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Object-based spatial attention in touch: holding the same object with both hands delays attentional selection

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Abstract

Previous research has shown that attention to a specific location on a uniform visual object spreads throughout the entire object. Here we demonstrate that, similar to the visual system, spatial attention in touch can be object-guided. We measured event-related brain potentials (ERPs) to tactile stimuli arising from objects held by observers' hands, when the hands were placed either near each other or far apart, holding two separate objects, or when they were far apart but holding a common object. Observers covertly oriented their attention to the left, the right or both hands, following bilaterally presented tactile cues indicating likely tactile target location(s). Attentional modulations for tactile stimuli at attended compared to unattended locations were present in the time range of early somatosensory components only when the hands were far apart, but not when they were near. This was found to reflect enhanced somatosensory processing at attended locations rather than suppressed processing at unattended locations. Crucially, holding a common object with both hands delayed attentional selection, similar to when the hands were near. This shows that the proprioceptive distance effect on tactile attentional selection arises when distant event locations can be treated as separate and unconnected sources of tactile stimulation, but not when they form part of the same object. These findings suggest that, similar to visual attention, both space- and object-based attentional mechanisms can operate when we select between tactile events on our body surface.

INTRODUCTION

For vision, it is known that attentional orienting toward locations can be both space- and object-based. Egly, Driver, and Rafal (1994) showed that covert attention can be shifted more rapidly between spatially separate locations when these appear on the same perceptual object than when they appear on different objects (see also Baylis and Driver, 1992; Marino and Scholl, 2005). In other words, space-based attentional costs of responding to visual signals at invalidly cued locations compared to validly cued locations were larger when the target appeared on another object than when it appeared on the same object at an equivalent distance. Egly et al. (1994) suggested that there may be interactions between a space-based system that selectively activates specific locations and an object-based segmentation system that links separate locations on the basis of grouping operations dependent on the current input (see also Humphreys and Riddoch, 1993). It has been proposed by several other researchers that the functional mechanism of this object-based spatial selection is founded on a strengthening of the sensory representation of an entire object because attention spreads throughout the object's boundaries (Vecera and Farah, 1994; Weber, Kramer, and Miller, 1997; Davis, Driver, Pavani, and Shepherd, 2000).

Recently, Martinez, Ramanathan, Foxe, Javitt, and Hillyard (2007) provided electrophysiological evidence that spatial attention directed to one part of a real or illusory object spreads throughout the entire object. Observers were cued to attend to one of four corners of a square, which was either intact or fragmented into four uneven sections (Experiment 1), and either illusory (induced by Kanisza figures) or absent (modified Kanisza figures, Experiment 2). Visual evoked potentials (VEPs) were recorded to brief offsets of either attended or unattended corners. Offsets at attended locations gave rise to enhanced P1 and N1 components of the VEP compared to offsets at unattended locations. Importantly, the space-based attentional effects over N1 (140-180ms post-stimulus onset) were found to be modified by the type of object configuration: attentional effects in this time range were larger when the square was fragmented or absent than when it was an intact perceptual object, whether real or illusory. In other words, these results concur with those of Egly et al. (1994) in demonstrating that the prioritization of processing at one visual event location over another is smaller when these locations can be perceptually grouped. Because grouping effects also occurred for illusory objects, this study confirms that attentional selection can be truly object-based rather than guided by simple stimulus features such as parallel lines, as may have occurred in previous studies (see Avrahami, 1999; Marino and Scholl, 2005).

To the best of our knowledge, no study has so far investigated whether a similar object-based spatial-selection mechanism operates in touch. It is possible that the spatial selection between tactile events may be modulated by the processing of non-spatial stimulus attributes, such as object-related information. Several recent studies have demonstrated that, similar to visual and auditory systems, the somatosensory system extracts information about the identity and the spatial location of tactile stimuli in parallel, functionally specialized pathways (so-called *what* and *where* pathways; De Santis, Spierer, Clarke, and Murray, 2007; Forster and Eimer, 2004; Reed, Klatzky, and Halgren, 2005; Van Boven, Ingeholm, Beauchamp, Bikle, and Ungerleider, 2005), which may interact with one-another in spatial selective attention.

To investigate whether the spread of spatial attention in touch can, like in vision, be modulated by object-based information, the present study utilized the so-called proprioceptive distance effect. Studies of this effect show that attentional selection between tactile events at different locations on the body is affected by their separation in external space, as perceived by proprioceptive feedback ("proprioceptive distance") (Driver and Grossenbacher, 1996; Eimer, Forster, Fieger, and Harbich, 2004; Lakatos and Shepard, 1997; Moscovitch and Behrmann, 1994; Rinker and Craig, 1994; Schicke and Röder, in press; Soto-Faraco, Ronald, and Spence, 2004), analogous to effects of eccentricity on visual spatial attention (e.g. Driver and Baylis, 1991; Eriksen and Eriksen, 1974; Intriligator and Cavanagh, 2001), and related to proprioceptive modulations of auditory attention (Simon-Dack and Teder-Sälejärvi, 2008). For example, Driver and Grossenbacher (1996) demonstrated that response times (RTs) to targets on an attended hand were slower when simultaneously presented distractors on the unattended hand were incongruent, compared to when they were congruent with the target stimulation. Critically, this interference effect was less pronounced when the hands were far apart than when they were close together. Event-related potential (ERP) studies have confirmed that proprioceptive distance affects early somatosensory processing. Eimer et al. (2004) cued observers to direct attention to the left or right hand for a tactile discrimination task, and found that tactile stimuli at attended compared to unattended locations resulted in modulations of both the somatosensory N140 component and the subsequent negative difference (Nd) at longer latencies (200-300ms). In the time range of the N140 component, effects of attention were more pronounced when the hands were far apart than when they were close together. These findings show that tactile spatial attention to the relevant hand operates more effectively when the distance of a distracting stimulus is increased in external space, even though the somatotopic location of the distractor (irrelevant hand) remained unchanged, suggesting that tactile spatial selectivity operates in a spatial frame of reference that is based primarily on external (proprioceptive), rather than somatotopic, coordinates (see Azañón & Soto-Faraco, 2008, for a recent discussion on the deployment of both somatotopic and external reference frames in touch).

In this present study, we compared the temporal dynamics of attentional selection for proprioceptively distant tactile events that arise from the same object (a bar held jointly by both hands) to events that arise from unconnected objects, which were either separated by the same distance or placed near each other. Tactile stimulators were embedded in two horizontal wooden bars, which observers held with their hands. The bars, and observers' hands, were positioned either near each other (Near condition) or far apart (Far condition), or they were positioned far apart but solidly linked to each other via a connecting bar that could be attached between them (Object condition). Tactile stimuli were preceded by tactile directional cues indicating the to-be-attended hand or directionally neutral cues instructing observers to attend to both hands. To assess the effects of covert spatial attention on somatosensory processing, we analyzed somatosensory event-related potentials (ERPs) in response to tactile stimuli when preceded by valid (indicating the hand that receives the tactile stimulus), invalid (indicating the opposite hand) and neutral (indicating both hands as possible stimulus locations) cues. Directionally neutral cues were included in order to investigate whether tactile attentional selection, and its modulation by proprioceptive distance and object conditions, primarily reflect enhancement of processing at attended locations, or suppression of processing at unattended locations. Similar to other studies of visual (e.g. Luck, Hillyard, Mouloua, Woldorff, Clark, and Hawkins, 1994), auditory (Schröger and Eimer, 1997) and tactile (Forster and Eimer, 2005) attention, attentional enhancement was defined as a difference between ERPs to validly and neutrally cued stimuli in the same direction as that of the general attentional effect (ERPs to validly vs. invalidly cued stimuli), and attentional suppression was defined as a difference between ERPs to invalidly and neutrally cued stimuli in the opposite direction as that of the general attentional effect.

As our aim was to investigate space- and object-based tactile attentional selection in the absence of any visuospatial information, we covered the hands and bars from view. In order to manipulate observers' assumption of tactile events arising from common or separate objects, we included trials during which observers were cued to lift the bars off the tabletop a few times throughout each block. The lifting of the two bars when not connected (Near and Far conditions) would provide sensory feedback of two separate unimanual actions, while the lifting of the bars when connected to form a solid object (Object condition) would result in analogous sensory feedback from both hands, which was expected to reinforce the assumption that tactile event locations were unconnected, or arose from a common object, respectively.

We expected to find an effect of proprioceptive distance on tactile attentional selection similar to Eimer et al. (2004). That is, effects of tactile attention (ERPs to validly vs. invalidly cued stimuli) were expected to be larger, or arise earlier, in the Far than in the Near condition, based on the assumption that the gain control over the flow of information exerted by spatial attention (e.g. Mangun & Hillyard, 1995) is greater when the selected location (in our case, the hand) is more spatially separated from a distractor location (the other hand). We further hypothesized that, if tactile spatial attention is object-guided like visual spatial attention (Egly et al., 1994, Martinez et al., 2007), attention should spread throughout the object. That is, effects of attentional selection between the hands should be smaller, or arise later, when the hands are touching a common object (Object condition) than when they are separated by an equivalent distance but are touching two separate objects (Far condition). If, unlike in vision, attentional selection in touch is not object-guided, and proprioceptive distance alone determines the extent to which processing at one tactile event location can be prioritized over those at another, there should be no difference between Far and Object conditions.

METHODS

Participants

Sixteen paid volunteers participated in the experiment. Four participants were excluded due to poor eye fixation control (see below), so that twelve participants (eight males, aged 20-37 years, mean 26.5 years) remained in the sample. All participants were right-handed and had normal or corrected-to-normal vision by self-report.

Stimuli and Apparatus

Participants sat in a dimly lit experimental chamber, fixating on a small green LED about 65 cm in front of the body midline. A tabletop microphone was placed in front of them to record vocal response latencies. A video camera monitored participants throughout the experimental session. Participants were holding on to bars with their left and right hands, and with their left and right index and middle fingers placed onto tactile stimulators which were embedded in the bars. The bars were constructed so that they were about 6cm above the tabletop, affording a grip-like hand position (see Fig. 1). In different conditions, the bars, and therefore the hands, were either placed close together (Near condition), far apart (Far condition), or far apart but solidly connected to one another through an additional bar between them (Object condition)[1]. In the Near condition, the bars were placed so that the left and right index fingers were 6 cm apart. In the Far and in the Object condition, left and right index fingers were 56 cm apart. The bars were held at a distance of about 30 to 45 cm from the body, depending on what distance felt comfortable for each participant while maintaining their grip. The bars and participants' hands were covered from view by a black wooden board, which was placed about 30 cm above the tabletop.

Figure 1 about here

Tactile stimuli were presented using four 12-volt solenoids, driving a metal rod with a blunt conical tip to the fingertips of the left and right index and middle fingers, making contact with the finger whenever a current was passed through the solenoid. 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 to the left and the right middle finger simultaneously, and consisted of simple taps or vibrations. Vibrations, generated by presenting a sequence of rapidly delivered brief pulses, were used as directional cues, indicating the left or right hand as the likely target location. One of the two target locations was associated with a 'flutter' vibration, and the other with a 'continuous' vibration. For 'flutter' vibrations, the stimulus onset asynchrony (SOA) between

[1] To ensure that tactile stimulation at one end of the bar did not travel along the object and contaminate ERPs to stimuli at the other end, we recorded EEG during the presentation of stimuli at the side held by one hand, at the other side (not held), and when no stimuli were presented, and found that no somatosensory ERPs were evoked from stimulation at the other side of the object, similar to when no stimuli were presented.

successive 6 ms pulses was 54 ms, corresponding to a rectangular stimulation frequency of about 16.7 Hz. For 'continuous' vibrations, the SOA between successive 2 ms pulses was 18 ms, corresponding to a frequency of 50 Hz. Simple taps, where the rod of the solenoid contacted both middle fingers continuously for 300 ms, were used as directionally neutral cues (indicating both target locations). 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 simple taps, 'flutter' vibrations, and 'continuous' vibrations alike. There was a fourth type of cue, indicating that participants should briefly lift up the bars, which consisted of a 'flutter' vibration at all four fingers. Left and right middle fingers were contacted for 30 ms, followed by a 30 ms contact of both left and right index fingers, repeated 5 times, such that the total duration of the Lift bar(s) cue was 300 ms. 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 twelve blocks, each consisting of 144 trials (see Table 1 for trial types and their frequency). Four blocks of each condition (Near, Far, Object) were presented successively, with the order counterbalanced across participants. Each trial started with a 302 ms presentation of the directional or non-directional tactile cue, or a 300ms presentation of the Lift bar(s) cue. 1000 ms after cue offset, a tactile target or non-target stimulus was presented to the left or right index finger. Lift bar(s) cues were never followed by a tactile stimulus, but by a 2000 ms pause before the onset of the next cue. Otherwise, the inter-trial interval was 1000 ms. Participants were instructed to keep their eyes open and to fixate their gaze straight ahead on the green LED, to respond vocally (“pa”) whenever a target stimulus (a double tap) was detected at the attended location, and to ignore all tactile non-target stimuli (single taps) as well as target stimuli at the unattended location. Tactile cues indicated the most likely location for a target to occur. For six participants, a ‘flutter’ vibration was associated with the left hand and a ‘continuous’ vibration was associated with the right hand, and for the other six participants, cues and target locations were associated in the reverse manner. Neutral cues (simple taps) were associated with both target locations for all participants. Since participants responded to targets at attended locations only on validly and neutrally cued trials, behavioral performance was not analyzed further.

Table 1 about here

EEG Recording

EEG was recorded with Ag-AgCl electrodes and online linked-earlobe reference 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). Horizontal EOG was recorded bipolarly from the outer canthi of both eyes. To encourage participants to lift the bars quickly, and to enable monitoring their performance during Lift bar(s) trials, additional electrodes were placed on the deltoid muscles of the left and right arms, although muscle EMG was recorded from the right arm only. 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. Amplifier band-pass was 0.01 – 100 Hz, and digitisation rate was 500 Hz. EEG was filtered off-line with a digital low pass filter of 40 Hz. EEG and HEOG were epoched in separate offline analysis and were extracted for a period from 100 ms before to 400 ms after the onset of the tactile stimulus. To check for eye movements in the interval between cue and tactile stimulus onsets, epochs were also extracted for the 1000 ms period between the onset of the cue and the onset of the tactile stimuli. Averaged HEOG waveforms obtained in this interval were scored for systematic deviations of eye position, indicating a tendency to move the eyes towards the cued side. Four participants were disqualified due to residual HEOG deflections exceeding ±4 μV in the cue-tactile stimulus interval. Analyses were only conducted for ERPs obtained in response to tactile non-target stimuli. Trials with horizontal eye movements (HEOG exceeding ± 40 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 100 ms before cue onset and ending 400 ms after the onset of the non-target stimulus, were excluded from analysis.

ERP Analysis

ERPs to tactile non-targets were averaged relative to a 100 ms pre-stimulus baseline for all combinations of cue type (valid vs. invalid vs. neutral), stimulated hand (left vs. right), and hand condition (Near vs. Far vs. Object). ERP mean amplitudes were computed within successive measurement windows centred on the latencies of early somatosensory ERP components P100 and N140 (96-150 ms post-stimulus). To investigate longer-latency effects of attention, mean amplitudes were also computed between 170 ms and 300 ms post-stimulus. For each of these two time windows, statistical analyses of ERP mean amplitudes were conducted initially to compare the effect of hand condition (Near vs. Far vs. Object) on overall effects of attention (validly vs. invalidly cued trials)[2]. These analyses were conducted separately for lateral recording sites F3/4, F7/8, FC1/2, FC5/6, C3/4, CP1/2, CP5/6, P3/4, P7/8, and O1/2, and for midline electrodes Fz, FCz, Cz, and Pz. Lateral recording sites were grouped into four quadrants of five electrodes each, as defined by lateral and anteroposterior axes (anterior-ipsilateral: F3/4i, F7/8i, FC1/2i, FC5/6i, C3/4i; anterior-contralateral: F3/4c, F7/8c, FC1/2c, FC5/6c, C3/4c; posterior-ipsilateral: CP1/2i, CP5/6i, P3/4i, P7/8i, O1/2i; posterior-contralateral: CP1/2c, CP5/6c, P3/4c, P7/8c, O1/2c). For lateral recording sites, repeated measures ANOVAs were conducted for the within-subject factors cue type (valid vs. invalid), hand condition (Near vs. Far vs. Object), laterality (contralateral vs. ipsilateral electrode sites), anterior-posterior location (anterior vs. posterior electrode sites) and electrode site (see above). For recording sites along the midline, repeated measures ANOVAs were conducted for the within-subject factors cue type (valid vs. invalid), hand condition (Near vs. Far vs. Object) and electrode (Fz vs. FCz vs. Cz vs. Pz). Follow-up analyses were conducted for each combination of the three hand conditions (Near vs. Far, Far vs. Object, and Near vs. Object) in each time window and for the subsets of electrodes where overall effects of hand condition on attention were found. In these analyses, further follow-up analyses were conducted to identify effects of attention in each of the three hand

[2] We also analyzed earlier components P45 (30-60ms) and N80 (60-90ms), but these analyses are not reported since there were no effects of or interactions with attention for lateral or midline electrodes (all: $F(1,11) \leq 2.2$, $p \geq .136$), except the following. Over P45, there was a very marginal interaction between attention, hand condition and laterality ($F(1,11)=2.7$, $p=.095$), but pairwise comparisons showed no attentional effects at any levels of hand condition and laterality ($p \geq .208$). Over N80, there was an interaction between attention, laterality and anterior-posterior location ($F(1,11)=7.4$, $p=.020$), but pairwise comparisons showed no attentional effects at any levels of laterality and anterior-posterior location ($p \geq .125$).

conditions separately, for each time window and for the subsets of electrodes where effects of hand condition on attention were found. To test whether attentional effects were based on enhancement or suppression of processing at attended or unattended locations, respectively, separate analyses were conducted comparing conditions of cue type (valid vs. neutral, and neutral vs. invalid) for each hand condition, time window, and for the subsets of electrodes where overall effects of attention were found. When appropriate, Greenhouse-Geisser adjustments to the degrees of freedom were applied.

RESULTS

Figure 2 shows somatosensory ERPs in response to tactile non-target stimuli at a subset of electrodes ipsilateral and contralateral to the stimulated hand, as well as at midline electrode Cz. ERPs are presented separately for stimuli at validly (black lines), invalidly (light grey lines) and at neutrally cued locations (dark grey lines), when the hands were positioned near (Figure 2A), far (Figure 2B), and far but connected through an object (Figure 2C). Figure 3 shows ERPs to stimuli at validly and invalidly cued locations for one representative electrode over somatosensory cortex contralateral to the stimulated hand (C3/4c, panel A), and voltage difference maps (activations in response to validly cued vs. invalidly cued stimuli) for the time range in which attentional effects differed between hand conditions (panel B). ERPs and voltage difference maps are shown for each of the three hand conditions (Near: top panel, Far: middle panel, Object: bottom panel).

Figure 2(A,B,C) about here

In the *Near* condition (Fig. 2A, Fig. 3 top panel), modulations of attention were only present at later processing stages, in the time range following the N140 component, where they appeared as an Nd between tactile stimuli at validly and invalidly cued locations. In the *Far* condition (Fig. 2B, Fig. 3 middle panel), attentional modulations were present much earlier. ERPs in response to tactile stimuli at validly cued locations showed an enhanced positivity compared to stimulation at invalidly cued locations, which started in the time range of the P100 component and extended into the time range of the N140 component. These attentional modulations appeared to be far more prominent over anterior than over posterior electrode sites. Similar to the Near condition, there was also an Nd effect of attention. In contrast to the early somatosensory modulations present in the Far condition, when the hands were far apart but connected by an *Object* (Fig. 2C, Fig. 3 bottom panel), effects of attention appeared to be only present as an Nd effect, but not at earlier stages.

These informal observations were tested with an overall ANOVA investigating effects of hand condition (Near vs. Far vs. Object) on attention (valid vs. invalid) in the early and the late time window.

Figure 3 about here

Effects of hand condition on early attentional selection. For the time window of the earlier components (96-150 ms), effects of attention differed as a function of hand condition specifically over anterior electrodes for lateral electrode sites (hand condition * cue type * anterior-posterior location: $F(1,11)=3.8$, $p=.040$; hand condition * cue type * anterior-posterior location * electrode site: $F(1,11)=3.3$, $p=.016$), as well as for midline sites (hand condition * cue type * electrode site:

F(1,11)=4.6, p=.013). For lateral electrode sites, there were no effects of laterality (hand condition * cue type * laterality: F(1,11)<1, p=.975; hand condition * cue type * anterior-posterior location * laterality: F(1,11)<1, p=.618). Simple effects analyses revealed that there were significant effects of attention in the Far condition over lateral anterior (p=.007), but not over posterior sites (p=.317), and not over either lateral anterior or posterior sites in both Near or Object conditions (p≥.394). Effects of attention in the Far condition were present for all lateral anterior electrodes (p≤.029) as well as for anterior midline electrodes Fz, FCz and Cz (p≤.038), and marginal or absent for lateral posterior electrodes (p≥.075) as well as for posterior midline electrode Pz (p=.431). In both Near and Object conditions, effects of attention were absent for all lateral (p≥.190) and midline (p≥.318) electrodes.

Therefore, we separately compared the effects of hand condition on attentional selection for lateral anterior electrode sites and anterior midline sites Fz, FCz and Cz for each combination of the three hand conditions (Near vs. Far, Far vs. Object, and Near vs. Object). Effects of attention were larger in the Far compared to the Near condition (hand condition * cue type: all F(1,11)≥5.7, p≤.036 for lateral and midline electrode sites), irrespective of laterality (hand condition * cue type * laterality: F(1,11)<1, p=.687 for lateral electrode sites). Effects of attention were marginally larger in the Far compared to the Object condition for lateral electrode sites (hand condition * cue type: F(1,11)=4.1, p=.067), irrespective of laterality (hand condition * cue type * laterality: F(1,11)<1, p=.669 for lateral electrode sites). For midline sites, effects of attention were larger in the Far compared to the Object condition as a function of electrode sites (hand condition * cue type * electrode site: F(1,11)=5.7, p=.029). Separate analyses for each electrode site showed that effects of attention were larger in the Far compared to the Object condition for electrode Fz (hand condition * cue type: $F(1,11)=8.1$, $p=.016$), but not for electrodes FCz or Cz (hand condition * cue type: $F(1,11)<2.6$, $p\geq.136$). Importantly, effects of attention did not differ between Near and Object conditions (hand condition * cue type: $F(1,11)<1$, $p\geq.591$ for lateral and midline electrode sites), irrespective of laterality (hand condition * cue type * laterality: $F(1,11)<1$, $p=.952$ for lateral electrode sites).

For the same set of electrodes, analyses of attentional effects were also conducted for each of the three hand conditions separately. For the Far condition, effects of attention (cue type: all $F(1,11)\geq10.9$, $p\leq.007$ for lateral and midline electrodes) differed as a function of electrode site for lateral electrodes (cue type * electrode site: $F(1,11)=3.9$, $p=.036$), irrespective of laterality (cue type * laterality * electrode site: $F(1,11)=1.6$, $p=.212$), and differed marginally as a function of electrode site for midline electrodes (cue type * electrode site: $F(1,11)=4.4$, $p=.053$). Separate analyses for each electrode site showed that effects of attention were present for all lateral electrodes (cue type: all $F(1,11)\geq6.3$, $p\leq.029$), as well as for all midline electrodes (cue type: all $F(1,11)\geq5.6$, $p\leq.038$), but they were largest over frontal electrodes F3/4 and Fz (cue type: all $F(1,11)\geq14.4$, $p\leq.003$), followed by frontocentral electrodes FC1/2 and FCz (cue type: all $F(1,11)\geq10.5$, $p\leq.008$), and were smallest for central electrodes C3/4 and Cz (cue type: all $F(1,11)\geq14.4$, $p\leq.038$) and the more temporally situated frontal and frontocentral electrodes F7/8 and FC5/6 (cue type: all $F(1,11)\geq14.4$, $p\leq.029$).

For the Near condition, there were no effects of attention (cue type: all $F(1,11)<1$, $p\geq.831$ for lateral and midline electrodes), independently of electrode site (cue type * electrode site: all $F(1,11)<1$, $p\geq.663$ for lateral and midline electrodes). For lateral electrode sites, there was a marginally significant interaction between attention and laterality (cue type * laterality: $F(1,11)=4.1$, $p=.067$), but simple effects indicated that there were no effects of attention at either ipsi- or contralateral sites ($p \geq .625$).

For the Object condition, there were also no effects of attention (cue type: all $F(1,11)<1$, $p \geq .394$ for lateral and midline electrodes), independently of electrode site cue type * electrode site: all $F(1,11) \leq 1.7$, $p \geq .214$ for lateral and midline electrodes) or laterality (cue type * laterality: $F(1,11)=2.1$, $p=.179$ for lateral electrode sites).

Effects of hand condition on late attentional selection. For the time window of the Nd (170-300 ms), effects of attention (cue type: all $F(1,11) \geq 23.3$, $p \leq .001$ for lateral and midline electrode sites) did not differ as a function of hand condition (hand condition * cue type: all $F(1,11)<1$, $p \geq .540$ for lateral and midline electrode sites). Attentional effects were larger for ipsilateral than contralateral electrode sites (cue type * laterality: $F(1,11)=7.9$, $p=.017$; cue type * laterality * electrode site: $F(1,11)=6.8$, $p=.009$), especially over anterior electrode sites (cue type * laterality * anterior-posterior location: $F(1,11)=38.7$, $p<.001$; cue type * laterality * anterior-posterior location * electrode site: $F(1,11)=13.5$, $p<.001$). Attentional effects also differed as a function of electrode for midline sites (cue type * electrode: $F(1,11)=5.9$, $p=.024$). Simple effects analyses indicated that, across all hand conditions, attentional effects were marginal for anterior contralateral electrode F7/8c ($p=.051$) but otherwise present for all electrodes in all lateral quadrants ($p \leq .008$), as well as for all midline electrodes ($p \leq .005$), but they were largest over frontal electrodes F3/4i and Fz, frontocentral electrodes FC1/2i, FC1/2c and FCz, central electrodes C3/4i and Cz, and centroparietal electrodes CP1/2i and CP1/2c (all $p \leq .005$).

Effects of attentional enhancement and suppression. In this study, we also included trials where attention was cued to both hands, and compared somatosensory ERPs evoked by stimuli in these trials (neutrally cued stimuli) with those evoked in trials where only one hand was selectively attended in order to assess the relative contributions of attentional enhancement (validly vs. neutrally cued stimuli) and suppression (invalidly vs. neutrally cued stimuli) to overall attentional effects (validly vs. invalidly cued stimuli). Somatosensory ERPs in response to tactile non-target stimuli at validly, invalidly, and neutrally cued locations are shown in Figure 2 separately for the three hand conditions. The earliest attentional modulations were evident for the time range of the P100 and N140 components in the Far condition (Figure 2B). These early modulations appeared to reflect attentional enhancement rather than suppression, that is, ERPs in response to stimuli at validly cued locations differed, not only from those to stimuli at invalidly cued locations, but also from those at neutrally cued locations over most electrode sites, while ERPs to neutrally and invalidly cued stimuli did not differ. In addition to these early modulations, attentional modulations were also present as Nd effects in all three hand conditions. In contrast to earlier attentional modulations, Nd effects on somatosensory processing appeared to reflect primarily attentional suppression, that is, ERPs to stimuli at invalidly cued locations differed, not only from those to stimuli at validly cued locations, but also from those at neutrally cued locations, while ERPs to validly and neutrally cued stimuli did not differ.

To formally test these observations, ANOVAs were carried out for anterior lateral and midline electrode sites for the time window of earlier attentional effects in the Far condition, and for all electrode sites for the time window of the Nd for all three hand conditions. The contribution of *attentional enhancement* to earlier attentional effects were shown by differences between waveforms to validly and neutrally cued stimuli (cue type: all $F(1,11) \geq 8.5$, $p \leq .014$ for lateral and midline electrode sites) in the absence of differences between waveforms to neutrally and invalidly cued stimuli (cue type: all $F(1,11)<1$, $p \geq .703$ for lateral and midline electrode sites). Similar to the overall attentional effect (validly vs. invalidly cued stimuli), attentional enhancement for validly compared to neutrally cued stimuli was present irrespective of laterality (cue type * laterality: $F(1,11)=1.5$, $p=.243$ for lateral electrode sites). Enhancement did not differ across electrode site (cue type * electrode site: all $F(1,11) \leq 2.6$, $p \geq .128$ for lateral and midline electrode sites).

For the Nd, effects of *attentional suppression* were shown by differences between waveforms to neutrally and invalidly cued stimuli (cue type: all $F(1,11) \geq 29.0$, $p<.001$ for lateral and midline electrode sites) in the absence of differences between waveforms to validly and neutrally cued stimuli (cue type: all $F(1,11) \leq 1.3$, $p \geq .273$ for lateral and midline electrode sites). Similar to the overall attentional effect (validly vs. invalidly cued stimuli), attentional suppression for invalidly compared to neutrally cued stimuli was larger for ipsilateral than contralateral electrode sites specifically over anterior electrode sites (cue type * laterality * anterior-posterior location: $F(1,11)=5.4$, $p=.040$), although it was not larger for ipsilateral sites overall (cue type * laterality: $F(1,11)=1.5$, $p=.248$). Attentional suppression also differed as a function of electrode (cue type * electrode: all $F(1,11) \geq 4.9$, $p \leq .031$ for lateral and midline sites). Although suppression was present for all lateral and midline electrodes ($p \leq .003$), it was largest for frontocentral electrodes FC1/2i, FC1/2c and FCz, central electrodes C3/4i, C3/4c and Cz, and centroparietal electrodes CP1/2i and CP1/2c (all $p<.001$).

DISCUSSION

To investigate whether tactile spatial attention can be object based, analogous to visual spatial attention (Egly et al., 1994; Martinez et al., 2007), we recorded ERP correlates of the proprioceptive distance effect on tactile spatial attention (Driver and Grossenbacher, 1996; Eimer et al., 2004; Soto-Faraco et al., 2004), and tested whether spatial attentional selection between proprioceptively distant hands is attenuated, or arises later, when the hands are connected by a jointly held object. Based on Eimer et al.'s (2004) study, which showed that ERP correlates of tactile spatial attention are modulated by the proprioceptive distance of the site of tactile stimulation (hands), we devised a task in which participants were holding either one or two objects while their hands were positioned either near or far apart. We compared attentional selection for tactile events on the hands in three different conditions: when tactile stimulation arose from two separate objects that observers held in their hands, when the hands were placed either near together or far apart, and when tactile stimulation arose from a common object held by both hands that were placed far apart. We induced the perception of whether or not tactile event locations were separate or connected by occasionally cueing observers to lift the object(s) they were holding as part of each experimental block. In order to investigate tactile attentional selection in the absence of any engagement of visuospatial orienting mechanisms we cued observers' attention tactually, rather than visually as done in most previous studies of tactile spatial attention. In addition, we included directionally neutral cues in order to explore the relative contributions of enhancement at attended locations and suppression at unattended locations to effects of tactile attentional selection.

Previous studies have shown that the representation of hand positions in external space profoundly affects tactile attentional selection (Driver and

Grossenbacher, 1996; Soto-Faraco et al., 2004). In line with equivalent effects on early somatosensory processing (Eimer et al., 2004), the present study shows that proprioceptive information about hand location modulates the mechanisms underlying tactile spatial attention. For this modulation to occur, integration between tactile and proprioceptive information must have taken place prior to the operation of attentional selection. We found that effects of attentional selection arose earlier (96-150 ms post-stimulus) when the hands were placed far apart than when they were near each other (170-300 ms post-stimulus). These earlier attentional effects were present over anterior electrodes as an enhanced positivity for attended compared to unattended stimuli. Interestingly, effects of attentional selection were also delayed (170-300 ms post-stimulus) when hands were placed far apart, but were holding the same object. In fact, evoked responses in the Object condition did not differ from those observed when the hands were placed near each other. These findings show for the first time that object-based information about tactile events on the hands affects the temporal dynamics of tactile attentional selection, suggesting that tactile spatial attention, analogous to visual attention, can be both space- and object-based.

Our findings also show that early effects (96-150 ms post-stimulus) of proprioceptive distance on attentional selection (Far condition) consist primarily of an enhancement of processing for stimuli at the attended hand, rather than of a suppression of processing at the unattended hand. At later processing stages, attentional selection was unaffected by the distance between the hands or whether they were holding an object; all three hand conditions showed a similar Nd between tactile stimuli at attended and unattended locations. Attentional effects in the time range of the Nd were found to consist primarily of a suppression of processing for tactile stimuli at invalidly cued locations, compared to those at validly or neutrally cued locations, which is in line with previous findings (Forster and Eimer, 2005). In addition, our results suggest that early enhancement of tactile processing at attended locations is only present when tactile stimulus locations originate from separate sources that are sufficiently distant in external space. These findings are in contrast to Driver and Grossenbacher's (1996) suggestion that the more effective attentional selection between proprioceptively distant hands is due to better suppression of events at the unattended, distractor hand, rather than enhancement of events at the attended, target hand. However, in their study participants where presented with tactile stimuli presented simultaneously to both hands. It is conceivable that mechanisms underlying tactile spatial selection may differ with stimulus presentation and task demands. Similar to Forster and Eimer (2005), we have found that attentional enhancement, if present, arises at earlier stages than suppression, which is in contrast to similar studies of visual (Luck et al., 1994) and auditory attention (Schröger and Eimer, 1997), where suppression typically precedes enhancement, and suggests that the component stages of attentional mechanisms in somatosensation differ from those in other modalities. In contrast to our results, however, Forster and Eimer (2005) found that attentional suppression accompanied enhancement at early stages of *visually* cued tactile selection. This difference between the two studies suggests that mechanisms of tactile spatial attention may also be affected by cueing modality.

The most important novel finding of this study is that the proprioceptive distance effect on early tactile attentional selection disappeared when the two hands were separated in external space but connected through a jointly held object. In this condition, effects of attentional selection did not arise until later stages of processing, similar to when the hands were placed near each other. The present findings mirror analogous findings made for visual spatial attention, and show for the first time that tactile attention can be both space- and object-based. Behavioral (e.g. Egly et al., 1994) and electrophysiological (e.g. Martinez et al., 2007) studies have shown that visual spatial attention spreads along object boundaries: effects of attentional selection between two equidistant locations are smaller when these locations form part of the same perceptual object than when they do not. Similarly, the present study demonstrates that effects of attentional selection between the hands are delayed when the hands are connected by a jointly held object than when they are separated by the same distance but hold two unconnected objects. This suggests that, at these stages, no location along a jointly held object receives prioritized processing because, like visual attention, tactile attention spreads along object boundaries. In addition to a space-based selection system that activates specific tactile event locations over others, the tactile modality may have an object-based system that links or segments tactile event locations on the basis of grouping operations that can or cannot be performed on the current input. Previous studies have shown that non-spatial attributes of tactile stimuli (e.g. frequency) are selected in parallel with spatial attributes in functionally segregated pathways (De Santis et al., 2007; Forster and Eimer, 2004; Reed et al., 2005; Van Boven et al., 2005). Our results extend these findings by showing that object-related information can modulate the spatial processing of tactile events, suggesting that specialized somatosensory *what* and *where* pathways may interact at early stages of spatial processing. Our findings also suggest that tactile and visual attentional systems may operate in similar ways. Just as the spread of spatial attention throughout an entire visual object may be useful for object perception, and indeed occurs at the level of regions implicated in object encoding (see Martinez et al., 2007), the absence of prioritized processing for locations along an object held by the two hands might be useful for purposes such as the bimanual handling of objects.

In line with previous studies we have shown that tactile attentional selection is modulated by the proprioceptive distance between stimulus locations (Driver and Grossenbacher, 1996; Eimer et al., 2004). In addition, our findings suggest that larger, or earlier, effects of tactile attentional selection with greater separation between the hands are driven by the system's assumption that proprioceptively distant event locations can be represented as unconnected sources of information. The proprioceptive distance effect on tactile attentional selection necessitates that proprioceptive information about current limb position is integrated with tactile processing prior to the operations of tactile spatial attention mechanisms. If tactile attentional selection is object-based, prior knowledge about whether or not tactile event locations arise from the same or different objects must be integrated with tactile processing in a similar manner.

Recently, Helbig and Ernst (2007) showed that prior knowledge about two events arising from a common source can affect how these events are treated by the perceptual system. Observers judged the shape of objects they simultaneously touched and viewed either when they had direct vision of their hand (co-located visual and haptic information) or when vision of their hand was provided via a mirror (creating a spatial separation between visual and haptic information). Typically, with greater spatial separations between the sources of visual and haptic information, their beneficial effect on one another gradually declines (Gepshtein, Burge, Ernst, and Banks, 2005), but integration did not differ between viewing conditions in Helbig and Ernst's study. This suggests that when observers have prior knowledge about object identity, that is, when they believe that vision and touch provide redundant information about the same object, information from both modalities is integrated, overcoming even substantial spatial separations between them. Helbig and Ernst (2007) proposed that the system must first decide whether information from different sources (different sensory modalities) pertain to the same object or event. If so, perceptual integration, which does not typically occur for spatially separate multimodal events, can take place in the same way as it would for co-located events. In line with this, we suggest that prior knowledge modulated the integration of proprioceptive information with tactile input in our study. Because tactile event locations could be treated as arising from a common source of stimulation in our Object condition, but as arising from separate sources in our Far condition, the proprioceptive or spatial distance between them was reflected in attentional modulations of early somatosensory processing stages only in the Far condition.

Our findings suggest that when the hands were proprioceptively distant but connected by a common object, attentional selection operated as if the hands were near, at least at early stages of processing. The question that arises from these findings is whether object-based effects occur despite proprioceptive distance, such that distance information is essentially preserved, or whether the nature of the proprioceptive information is fundamentally changed through the assumption that tactile events on both hands have a common source. That is, object-based effects may lead to a representation of the hands as ‘near’, or as ‘connected’, thereby essentially changing the current body schema with respect to the functional relationship between the hands. Future studies should address the question of how the functional relationship between the hands is affected, for example by investigating the consequences of object-guided selection for the preparation of hand movements.

Acknowledgments

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Figure captions

Figure 1. Experimental setup showing the bars participants held with their left and right hands in the Far condition. Dotted lines indicate the outline of the connecting bar used in the Object condition. The inset shows the location of the tactile stimulators used to present tactile cues (middle fingers), targets and non-targets (index fingers).

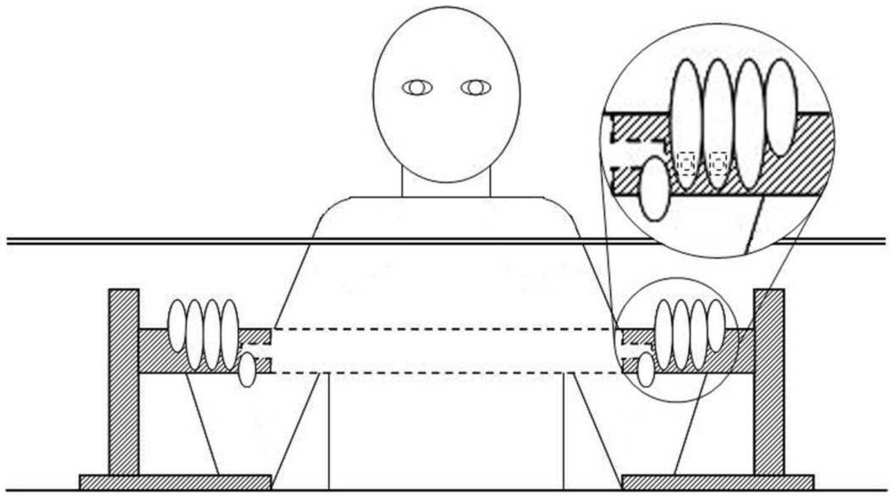
Figure 2. Grand-averaged somatosensory ERPs elicited at a subset of sites ipsilateral (i) and contralateral (c) to the stimulated hand and at midline electrode Cz by tactile non-target stimuli at validly cued locations (black lines), at invalidly cued locations (grey lines) and at neutrally cued locations (dashed lines) in the 400 ms interval following stimulus onset. A: Near. B: Far. C: Object.

Figure 3. A: Enlarged image of ERPs elicited at one representative electrode (C3/4c) by tactile stimuli at validly cued (black lines) and invalidly cued (grey lines) locations. The shaded area indicates the 96-150 ms time range. B: Voltage difference maps (activations elicited by validly cued vs. invalidly cued stimuli) for the 96-150 ms time range in which attentional effects differed between hand conditions. Black contour lines indicate levels of negative difference, white contour lines indicate levels of positive difference. Black x indicates the location of C3/4c. Top: Near. Middle: Far. Bottom: Object.

Table 1. Trial types defined by conditions of cueing and target/non-target presentation for one block of 144 trials. Left and Right refer to left hand and right hand, respectively.

Cue type (number per block)	*Target / Non-target (number per block)*
Directional	
Left (47)	Left (12), Right (3) / Left (16), Right (16)
Right (47)	Left (3), Right (12) / Left (16), Right (16)
Non-directional (neutral)	
Left and Right (44-48)*	Left (6-8)*, Right (6-8)* / Left (16), Right (16)
Lift bar(s) (2-6)*	-

* In all blocks, a total of 138 directional and neutral cueing trials were presented. An additional six trials were drawn from a pool of Lift bar(s) and neutral cue trials, such that at least two, but never more than six, Lift bar(s) trials were selected per block in order to vary the number of such trials across blocks. The remainder (0-4 trials) were trials in which neutral cues were followed by left (0-2) or right (0-2) targets.



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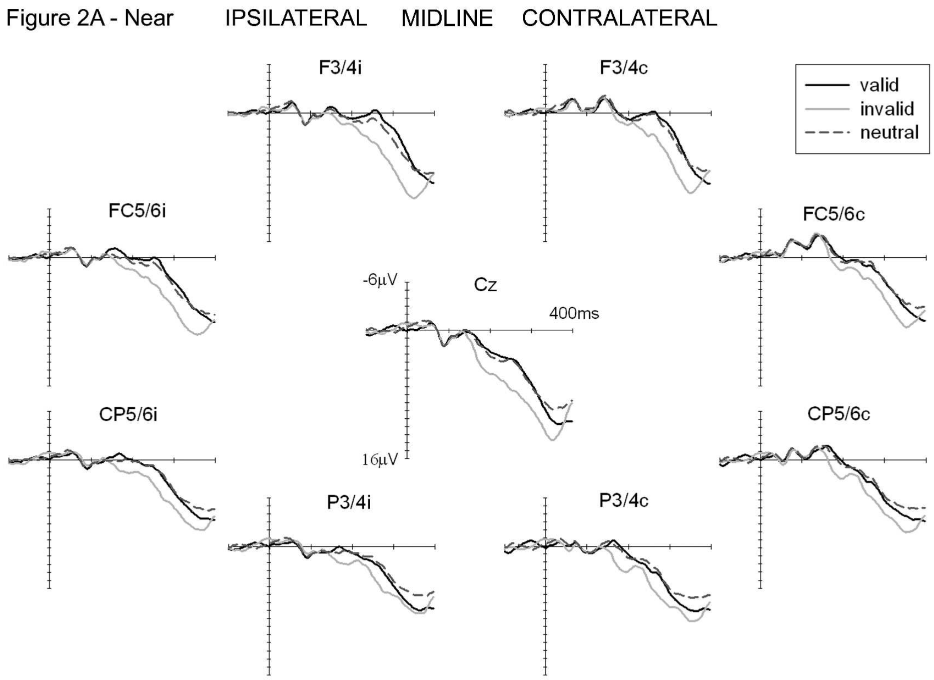

Figure 2. Grand-averaged somatosensory ERPs elicited at a subset of sites ipsilateral (i) and contralateral (c) to the stimulated hand and at midline electrode Cz by tactile non-target stimuli at validly cued locations (black lines), at invalidly cued locations (grey lines) and at neutrally cued locations (dashed lines) in the 400 ms interval following stimulus onset. A: Near. B: Far. C: Object.
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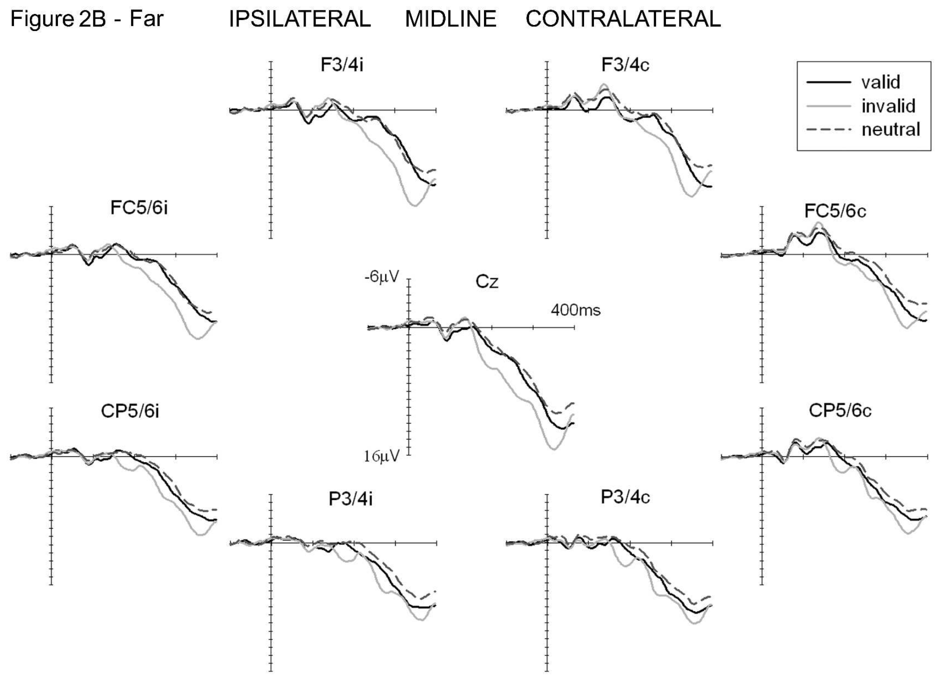

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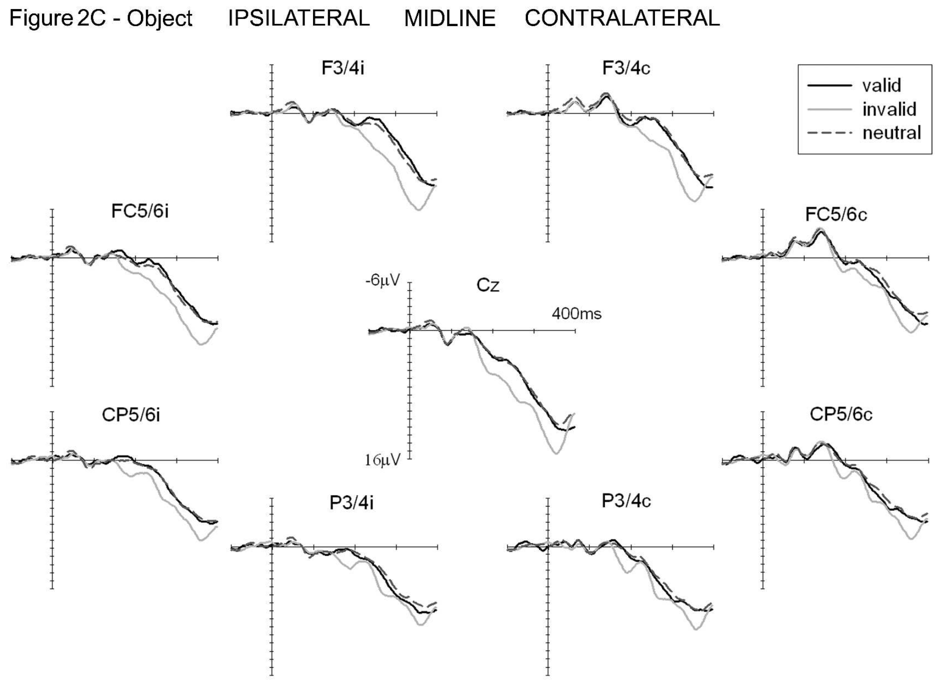
277x200mm (500 x 500 DPI)



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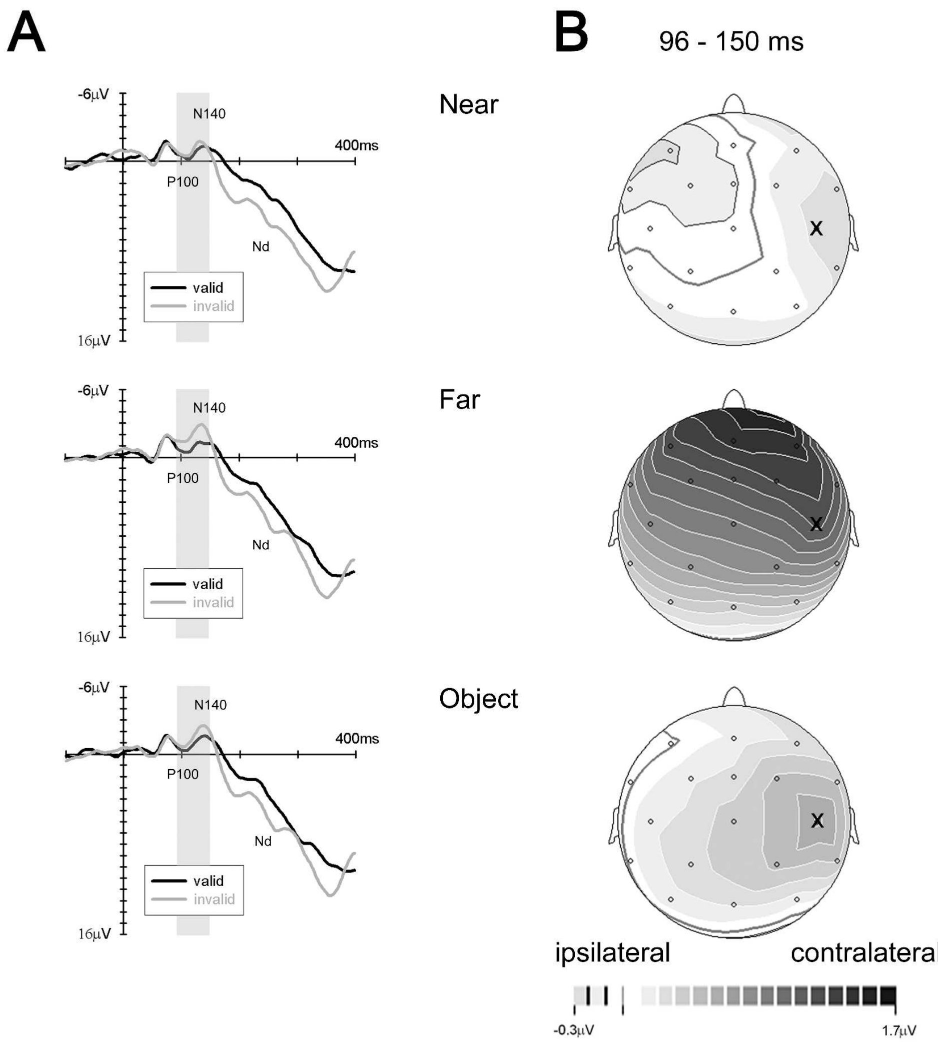

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178x194mm (500 x 500 DPI)