERPs and RTs on non-directional cue trials fall between those on directional (valid and invalid) cue trials, and the common interpretation is that any difference between valid and neutral cue trials is an indication of enhancement of processing at attended locations, while any difference between invalid and neutral cue trials is an indication of suppression of processing at unattended locations on directional cue trials. For the short CTI, we found that attentional modulations on directional cue trials were present for the time range of the N140 and P200 components, as well as at longer latencies. Comparison of these attentional modulations with ERP responses on non-directional cue trials suggests that mid- to long-latency attentional modulations (N140 and P200 time ranges) were mainly due to enhancement of processing at the currently attended location, followed by mainly suppression of processing at the unattended location at longer latencies (244–374 ms post-stimulus). While for the long CTI attentional modulations were only present for longer latencies, comparison of directional and non-directional cue trials suggests that attentional modulations on directional cue trials were due to suppression of processing, not only at the unattended location, but also at the attended location.

Importantly, previous ERP studies of visual (Luck et al., 1994; Talsma et al. 2007), auditory (Golob et al., 2002; Schröger & Eimer, 1997) and crossmodal tactile (Forster & Eimer, 2005) spatial attention, using a paradigm analogous to the present study, have reported different *patterns* of enhancement and suppression of sensory processing. That is, previous studies of vision and audition have reported a pattern of initial suppression of sensory information at unattended locations, followed by enhancement of stimulus processing at attended locations. In contrast, our results suggest that in touch spatial attention exerts amplification of attended inputs between 125 to 250 ms after stimulus onset, which is short lived (only present for short CTI) and suppression of irrelevant information at later processing stages suggesting that mechanisms underlying attentional selection differ between touch and other modalities. In addition, our pattern of findings also differs from our previous study (Forster & Eimer, 2005) of crossmodally cued tactile attention, which used visual (arrow) cues and a CTI similar to the short CTI used in our present study. Forster & Eimer (2005) reported attentional modulations on directional cue trials from the time range of the P100 component, with enhancement as well as suppression of stimulus processing reliably present at the N140 component. This was followed by mainly suppression of stimulus information at unattended locations at longer latencies. In contrast, in the present study attentional modulations on directional cue trials were only present from the N140 component, and were found to reflect mainly enhancement of processing at the attended location at this latency and the subsequent P200 component. This difference in findings between crossmodally and tactually cued tactile attention suggests that engagement of the visual system is associated with the presence of earlier spatial-attentional modulations (c.f. Forster et al., 2009) as well as with earlier suppression of processing of tactile stimuli at the currently unattended location. Taken together, these findings suggest that mechanisms underlying tactile attentional selection can vary depending on interactions with other sensory modalities.

Studies investigating the contributions of suppression and enhancement of stimulus processing to behavioral and ERP spatial attention effects in vision have reported that behavioral responses on non-directional cue trials fall between directional

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(valid and invalid) cue trials while ERP recordings have shown that different early sensory processing stages are linked to suppression (P1) of unattended and enhancement of attended information (N1), followed by both suppression of stimuli at unattended and enhancement at attended locations at later processing stages (Luck et al., 1994; Talsma et al., 2007). Furthermore, attentional modulations of the N1 component have been linked to speeded behavioral responses (c.f. Talsma et al., 2007). Analogously, one might expect that in touch attentional modulations of early- or mid-latency components relate to attentional effects on response times. We found that behavioral responses indicated mainly enhancement of processing at attended locations, regardless of CTI, and further, that response times for the different attention conditions were similar across CTIs. In contrast, attentional modulations of sensory processing were present in the time range of the N140 and P200 components, but only for the short CTI. However, comparison of directional and non-directional cue trials suggests that attentional modulations in this mid- to late-latency time range reflect mainly enhancement of processing of stimuli at attended locations, analogous to the behavioral results. Linking behavior and ERPs in a similar fashion, when attention to locations on the body is cued crossmodally (Forster & Eimer, 2005), comparison of directional and non-directional cue trials suggests that both enhancement at the attended and suppression at the unattended location contribute to attentional modulations of response times and the N140 component. Taken together, there is some indication for a link between spatial attentional effects on behavioral responses on mid- to long-latency ERP modulations in touch. However, with longer intervals between cue and imperative stimulus, behavioral and ERP recordings suggest seemingly opposing consequences of shifts of attention to locations on the body. That is, ERP modulations of attention were only present at longer latencies and reflect mainly suppression of information processing at the unattended location, while behavioral responses reflect mainly enhancement of processing of stimuli at the attended location. Thus, further research is needed to clarify the links between early somatosensory processing and behavioral responses.

While most previous studies investigating effects of transient shifts of attention on sensory processing in vision, audition, and touch have employed simple visual or auditory symbolic cues (arrows or tones), studies investigating pure tactile attentional processes have used more complex frequency cues, which may take longer to decode. Therefore, a plausible explanation for any differences found between crossmodally and tactually cued attention to locations on the body may be that it takes longer to decode tactile frequency cues in comparison to symbolic cues in other modalities. If this were the case, we would have expected to find attentional modulations in directional cue trials at later stages in the short (600 ms) compared to the long (1200 ms) CTI, because the longer interval should have allowed for better decoding of the cue. However, attentional modulations on directional cue trials were present earlier for tactile stimuli following short rather than long CTI. That is, attentional modulations for the time range of the N140 and P200 components were present only for the short CTI, while at longer latencies attentional modulations were present for both short and long CTI. This finding therefore clarifies that decoding of tactile cues does not delay effects of attentional selection. Furthermore, our results are in line with a previous study of crossmodally cued tactile attention (Van Velzen, Forster, & Eimer, 2002), which showed that in touch early attentional modulations were abolished with longer time intervals between directional cues and imperative stimuli, suggesting that in touch early spatial-attentional modulations of somatosensory processing are short-lived.

When comparing attentional modulations on directional and non-directional cue trials, we found that attentional modulations on directional cue trials were only present from the time range of the N140 component for short CTI. That is, tactile stimuli presented at the hand that was cued (currently attended) compared to stimuli presented at the other hand (currently unattended) elicited an enhanced negativity starting in the time range of the N140 component. In contrast, on non-directional cue trials, when the cue indicated both hands as possible target location, tactile stimuli elicited an enhanced positivity already in the time range of the P100 component compared to stimuli presented on directional cue trials (at both attended and unattended locations).[1] This modulation of somatosensory processing when both hands were attended was present for both CTIs; however, in the graphs it is mainly visible for short intervals between cue and imperative stimulus presentations (short CTI) and may suggest that in touch attention is initially allocated to all possible target locations. In addition, an enhancement of non-directional compared to directional cue trials was also present at longer latencies (244–374 ms post-stimulus). This suggests that somatosensory processing may be enhanced, albeit at later stages, when attending to multiple compared to a single location on the body with longer time intervals between cues and imperative stimuli. Interestingly, such enhancement of processing on non-directional compared to directional cue trials has, to our knowledge, not been reported previously in similar studies involving other modalities, and may indicate that in touch different mechanisms underlie attentional selection when multiple locations on the body are attended compared to when only one location is attended; that is, attention appears to be fully allocated to both hands leading to modulations, even exceeding those seen on validly cued trials.[2] This may question whether the comparison of non-directional and directional cue trials is appropriate for evaluating the relative contributions of suppression of irrelevant and enhancement of relevant somatosensory information through tactile-spatial attentional selection. However, more research is needed to investigate the mechanisms underlying allocation of attention to multiple locations on the body and their effects on different somatosensory processing stages as indexed by ERP modulations.

In summary, this is the first study to investigate the mechanisms underlying pure tactile attentional selection processes while minimizing any crossmodal influences. We employed a commonly used cueing paradigm to investigate early sensory and behavioral modulations by tactually induced transient shifts of attention to locations on the body. Our findings indicate that the suggested neural basis of attentional modulations differs from

[1]We found a comparable early modulation on non-directional compared to directional cue trials in a pilot study (unpublished data). In that study, we employed bilateral tactile cues simultaneously presented to the middle fingers of both hands while every other aspect was identical to the present study. We initially attributed this early modulation to exogenous effects due to the use of peripheral cues close to the imperative stimulus locations (attracting attention to both hands in neutral cue trials).

[2]Participants were instructed to attend to both hands under neutral cue conditions. However, if they randomly attended to one of the locations, split their attention between them, or attended somewhere else, ERP traces should be somewhere between or identical to ERPs on validly and invalidly cued trials.

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that of previous studies, which have employed comparable paradigms but presented imperative stimuli and/or attentional cues in a different sensory modality. In addition, we also report enhancement of somatosensory processing when both hands were attended (i.e., non-directional cue trials) that preceded (short and long CTIs) or was over and above (long CTI) ERP modulations by stimuli at the currently attended or unattended location when only one hand was attended (i.e., directional cue trials). This latter result may suggest that in touch mechanisms underlying attentional selection differ when attending to multiple locations compared to attending to a single location.

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