Psychophysiology, 40 (2003), 924–933. Blackwell Publishing Inc. Printed in the USA.

DOI: 10.1111/1469-8986.00110

Anterior and posterior attentional control systems use different spatial reference frames: ERP evidence from covert tactile-spatial orienting

MARTIN EIMER, BETTINA FORSTER, AND JOSÉ VAN VELZEN
Department of Psychology, Birkbeck College, University of London, London, UK

Abstract

To investigate whether processes controlling preparatory covert shifts of spatial attention operate within external and anatomically defined spatial coordinates, lateralized event-related potentials components sensitive to the direction of attentional shifts were measured in response to visual precues directing attention to the relevant location of tactile events. Participants had to detect infrequent tactile targets delivered to the hand located on the cued side. In different blocks, hands were uncrossed or crossed, so that external and anatomical codes specifying task-relevant locations were either congruent or incongruent. With uncrossed hands, an anterior directing attention negativity and a posterior directing attention positivity were elicited in the cue-target interval contralateral to the side of a cued attentional shift. Although the posterior effect was unaffected by hand posture, the anterior effect was delayed and reversed polarity with crossed relative to uncrossed hands. This pattern of results provides new evidence that different spatial coordinate systems may be used by separable attentional control processes. It is suggested that a posterior process operates on the basis of external spatial coordinates, whereas an anterior process is based primarily on anatomically defined spatial codes.

Descriptors: Spatial attention, Somatosensory processes, Attentional control, Spatial representation, Event-related brain potentials

It is well known that covertly directing spatial attention to a particular location enhances the sensory processing of stimuli within the current focus of attention. Numerous event-related potential (ERP) studies have shown that early, modality-specific sensory components show larger amplitudes for stimuli presented at covertly attended versus unattended locations. This has been demonstrated repeatedly for vision (e.g., Mangun & Hillyard, 1991), audition (e.g., Alho, 1992), and touch (e.g., García-Larrea, Lukaszewicz, & Mauguière, 1995). The combination of ERP and hemodynamic imaging methods has now also revealed detailed information about the likely neural generators of such attentional effects on the amplitude of early sensory-specific ERP components (e.g., Hopfinger, Jha, Hopf, Girelli, & Mangun, 2000; Mangun, 1995).

Although research on spatial attention has primarily been focused on sensory modulations, there has recently been an increasing interest in identifying preparatory control processes responsible for such attentional effects on stimulus processing. Numerous functional imaging studies have consistently found fronto-parietal networks to be involved in the control of attentional shifts (for recent reviews, see Corbetta & Shulman, 2002; Kastner & Ungerleider, 2000). ERP measures have also been used to examine preparatory control states arising in anticipation of expected stimuli at specific locations. In these studies, ERPs were measured during the anticipatory orienting of visual-spatial attention in the interval between a symbolic cue directing attention to the left or right side and the onset of a subsequent peripheral visual event (cf. Harter, Miller, Price, LaLonde, & Keyes, 1989; Hopf & Mangun, 2000; Hopfinger, Buoncore, & Mangun, 2000; Mangun, 1994; Nobre, Sebestyen, & Miniussi, 2000; Yamaguchi, Tsuchiya, & Kobayashi, 1994, 1995). Several lateralized ERP components were found contralateral to the direction of a cued attentional shift. An early negative deflection at contralateral occipital electrodes (early directing attention negativity or EDAN) was followed by an enhanced negativity at contralateral frontal electrodes (anterior directing attention negativity or ADAN), and an enhanced contralateral positivity at posterior electrode sites (late directing attention positivity or LDAP). These lateralized effects were assumed to reflect successive phases in the control of covert visual-spatial orienting, such as the decoding of the attentional cue, the initiation of an attention shift, and the preparatory activation of visual cortex.

However, more recent experiments (Eimer & Van Velzen, 2002; Eimer, Van Velzen, & Driver, 2002; Eimer, Van Velzen,

---

This research was supported by grants from the Medical Research Council (MRC) and from the Biotechnology and Biological Sciences Research Council (BBSRC).

Address reprint requests to: Martin Eimer, Department of Psychology, Birkbeck College, University of London, Malet Street, London WC1E 7HX, England. E-mail: m.eimer@bbk.ac.uk.

Forster, & Driver, 2003; Van Velzen, Forster, & Eimer, 2002) have demonstrated that these lateralized ERP components are not only elicited during visual-spatial orienting, but can also be observed during anticipatory attentional shifts toward expected locations of auditory or tactile events.[1] This suggests that these components may at least in part reflect supramodal attentional control processes (see Driver, Eimer, Macaluso, & Van Velzen, in press; Eimer & Driver, 2001; Eimer et al., 2002, for more detailed discussion).

Although potential correlates of preparatory attentional control processes have been identified with fMRI as well as ERP measures, the nature of these processes is still poorly understood. An important unresolved question concerns the spatial coordinates used in the control of spatial orienting. Attentional shifts toward expected visual stimuli on the left or right side or toward tactile stimuli delivered to the left or right hand may be based on representations in external or body-centered space (i.e., representations of task-relevant locations relative to the body midline). Alternatively, shifts of attention may be mediated by representations of anatomical space (i.e., left and right retinotopic space for shifts of visual attention; somatotopic representations of the left and right hand for shifts of tactile attention). A third possibility is that both external and anatomically defined spatial coordinate systems are involved in the control of attentional orienting.

The relative roles of external and anatomical spatial codes in the control of spatial orienting can be investigated by studying attentional control processes under conditions where these codes are in conflict. A simple way to induce a conflict between external and anatomical codes is to vary hand posture. When hands and arms are crossed, these codes are incongruent, because the anatomically left hand is located on the right side of external space, and the right hand on the left side. In contrast, external and anatomical codes are congruent when hands and arms are resting in their normal uncrossed position. It is well known that such variations in hand posture have strong effects on behavioral performance. Choice reaction times (RTs) are delayed when hands are crossed relative to an uncrossed hand posture, and this "hand posture effect" is assumed to result from conflicting external and anatomical spatial codes (cf. Nicoletti, Anzola, Luppino, Rizzolatti, & Umiltà, 1982; Nicoletti, Umiltà, & Ladavas, 1984; Riggio, Gawryszewski, & Umiltà, 1986).

In the present experiment, hand posture was manipulated to investigate the role of external and anatomical spatial codes in the control of attention shifts toward the location of relevant tactile stimuli delivered to the left or right hand. More specifically, we studied lateralized ERP components elicited during preparatory attentional orienting (ADAN, LDAP) when these spatial codes were either congruent or incongruent. On each trial, a central symbolic precue instructed participants to direct attention to the left or right side of external space to detect infrequent tactile targets delivered to the hand located there. In the uncrossed hands condition, both hands rested in their standard position, with the left hand on the left side, and the right hand on the right. In the crossed hands condition, the left hand was placed to the right of the body midline and the right hand to the left. Thus, external and anatomical codes specifying task-relevant locations were congruent with uncrossed hands, whereas these codes were incongruent when hands were crossed.

With hands uncrossed, ADAN and LDAP components elicited in the cue-target interval in response to cues directing attention to the left or right side of external space were expected to be similar to the effects observed in earlier studies on tactile-spatial orienting (Eimer & Van Velzen, 2002; Eimer et al., 2002, 2003; Van Velzen et al., 2002). Crucially, to investigate for the first time whether attentional control processes mediating attentional shifts (as reflected by ADAN and LDAP components) operate within external or anatomically defined space, lateralized ERP components observed in the uncrossed hands condition were compared to ERPs elicited when hands were crossed. If these control processes were mediated exclusively by representations of external space, the polarity of ADAN and LDAP components elicited in response to cues directing attention to the left or right side of external space should be unaffected by manipulations of hand posture. That is, in the crossed hand condition, anterior negativities (ADAN) and posterior positivities (LDAP) should still be elicited contralateral to the cued side. In contrast, if these processes were to operate on the basis of anatomically defined spatial coordinates, hand posture should have a strong effect on polarity of these preparatory components. With crossed hands, ADAN and LDAP should be elicited contralateral to anatomical side of the relevant hand, and thus should be observed *ipsilateral* to the cued side of external space. In other words, when considered in terms of external space, the polarity of these components should reverse for crossed relative to uncrossed hands.

Another aim of the present study was to investigate the contribution of attentional factors to the hand posture effect observed in previous behavioral studies. It is possible that the conflict between incongruent external and anatomical codes arising when hands are crossed may disrupt the attentional selection of task-relevant effectors. If this disruption was already present during preparatory attentional shifts, this could be reflected in systematic effects of hand posture on the latency of preparatory ERP components (ADAN, LDAP) observed during the cue-target interval. If conflicting spatial codes were to interfere with the attentional processing of tactile stimuli, effects of tactile-spatial attention on somatosensory ERPs elicited in response to peripheral tactile events should be attenuated and/or delayed when hands are crossed. Initial evidence for this comes from a recent ERP study investigating crossmodal links in spatial attention (Eimer, Cockburn, Smedley, & Driver, 2001). Here, attentional modulations of somatosensory ERPs elicited when hands were crossed were substantially delayed relative to an uncrossed hand posture. To confirm these observations and extend them to a unimodal tactile task, the present experiment also compared attentional effects on ERPs elicited in response to tactile stimuli at cued versus uncued locations with uncrossed hands to attentional modulations elicited in the crossed hands condition.

Methods

Participants

Twenty-two paid volunteers participated in the experiment. Two participants were excluded due to poor eye fixation control in the

---

[1] It should be noted that although ADAN and LDAP components were reliably elicited in these recent experiments, no posterior EDAN component was observed. This discrepancy with previous findings may be due to the fact that asymmetrical visual precues were employed in earlier studies, whereas auditory cues or fully symmetrical visual cues were used in our recent studies. Instead of reflecting genuine attentional processes, the EDAN is likely to represent a lateralized response to asymmetric visual cue stimuli (such as arrows; see Van Velzen & Eimer, 2003, for ERP evidence supporting this view).

cue-target interval (see below), and 2 other participants were excluded because of artefacts during EEG recording (large drifts at lateral electrodes; excessive occipital α wave activity). Thus 18 participants (8 women, 10 men, aged 20–39 years with a mean of 28 years) remained in the sample. Seventeen participants were right-handed and 1 was left-handed, and all had normal or corrected-to-normal vision by self-report.

Stimuli and Apparatus

Participants sat in a dimly lit experimental chamber, wearing a head-mounted microphone. Tactile stimuli were presented using 12-V solenoids, driving a metal rod with a blunt conical tip to the radial side of the middle phalanx of the index fingers, making contact with the fingers whenever a current was passed through the solenoid. The solenoids were attached to the fingers with white medical tape, which also prevented visibility of the rod movements. White noise (65 dB SPL, measured from the position of the participant's head) was continuously present to mask any sounds made by the tactile stimulators.[2] Two adjacent triangles, presented centrally on a computer screen at a viewing distance of 55 cm (total visual angle covered: 3.5° × 2.5°; visual angle of each triangle: 1.2° × 2.5°), served as cue stimuli. One triangle was red (luminance: 14 cd/m^2), the other blue (luminance: 19 cd/m^2), and they always pointed in opposite directions (◀ ▶ or ▶ ◀). A central fixation cross, located between both triangles, was continuously present throughout the experimental blocks. Tactile nontarget stimuli consisted of one rod contacting a finger for 200 ms. Tactile target stimuli had a gap, where this contact was interrupted for 10 ms after a duration of 95 ms.

Procedure

The experiment consisted of 12 blocks, each consisting of 64 trials. Each trial started with a 100-ms presentation of the cue. Six hundred milliseconds after cue offset, a tactile stimulus (200 ms duration) was presented to the left or right hand. Intertrial interval was 1,000 ms. Participants were instructed to keep their gaze focused on the central fixation cross, and to respond vocally ("yes") whenever a target (gap) stimulus was detected on the cued side. This task-relevant side was cued by the direction of one of the triangles. For 9 participants, blue triangles were relevant, and red triangles were relevant for the other 9 participants. Relevant left-pointing or right-pointing triangles were presented with equal probability to the left or right of fixation. In 48 trials, nontarget stimuli were presented with equal probability to the left or right hand, and were preceded with equal probability by a left or right cue, resulting in 12 trials for each of the four combination of cued location and stimulus location. The remaining 16 trials contained gap targets, and these were equally likely to be delivered to the left or right hand and to be preceded by a left or right cue. Thus, eight targets were delivered on the cued side and thus required a vocal response, and eight targets were delivered on the uncued side.

Hand posture was varied between block, with six successively presented blocks where hands rested in their normal uncrossed position and six successive blocks were hands were crossed. In the crossed hands condition, the left hand was thus located to the right of the body midline and the right hand on the left side. The order in which these two hand posture conditions were delivered was balanced across participants. In both conditions, hands were placed on a table, so that the index finger of each hand was located approximately 26 cm to the right and left of the body midline.

Recording and Data Analyses

EEG was recorded with Ag–AgCl electrodes and linked-earlobe reference from 23 scalp electrodes. Horizontal EOG was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 5 kΩ, and efforts were made to equalize the impedance of the earlobe electrodes. Amplifier bandpass was 0.1–40 Hz, and digitization rate was 200 Hz. Trials with eyeblinks, horizontal eye movements, or muscle artefacts were excluded. Separate analyses were conducted for ERPs obtained in the cue-target interval, and for ERPs in response to tactile nontarget stimuli.

ERPs in response to cue stimuli were averaged relative to a 100-ms precue baseline for the time interval between cue onset and 700 ms after cue onset (corresponding to the onset of the subsequent tactile stimulus), for all combinations of hand posture (uncrossed vs. crossed) and cue direction (left vs. right). Averaged HEOG waveforms obtained in the cue-target interval in response to cues directing attention to the left versus right hand were scored for systematic deviations of eye position, indicating a tendency to move the eyes toward the cued side. Two participants were disqualified due to residual HEOG deflections exceeding $\pm 3\,\mu$V.

ERP mean amplitudes obtained in the cue-target interval were analyzed with repeated measures ANOVAs, separately for lateral anterior (F7/8, F3/4, FC5/6), lateral central (C3/4, T7/8, CP5/6), and lateral posterior sites (OL/R, P3/4, P7/8), for the factors electrode site, hand posture, cue direction, and hemisphere (left vs. right). In these analyses, ERP lateralizations sensitive to the cued direction of an attentional shift will be reflected by Hemisphere × Cue Direction interactions. As in previous studies, these analyses were based on ERP mean amplitudes obtained between 350 and 500 ms, and between 500 and 700 ms after cue onset. Initial analyses of cue-target ERP waveforms were conducted with order of hand posture condition (uncrossed followed by crossed hands, or vice versa) as the between-subject factor. As no main effects or significant interactions of this factor with other factors were observed (reflecting the absence of any systematic task order effects), this factor was not included in the main analyses.

ERPs to tactile nontargets (tactile stimuli without gaps) were averaged relative to a 100-ms prestimulus baseline for all combinations of hand posture, cue direction, and stimulated hand (left vs. right). ERP mean amplitudes were computed within successive measurement windows centered on the latencies (in milliseconds poststimulus) of early SEP components: P45 (35–55 ms), N80 (60–90 ms), P100 (90–120 ms), N140 (130–160 ms). To investigate longer-latency effects of attention, mean amplitudes were also computed between 200 ms and 300 ms poststimulus. Statistical analyses were restricted to recording sites close to somatosensory areas (F3/4, Fz, FC5/6, C3/4, Cz, CP5/6), where early ERP components are maximal. Because these early components are strongly lateralized in response to left-hand and right-hand tactile stimulation, separate analyses were conducted for midline electrodes, as well as for electrodes

---

[2] The noise intensity level sufficient for complete masking was determined in a pilot study, where 2 participants were seated next to each other. Tactile stimuli were delivered at variable intervals to the left or right hand of 1 participant, while the other participant had to report any audible occurrence of tactile stimulation. With white noise at 65 dB SPL, participants were consistently unable to detect tactile stimulus presentation.

contralateral and ipsilateral to the anatomical side of the stimulated hand. Initial analyses of somatosensory ERP waveforms were conducted with the factor order of hand posture condition (uncrossed first vs. crossed first) as the between-subject factor. No main effects or significant interactions of this factor with other factors were observed, and this factor was therefore not included in the main analyses. Here, mean amplitude values were analyzed with repeated measures ANOVAs for the factors hand posture, attention (stimulus at attended vs. unattended side), stimulated hand, and electrode site (frontal vs. frontocentral vs. central vs. centroparietal for contralateral and ipsilateral electrodes; Fz vs. Cz for midline sites). When appropriate, Greenhouse–Geisser adjustments to the degrees of freedom were performed. When interactions between attention and electrode site were found (for brevity, these are not reported in full), additional analyses were conducted for single electrode sites. For vocal response times (RTs; recorded with a voice key, and measured relative to the onset of the target-defining gap) and arcsin-transformed error rates, repeated measures ANOVAs were performed for the factors hand posture and stimulated hand.

Results

Behavioral Performance

Vocal RTs to correctly detected infrequent gap targets at attended locations were faster when hands were uncrossed (495 ms) than with crossed hands (530 ms), and this was reflected in a main effect of hand posture, $F(1,17) = 10.1$, $p < .01$. Participants missed 4.2% and 3.6% tactile targets at attended locations with uncrossed and crossed hands, respectively, and this difference was not significant. False alarms to targets presented to the unattended hand occurred on less than 1% of these trials, and false alarms to nontarget (nongap) stimuli were virtually absent (less than 0.2% of all trials).

ERP Correlates of Anticipatory Spatial Orienting in the Cue-Target Interval

Figures 1 and 2 show ERPs elicited in the interval between the onset of the central visual cue and the onset of the subsequent peripheral tactile stimulus. ERPs are displayed separately for cues directing attention to the left versus right side of external space, with hands either uncrossed (Figure 1) or crossed (Figure 2). When hands were in their normal uncrossed position, the expected ERP lateralizations sensitive to the direction of attentional shifts were present (Figure 1). At frontocentral electrodes, a negativity contralateral to the direction of an attentional shift (anterior directing attention negativity; ADAN) was observed, which appeared more pronounced over the left hemisphere. In addition, a contralateral positivity was elicited at lateral posterior sites (late directing attention positivity; LDAP). When hands were crossed (Figure 2), the posterior LDAP appeared similar to the LDAP elicited with uncrossed hands. In contrast, the polarity of the ADAN component was found to be reversed relative to uncrossed hands condition.

The presence of ERP lateralizations sensitive to the direction of attentional shifts, and their sensitivity to manipulations of hand posture, can be seen more clearly in the difference waveforms shown in Figure 3, which were constructed to simplify graphical presentation, not for formal statistics. These waveforms were generated by first subtracting ERPs recorded

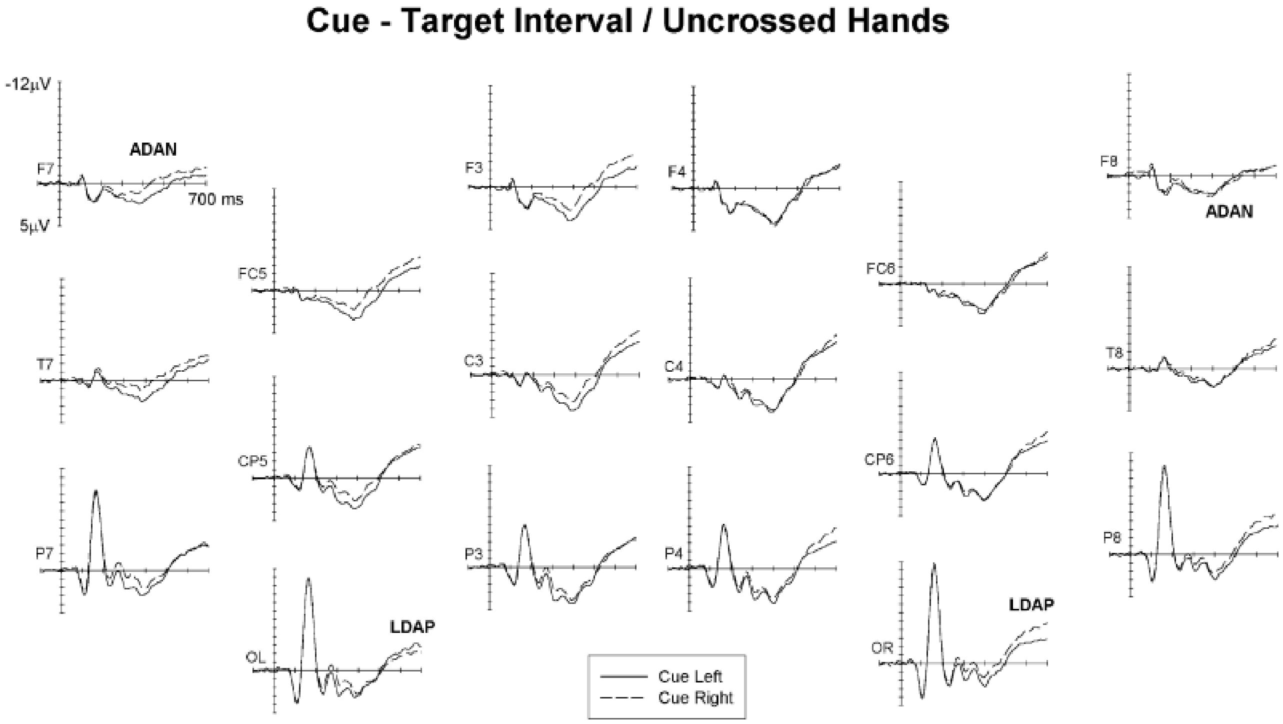

Figure 1. Grand-averaged ERPs elicited in the uncrossed hand condition at lateral electrodes in the interval between cue onset and the onset of the subsequent peripheral tactile stimulus in response to visual cues directing attention to the left side (solid lines), or cues directing attention to the right side (dashed lines), showing a left-lateralized anterior directing attention negativity (ADAN) and a bilateral late directing attention positivity (LDAP) contralateral to the direction of an attentional shift.

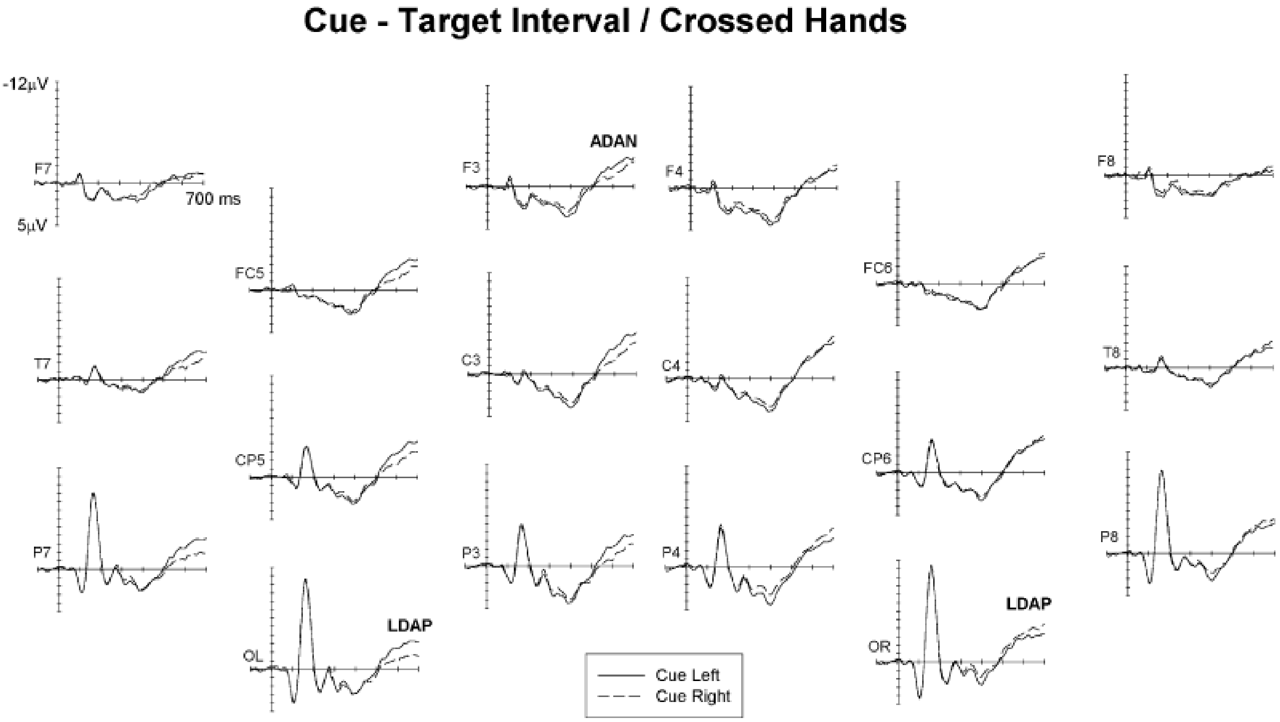

Figure 2. Grand-averaged ERPs elicited in the crossed hand condition at lateral electrodes in the interval between cue onset and the onset of the subsequent peripheral tactile stimulus in response to visual cues directing attention to the left side (solid lines), or cues directing attention to the right side (dashed lines). Both anterior directing attention negativity (ADAN) and late directing attention positivity (LDAP) are visible, but the polarity of the ADAN is reversed relative to the uncrossed hands condition.

during attentional shifts to the right side of external space from ERPs elicited during leftward attentional shifts, to obtain differential ERP responses during leftward versus rightward attentional shifts at all recording sites. To visualize the lateralized portion of these differential responses, difference waveforms obtained for right-hemisphere electrodes were then subtracted from the difference waveforms emerging at homologous electrodes over the left hemisphere. In the resulting double subtraction waveforms, a negativity contralateral to the direction of attentional shifts is reflected by positive amplitude values (downward-going deflections), and a contralateral positivity is indicated by negative values (upward-going deflections). Figure 3 shows difference waveforms obtained for anterior (top), central (middle), and posterior (bottom) electrode pairs, displayed separately for the uncrossed hands condition (solid lines) and the crossed hands condition (dashed lines). Whereas the posterior LDAP component seems largely unmodulated by hand posture, frontocentral lateralizations were strongly affected. A negativity contralateral to the side of an attentional shift (ADAN) was observed with uncrossed hands, starting at about 300 ms after cue onset. In contrast, a lateralized activity of opposite polarity was present in the final 200 ms of the cue–target interval when hands were crossed.

These informal observations were confirmed by statistical analyses. No systematic ERP modulations sensitive to the direction of attentional shifts were observed within the first 350 ms following cue onset. In the 350–500-ms measurement window, significant Hemisphere × Cue Direction interactions were present at anterior and central electrode pairs, $F(1,17) = 25.8$ and 10.9, $p < .001$ and .004, respectively. More importantly, significant three-way interactions (Hand Posture × Hemisphere × Cue Direction) were found for both sets of electrodes, $F(1,17) = 24.0$ and 8.2, $p < .001$ and .011, respectively, due to the fact that an increased negativity contralateral to the direction of an attentional shift (ADAN) was present with uncrossed hands, but not in the crossed hands condition (see Figure 3). This was confirmed by follow-up analyses, which revealed significant Hemisphere × Cue Direction interactions at anterior and central sites with uncrossed hands, $F(1,17) = 35.5$ and 13.2, $p < .001$ and .002, respectively, whereas no such interactions were obtained for the crossed hands condition. No Hemisphere × Cue Direction interactions were present between 350 and 500 ms at lateral posterior electrodes.

In the subsequent 500–700-ms measurement window (corresponding to the final 200 ms of the cue-target interval), significant three-way interactions (Hand Posture × Hemisphere × Cue Direction) were again present for lateral anterior and central electrode pairs, $F(1,17) = 21.6$ and 12.4, $p < .001$ and .003, respectively. With uncrossed hands, Hemisphere × Cue Direction interactions were found at lateral anterior sites, $F(1,17) = 20.1$, $p < .001$, reflecting the late phase of the ADAN component (Figure 3, top). More importantly, reliable Hemisphere × Cue Direction interactions were now also obtained when hands were crossed, both at lateral anterior and at lateral central electrode pairs, $F(1,17) = 6.3$ and 18.5, $p < .022$ and .001, respectively. As can be seen from Figure 3 (where lateralized components are plotted with respect to the cued side of external space), the polarity of the lateralizations observed in the final 200 ms of the cue-target interval with crossed hands was reversed relative to the ADAN obtained in the uncrossed hands condition. Note that if frontocentral lateralizations had been plotted in terms of the anatomical side of the cued hand, rather

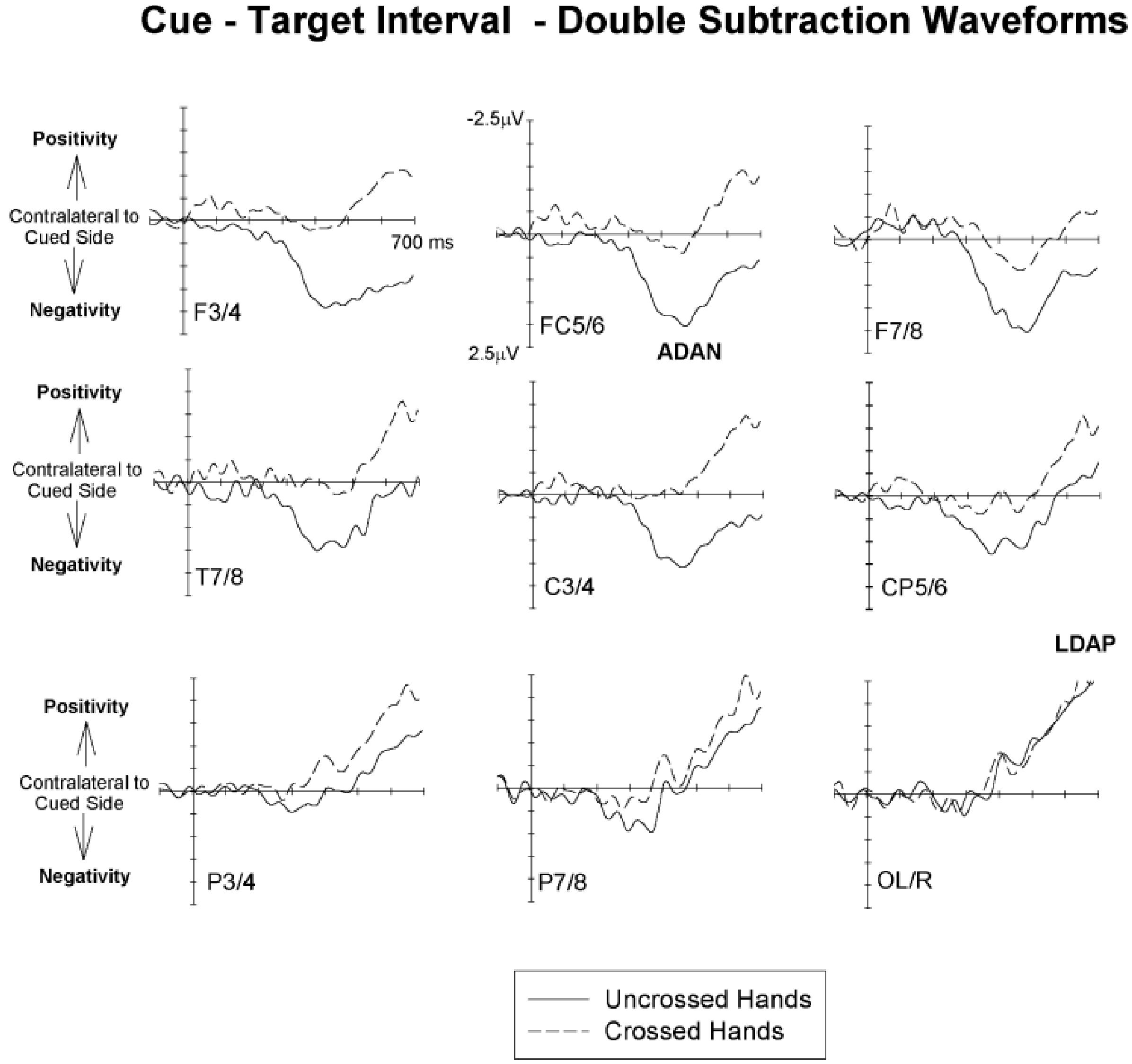

Figure 3. Difference waveforms obtained at lateral anterior (top), central (middle), and posterior (bottom) electrodes in the 700-ms interval between cue onset and onset of the subsequent peripheral tactile stimulus in the uncrossed hands condition (solid lines) and in the crossed hands condition (dashed lines), reflecting lateralized ERP modulations sensitive to the direction of attentional shifts. Difference waveforms were generated by first subtracting ERPs in response to cues directing attention to the right side of external space from ERPs in response to cues directing attention to the left side, and then subtracting the resulting difference waves at right electrodes from the difference waveform obtained for the corresponding left-hemisphere electrode. Enlarged negativities contralateral to the direction of attentional shifts are reflected by positive amplitude values (downward-going deflections), and larger positivities at contralateral sites are reflected by negative values (upward-going deflections). The resulting waveforms show a frontocentral directing attention negativity (ADAN) with uncrossed hands that reverses polarity in the crossed hand condition, and a posterior directing attention positivity (LDAP) that is very similar for both hand postures.

than in terms of external space, no such polarity reversal would have been present (although the onset of this lateralized effect would still be substantially delayed with crossed hands).

As can be seen from Figures 1 and 2, the size of the ADAN and "reversed ADAN" effects was considerably larger over the left hemisphere than at right electrode sites. To further explore this difference, additional analyses tested effects of cue direction separately for left and for right frontocentral electrodes. Significant effects of cued direction was present over the left hemisphere between 350 and 500 ms with uncrossed hands and between 500 and 700 ms with crossed hands, but these effects failed to reach significance over the right hemisphere (see Eimer et al., 2002, for similar findings).

The presence of a posterior LDAP was reflected in a Hemisphere × Cue Direction interaction obtained at lateral posterior electrodes in the 500–700-ms measurement window, $F(1,17) = 25.4$, $p < .001$. Importantly, there was no Hand Posture × Hemisphere × Cue Direction interaction, indicating that the LDAP component was unaffected by the manipulation of hand position (see Figure 3, bottom). Accordingly, reliable Hemisphere × Cue Direction interactions were observed for both uncrossed and crossed hands, $F(1,17) = 26.3$ and 15.9, both

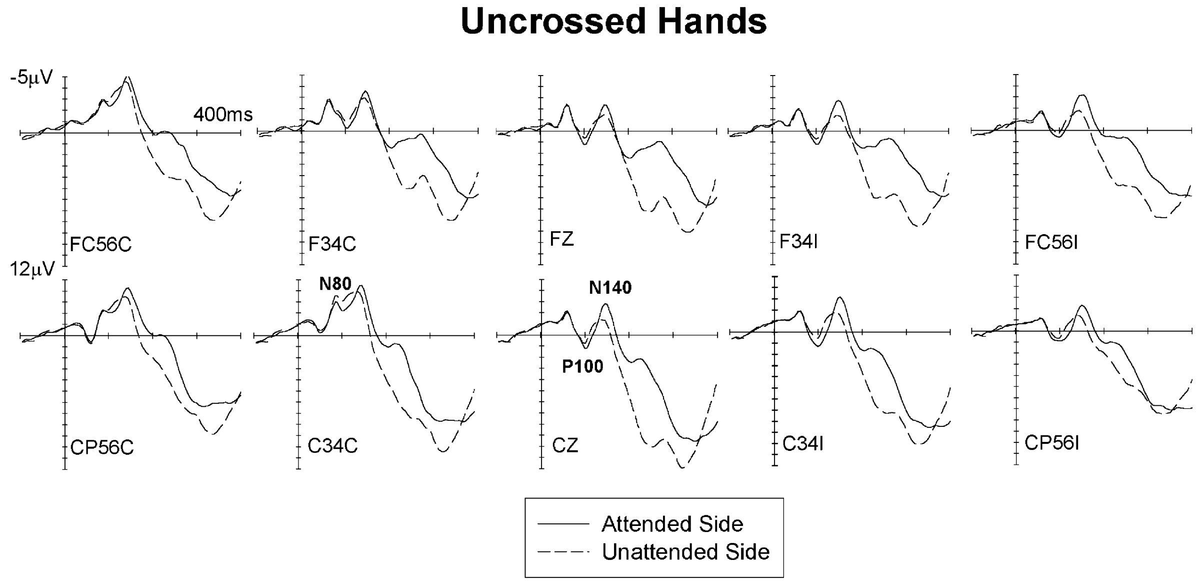

Figure 4. Grand-averaged somatosensory ERPs elicited in the uncrossed hands condition at midline electrodes and at sites contralateral (C) and ipsilateral (I) to the anatomical side of the stimulated hand by tactile nontarget stimuli at cued locations (solid lines) and uncued locations (dashed lines) in the 400-ms interval following stimulus onset.

$p < .001$. Additional analysis conducted separately for left and right posterior electrodes in the 500–700 ms analysis window revealed effects of cue direction for left as well as right recording sites, both $F(1,17) > 7.3$, both $p < .015$, thus confirming earlier observations that the LDAP is elicited bilaterally during shifts of tactile-spatial attention (Eimer & Van Velzen, 2002; Eimer et al., 2002; Van Velzen et al., 2002).

Effects of Spatial Attention on Somatosensory ERPs in Response to Peripheral Tactile Nontarget Stimuli

Figures 4 and 5 show ERPs elicited in response to tactile stimuli without gaps (nontargets) at attended (cued) and unattended (uncued) locations, displayed separately for midline electrodes and for electrodes contralateral (C) and ipsilateral (I) to the anatomical side of the stimulated hand. Figure 4 shows

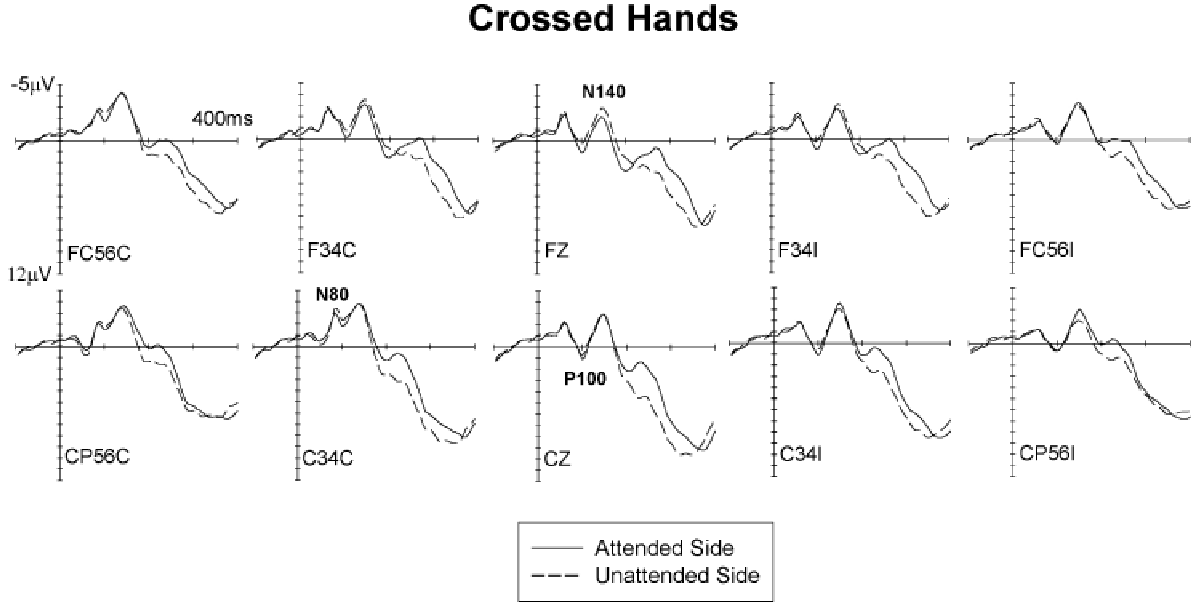

Figure 5. Grand-averaged somatosensory ERPs elicited in the crossed hands condition at midline electrodes and at sites contralateral (C) and ipsilateral (I) to the anatomical side of the stimulated hand by tactile nontarget stimuli at cued locations (solid lines) and uncued locations (dashed lines) in the 400-ms interval following stimulus onset.

somatosensory ERPs obtained in the uncrossed hand condition, and Figure 5 shows ERPs elicited in the crossed hands condition. Effects of spatial attention on somatosensory ERPs were strongly affected by variations in hand posture. With uncrossed hands, attentional modulations of the P100 and N140 components were followed by a sustained negativity for tactile stimuli at attended versus unattended locations (Figure 4). In contrast, no effects of spatial cueing on early P100 and N140 components appear to be present with crossed hands. Here, attentional effects seem to be restricted to a sustained enhanced negativity for tactile stimuli at cued locations beyond 200 ms poststimulus (Figure 5).

Again, these observations were confirmed by statistical analyses. No effect of attention was found for the P45 and N80 components. In the P100 measurement window (90–120 ms poststimulus), significant attentional modulations were observed with uncrossed hands at contralateral sites, $F(1,17) = 4.5$, $p < .05$, and at ipsilateral electrodes C3/4, $F(1,17) = 5.2$, $p < .04$, reflecting enlarged P100 amplitudes for tactile stimuli delivered to the cued hand (Figure 4). In contrast, no reliable effects of attention on P100 amplitudes were found in the crossed hand condition.[3]

In the N140 time window (130–160 ms poststimulus), significant Attention × Hand Posture interactions were found at midline electrodes and at electrodes ipsilateral to the stimulated hand, both $F(1,17) > 7.8$, both $p < .02$, and this interaction was nearly significant at contralateral sites, $F(1,17) = 4.0$, $p < .07$. Significant attentional enhancements of N140 amplitudes were present contralaterally, ipsilaterally, and at midline sites when hands were uncrossed, all $F(1,17) > 5.3$, all $p < .04$, but were absent in the crossed hands condition.[4]

In the 200–300-ms time interval, main effects of attention were present contralaterally, ipsilaterally, and at midline electrodes, all $F(1,17) > 11.2$, all $p < .004$, and were accompanied by Hand Posture × Attention interactions at all these sites, all $F(1,17) > 12.6$, all $p < .002$. A comparison of Figures 4 and 5 shows that sustained enhanced negativities for attended tactile stimuli side beyond 200 ms poststimulus were more pronounced when hands were in their usual uncrossed position than with crossed hands. However, follow-up analyses revealed that significant effects of attention were present at all analyzed recording sites not only for the uncrossed hands condition, all $F(1,17) > 14.0$, all $p < .002$, but also when hands were crossed, all $F(1,17) > 5.4$, all $p < .05$.

Discussion

Although numerous studies using hemodynamic and electrophysiological imaging methods have identified anterior and posterior networks involved in the control of attention shifts, the principles underlying the operation of these networks are not yet well understood. The aim of the present experiment was to investigate the role of external and anatomical spatial coordinate systems in the control of spatial orienting. ERPs were measured while participants were instructed to direct attention to the left or right side (as indicated by a visual precue presented centrally at the beginning of each trial) in order to detect infrequent tactile target stimuli delivered to the index finger of the hand located on the cued side while completely ignoring all tactile stimuli on the uncued side. In different experimental blocks, hands either rested in their standard uncrossed position, or were crossed, with the left hand located on the right side of external space, and the right hand on the left.

To find out whether control processes responsible for shifts of attention to the location of relevant tactile events operate on the basis of external or anatomically defined spatial codes, lateralized ERP components (ADAN, LDAP) elicited during preparatory attention shifts in the cue-target interval with uncrossed hands were compared to ERPs elicited when hands were crossed. When hands are uncrossed, external and anatomical spatial codes representing the index finger of the left and right hand are congruent. In contrast, these codes are incongruent when hands are crossed. With uncrossed hands, ADAN and LDAP components elicited in response to cues directing attention to the left or right side of external space were very similar to the effects observed in previous ERP studies of tactile-spatial orienting (Eimer & Van Velzen, 2002; Eimer et al., 2002, 2003; Van Velzen et al., 2002). In addition, these lateralized effects also closely resembled results obtained in earlier experiments investigating shifts of attention toward anticipated visual events (Harter et al., 1989; Hopf & Mangun, 2000; Nobre et al., 2000; Yamaguchi et al., 1994, 1995). A frontocentral directing attention negativity (ADAN) was observed contralateral to the direction of the cued attentional shift. This effect was maximal between 350 ms and 500 ms after cue onset, and remained present, albeit in an attenuated fashion, during later phases of the cue-target interval (Figure 3, top). At lateral posterior sites, an enhanced positivity contralateral to the direction of an attentional shift was observed in the final 200 ms of the cue–target interval (Figure 3, bottom), again in line with observations from earlier experiments. This pattern of results again confirms that these effects are not restricted to visual-spatial orienting, but are also elicited during shifts of attention in anticipation of relevant tactile events.

The central aim of this study was to compare ERP modulations obtained in the cue-target interval with uncrossed hands to results obtained in the crossed hand condition, in order to find out whether attentional control processes reflected by lateralized ERP components elicited during covert attentional shifts operate within coordinate systems based on external or anatomical space. If these processes were mediated by representations of external space, variations in hand posture should have no systematic effects on ADAN and LDAP components. That is, the polarity of these components (when considered in terms of the side of an attentional shift in external space) should remain unchanged regardless of whether hands are crossed or uncrossed. In contrast, if attentional control processes operate on the basis of anatomical spatial coordinates (i.e., code the direction of an attentional shift with respect to the anatomical identity of the cued hand), the polarity of ADAN and LDAP, again defined in terms of the cued side of external space, should reverse when hands are crossed.

The ERP results obtained for the cue-target interval in the crossed hand condition revealed a striking dissociation in the effects of hand posture on the frontocentral ADAN and the posterior LDAP component. The LDAP was virtually

---

[3] It should be noted that although attentional effects on the P100 component were significant for uncrossed hands, but not for crossed hands, this difference was not reflected in statistically reliable Attention × Hand Posture interactions in the P100 analysis window.

[4] Figure 5 suggests that with crossed hands, N140 amplitude at Fz was actually larger for stimulation of uncued relative to cued locations, and this difference turned out to be significant, $F(1,17) = 5.2$, $p < .04$. This fully replicates an earlier finding by Eimer et al. (2001; Exp. 2) for somatosensory ERPs and crossed hands in a crossmodal attention study.

unaffected by the hand posture manipulation. When hands were crossed, enhanced posterior positivities were elicited contralateral to the side of an attentional shift, and these lateralized effects were very similar in terms of amplitudes and latencies to the effects observed with uncrossed hands (Figure 3, bottom). This pattern of results strongly suggests that the attentional control processes responsible for the LDAP component operate on the basis of representations of external space, are not sensitive to the anatomical identity of the task-relevant hand, and are also unaffected by the incongruency between external and anatomical spatial codes in the crossed hands condition.

A very different pattern of results was obtained for the frontocentral ADAN component. When hands were crossed, no significant lateralizations were obtained between 350 and 500 ms after cue onset, when ADAN amplitudes were maximal in the uncrossed hands condition. In the final 200 ms of the cue-target interval, a reliable lateralized effect was present at frontocentral electrodes with crossed hands, but the polarity of this lateralization (considered in terms of the direction of an attentional shift in external space) was opposite to the polarity of the ADAN observed when hands were uncrossed (Figure 3, top). In other words, when the left hand was located on the right side and the right hand on the left, an anterior directing attention negativity was elicited contralateral to the anatomical side of the relevant hand, and thus ipsilateral to the cued side of external space. This result indicates that in contrast to the LDAP, the ADAN component is primarily sensitive to the anatomical identity of the task-relevant hand and not to the cued location of relevant tactile stimuli in external space.

Overall, these ERP results obtained during anticipatory covert shifts of attention to the location of tactile events strongly suggest that both external and anatomically defined spatial coordinate systems are involved in the control of attentional orienting. Most importantly, results indicate that different spatial codes are utilized independently by separable attentional control mechanisms. Anterior and posterior attentional networks, as identified in functional imaging studies (see Corbetta & Shulman, 2002; Kastner & Ungerleider, 2000), are often linked to different subprocesses involved in the control of spatial attention (cf. Posner & Petersen, 1990). If one assumes that the ADAN and LDAP components observed in this study and in previous ERP investigations of spatial orienting reflect the operation of anterior and posterior attentional networks, respectively, the present results indicate that these subprocesses differ not only with respect to their anatomical substrate (anterior vs. posterior, as reflected by the scalp distribution of ADAN and LDAP), and their time course (with the onset of the anterior process preceding the onset of the posterior process), but also, perhaps most importantly, with respect to the format of the spatial representations involved. Whereas the anterior process (reflected by the ADAN) appears to operate predominantly on the basis of anatomically defined representations, the posterior process (indicated by the LDAP) seems to be exclusively based on coordinates of external space. This latter observation is consistent with recent findings from single-cell recordings in monkeys, which demonstrated that regions of posterior parietal cortex encode the direction of planned reaching movements in eye-centered coordinates, rather than with respect to a limb-centered reference frame (for a review, see Andersen & Buneo, 2002).

Another aim of the present study was to investigate whether the "hand posture effect" (delayed response latencies when hands are crossed) is related to attentional factors. Vocal RTs to infrequent tactile targets at cued locations were delayed with crossed as compared to uncrossed hands, thus replicating the effect of hand posture observed in earlier behavioral studies (Nicoletti et al., 1982, 1984; Riggio et al., 1986). If conflicting external and anatomical spatial codes disrupted attentional selectivity, this may be reflected in effects of hand posture on preparatory ERP components elicited during the cue-target interval, as well as on attentional modulations of somatosensory ERPs in response to subsequent peripheral tactile stimuli. Such effects were indeed observed. Anterior lateralizations triggered in the cue-target interval were substantially delayed with crossed as compared to uncrossed hands (Figure 3, top). This delay may indicate an adverse effect of incongruent external and anatomical spatial codes on the timing of attentional control processes involved in selecting the task-relevant hand.

In addition, attentional modulations of somatosensory ERPs in response to subsequent peripheral tactile stimuli were delayed and attenuated with crossed as compared to uncrossed hands. With uncrossed hands, attention enhanced the amplitudes of sensory-specific somatosensory P100 and N140 components, and then resulted in a sustained negativity starting at about 200 ms poststimulus (Figure 4; cf. García-Larrea et al., 1995; Michie, Bearpark, Crawford, & Glue, 1987, for similar results). In the crossed hands condition, attentional P100 and N140 modulations were absent, and although a sustained attentional negativity was reliably elicited, it was reduced in amplitude relative to the uncrossed hands condition (Figure 5).

These results suggest that the attentional selection of one hand versus the other is strongly affected by changes in body posture. Attentional modulations of somatosensory processes are delayed and attenuated under conditions where crossing the hands results in mismatching external and anatomical codes (for similar findings, see Eimer et al., 2001). This observation is in line with the hypothesis that conflicts between external and anatomical spatial coordinates defining a task-relevant location disrupt the operation of spatial attention, and that this may also be responsible for the hand posture effect observed in earlier behavioral studies.

In summary, the present study provided novel findings that strongly suggest that anterior and posterior attentional control systems differ with respect to the spatial coordinates used to guide covert shifts of spatial attention. Whereas the anterior system appears to operate on the basis of anatomically defined codes, the posterior system employs representations of the location of relevant events in external space. The observation that attentional selectivity is disrupted when external and anatomical codes are incongruent indicates that both spatial coordinate systems are relevant, and may interact during covert attentional orienting. These preliminary conclusions need to be substantiated in future experiments, where target modalities other than touch should be included. For example, to study the relative contributions of retinotopic versus head- and body-centered spatial coordinates to covert visual-spatial orienting, ERP correlates of anticipatory attentional shifts toward relevant visual events should be measured while gaze direction is systematically varied.[5] Overall, the present findings show that ERP measures can be extremely useful tools when studying functional properties of covert attentional control processes.

---

[5] As gaze direction was held constant in the present experiment, the relative roles of head-centered and eye-centered spatial coordinate systems could not be dissociated.

REFERENCES

Alho, K. (1992). Selective attention in auditory processing as revealed by event-related brain potentials. *Psychophysiology*, *29*, 247–263.

Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience*, *25*, 189–220.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.

Driver, J., Eimer, M., Macaluso, E., & Van Velzen, J. (in press). Neurobiology of human spatial attention: Modulation, generation and integration. In N. Kanwisher & J. Duncan (Eds.), *Attention and Performance XIX*. Cambridge, MA: MIT Press.

Eimer, M., Cockburn, D., Smedley, B., & Driver, J. (2001). Cross-modal links in endogenous spatial attention are mediated by common external locations: Evidence from event-related brain potentials. *Experimental Brain Research*, *139*, 398–411.

Eimer, M., & Driver, J. (2001). Crossmodal links in endogenous and exogenous spatial attention: Evidence from event-related brain potential studies. *Neuroscience and Biobehavioral Reviews*, *25*, 497–511.

Eimer, M., & Van Velzen, J. (2002). Crossmodal links in spatial attention are mediated by supramodal control processes: Evidence from event-related potentials. *Psychophysiology*, *39*, 437–449.

Eimer, M., Van Velzen, J., & Driver, J. (2002). Crossmodal interactions between audition, touch and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *Journal of Cognitive Neuroscience*, *14*, 254–271.

Eimer, M., Van Velzen, J., Forster, B., & Driver, J. (2003). Shifts of attention in light and in darkness: An ERP study of supramodal attentional control and crossmodal links in spatial attention. *Cognitive Brain Research*, *15*, 308–323.

García-Larrea, L., Lukaszewicz, A. C., & Mauguière, F. (1995). Somatosensory responses during selective spatial attention: The N120-to-N140 transition. *Psychophysiology*, *32*, 526–537.

Harter, M. R., Miller, S. L., Price, N. J., LaLonde, M. E., & Keyes, A. L. (1989). Neural processes involved in directing attention. *Journal of Cognitive Neuroscience*, *1*, 223–237.

Hopf, J. M., & Mangun, G. R. (2000). Shifting visual attention in space: An electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology*, *111*, 1241–1257.

Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, *3*, 284–291.

Hopfinger, J. B., Jha, A. P., Hopf, J. M., Girelli, M., & Mangun, G. R. (2000). Electrophysiological and neuroimaging studies of voluntary and reflexive attention. In S. Monsell & J. Driver (Eds.), *Attention and Performance XVII* (pp. 125–153). Cambridge, MA: MIT Press.

Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, *23*, 315–341.

Mangun, G. R. (1994). Orienting attention in the visual fields: An electrophysiological analysis. In H.-J. Heinze, T. F. Münte & G. R. Mangun (Eds.), *Cognitive Electrophysiology* (pp. 81–101). Boston: Birkhäuser.

Mangun, G. R. (1995). The neural mechanisms of visual selective attention. *Psychophysiology*, *32*, 4–18.

Mangun, G. R., & Hillyard, S. A. (1991). Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception & Performance*, *17*, 1057–1074.

Michie, P. T., Bearpark, H. M., Crawford, J. M., & Glue, L. C. T. (1987). The effects of spatial selective attention on the somatosensory event-related potential. *Psychophysiology*, *24*, 449–463.

Nicoletti, R., Anzola, G. P., Luppino, G., Rizzolatti, G., & Umiltà, C. (1982). Spatial compatibility effects on the same side of the body midline. *Journal of Experimental Psychology: Human Perception & Performance*, *8*, 664–673.

Nicoletti, R., Umiltà, C., & Ladavas, E. (1984). Compatibility due to the coding of the relative positions of the effectors. *Acta Psychologica*, *57*, 133–143.

Nobre, A. C., Sebestyen, G. N., & Miniussi, C. (2000). The dynamics of shifting visuospatial attention revealed by event-related brain potentials. *Neuropsychologia*, *38*, 964–974.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42.

Riggio, L., Gawryszewski, L., & Umiltà, C. (1986). What is crossed in crossed-hand effects? *Acta Psychologica*, *62*, 89–100.

Van Velzen, J., & Eimer, M. (2003). Early posterior ERP components do not reflect the control of attentional shifts towards expected peripheral events. *Psychophysiology*, *40*, 827–831.

Van Velzen, J., Forster, B., & Eimer, M. (2002). Temporal dynamics of lateralized ERP components elicited during endogenous attentional shifts to relevant tactile events. *Psychophysiology*, *39*, 874–878.

Yamaguchi, S., Tsuchiya, H., & Kobayashi, S. (1994). Electroencephalographic activity associated with shifts of visuospatial attention. *Brain*, *117*, 553–562.

Yamaguchi, S., Tsuchiya, H., & Kobayashi, S. (1995). Electrophysiologic correlates of age effects on visuospatial attention shift. *Cognitive Brain Research*, *3*, 41–49.

(Received October 24, 2002; Accepted May 19, 2003)