Cross-Modal Interactions Between Audition, Touch, and Vision in Endogenous Spatial Attention: ERP Evidence on Preparatory States and Sensory Modulations

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Abstract

■ Recent behavioral and event-related brain potential (ERP) studies have revealed cross-modal interactions in endogenous spatial attention between vision and audition, plus vision and touch. The present ERP study investigated whether these interactions reflect supramodal attentional control mechanisms, and whether similar cross-modal interactions also exist between audition and touch. Participants directed attention to the side indicated by a cue to detect infrequent auditory or tactile targets at the cued side. The relevant modality (audition or touch) was blocked. Attentional control processes were reflected in systematic ERP modulations elicited during cued shifts of attention. An anterior negativity contralateral to the cued side was followed by a contralateral positivity at posterior

sites. These effects were similar whether the cue signaled which side was relevant for audition or for touch. They also resembled previously observed ERP modulations for shifts of visual attention, thus implicating supramodal mechanisms in the control of spatial attention. Following each cue, single auditory, tactile, or visual stimuli were presented at the cued or uncued side. Although stimuli in task-irrelevant modalities could be completely ignored, visual and auditory ERPs were nevertheless affected by spatial attention when touch was relevant, revealing cross-modal interactions. When audition was relevant, visual ERPs, but not tactile ERPs, were affected by spatial attention, indicating that touch can be decoupled from cross-modal attention when task-irrelevant. ■

INTRODUCTION

In everyday life, attention is often directed to information coming from different sensory modalities, but from the same location in space. When trying to follow a conversation in a noisy room, we may attend to seen lip movements as well as to the speaker's voice coming from the same location. When exploring an object manually, we may attend both to its visual appearance and to the tactile information produced at the same location. In general, adaptive control of behavior requires the integration and coordination of information originating from different input modalities, but from corresponding spatial locations. This may involve spatial synergies in selective attention across different sensory modalities.

Selective attention has traditionally been studied separately for different sensory modalities, with little direct contact between traditional research on "visual attention," "auditory attention," or "tactile attention." The issue of cross-modal interactions in spatial attention between vision, audition, and touch has been addressed only more recently (see Driver & Spence, 1998, for review). A few studies have also begun to examine neural correlates of such interactions, using event-related brain potentials (ERP) (e.g., Eimer & Schröger,

1998; Hillyard, Simpson, Woods, Van Voorhis, & Münte, 1984) or functional imaging measures (e.g., Macaluso, Frith, & Driver, 2000a, Macaluso, Frith, & Driver, 2000b). Several recent behavioral studies (e.g., Spence & Driver, 1996; Spence, Pavani, & Driver, 2000) found evidence for cross-modal interactions in endogenous (voluntary) spatial attention between vision and audition, and vision and touch. In these experiments, participants had to direct their attention to the expected location of target stimuli within one (primary) modality. On a few trials, stimuli of a different (secondary) modality were presented, but were somewhat more likely on the side opposite the expected location in the primary modality. Superior performance for stimuli at the location that was expected for the primary modality was observed not only for that modality, but also for stimuli in the secondary modality, thus demonstrating a spatial synergy in attention between the two modalities.

Such behavioral results demonstrate that cross-modal interactions exist between vision, audition, and touch, in endogenous spatial attention. However, the behavioral results alone cannot directly address two important questions. First, do such cross-modal interactions reflect a supramodal control system for spatial attention, which directs endogenous spatial attention together across the different modalities (Farah, Wong, Monheit, & Morrow, 1989); or do they instead reflect "horizontal" links

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between otherwise separate systems (Spence & Driver, 1996)? Second, what level(s) of processing (e.g., sensory, decision, response selection) are affected by cross-modal interactions in endogenous spatial attention?

The present study used ERP measures to investigate both of these issues. In different experimental blocks, participants were instructed to direct attention to the left or right side, in order to detect infrequent targets on that side only within the relevant modality. This relevant modality (audition or touch) was blocked. The relevant side for that modality was indicated, on a trial-by-trial basis, with a symbolic central cue. Single auditory, tactile, or visual stimuli were then presented at the cued or uncued side. Stimuli in the two currently irrelevant modalities had to be entirely ignored regardless of their position. To investigate whether control processes involved in shifts of spatial attention are supramodal or modality-specific, we measured and compared ERPs elicited by cues directing attention to the left or right in blocks where audition or touch was task-relevant. To study whether cross-modal interactions in spatial attention affect sensory-specific perceptual processes or only later postperceptual stages, we recorded ERPs to stimuli in task-irrelevant modalities at locations that were attended or unattended within the currently relevant modality.

ERP Correlates of Attentional Control Processes

Some previous studies have investigated ERP correlates of attentional control in the interval between a cue stimulus that indicates the direction of an attentional shift and a subsequent target stimulus. However, all such studies to date have been unimodal, focusing exclusively on processes underlying the control of visual–spatial attention. A major aim of the present study was to assess whether cued attentional shifts may be controlled by supramodal mechanisms. To this end, we investigated ERPs elicited during cued attentional shifts to one side or the other for auditory and for tactile tasks. If preparatory shifts of spatial attention for visual, auditory, and tactile tasks all reflect a supramodal control system, one could expect to find similar ERP correlates in the cue–target interval for these different modalities. By contrast, if separate modality-specific control systems were involved, this should be reflected in systematic differences in the ERPs recorded for the cue–target interval when the subject prepares for a stimulus in a different modality on the cued side.

In a pioneering ERP study of the control of spatial attention in a visual task, Harter, Miller, Price, LaLonde, and Keyes (1989) measured ERPs during leftward versus rightward shifts of visual attention. These were triggered by central arrow cues that indicated the side of an upcoming visual event. They found an early negative deflection at posterior electrodes contralateral to the direction of the induced attentional shift ("early-directing attention negativity," or EDAN; see also Nobre,

Sebestyen, & Miniussi, 2000; Yamaguchi, Tsuchiya, & Kobayashi, 1994; Yamaguchi, Tsuchiya, & Kobayashi, 1995). Subsequent to this an enhanced contralateral positivity at posterior electrodes ("late-directing attention positivity," LDAP) was found during later phases of the cue–target interval. In addition, Nobre et al. (2000) and Mangun (1994; see also Hopfinger, Jha, Hopf, Girelli, & Mangun, 2000) observed enhanced negativities at frontal electrodes contralateral to the direction of attentional shifts, between 300 and 500 msec after onset of the central cue ("anterior-directing attention negativity," ADAN). All these effects (i.e., the EDAN, LDAP, and ADAN) were assumed to reflect successive phases in the control of covert visual–spatial orienting. The EDAN has been linked (Harter et al., 1989) to the encoding of the spatial information provided by the cue and/or to the initiation of an attentional shift. The ADAN (Nobre et al., 2000; Mangun, 1994) has been linked to the activation of frontal structures involved in the control of spatial attentional shifts within visual space (Corbetta, Miezin, Shulman, & Petersen, 1993; Posner & Petersen, 1990). Finally, the LDAP has been linked to preparatory modulations in the excitability of sensory areas (Harter et al., 1989). The present study investigated whether similar ERP effects can be observed in the cue–target interval during shifts of attention to the location of relevant auditory or tactile events. This could be expected if the control of endogenous spatial attention is based on supramodal mechanisms.

ERP Effects of Cross-Modal Interactions in Endogenous Spatial Attention on Sensory Processing

While previous behavioral studies have uncovered the existence of cross-modal interactions in endogenous spatial attention between vision and audition, and between vision and touch (Spence & Driver, 1996; Spence et al., 2000), recent electrophysiological studies have provided additional insights into the processing stages affected by such cross-modal interactions. Eimer and Schröger (1998) investigated ERP effects of cross-modal attention for vision and audition. Attention had to be directed to the left or right to perform a task within one primary modality (vision or audition), while the other modality could be entirely ignored. Effects of spatial attention on sensory-specific N1 components were observed not only for the currently relevant primary modality, but also for stimuli in the currently irrelevant secondary modality, although these effects were typically somewhat larger in amplitude for the primary modality (see also Teder-Sälejärvi, Münte, Sperlich, & Hillyard, 1999; Hillyard et al., 1984, for similar results). Analogous ERP results were obtained by Eimer and Driver (2000) in a study of vision and touch, with the exception that touch can apparently be "decoupled" from the direction of endogenous spatial attention in

vision, provided that all tactile events are entirely task-irrelevant throughout a block of trials (see Ward, McDonald, & Lin, 2000, for further arguments about possible "decoupling," based on behavioral data).

These ERP results suggest that relatively early stages of visual, auditory, and tactile information processing (i.e., stages traditionally considered to be "unimodal") can be affected by cross-modal interactions between vision and audition, and between vision and touch (see also Kennett, Eimer, Spence, & Driver, 2001; McDonald & Ward, 2000, for related ERP evidence concerning exogenous rather than endogenous cross-modal spatial attention). This pattern of cross-modal interactions apparently influencing sensory-specific responses suggests that locations may initially be selected for attention at a multimodal level of spatial representation, with this selection then feeding down to influence "unimodal" sensory processes for incoming stimuli. If spatial selection does indeed operate supramodally, similar cross-modal interactions should also be found between audition and touch. The second major aim of the present study was to examine with ERP measures interactions in endogenous spatial attention between these two modalities. A final question was whether such interactions might be asymmetric, such that touch may be "decoupled" from multimodal influences when entirely task-irrelevant (as suggested by Eimer & Driver's, 2000, visual–tactile ERP study). In addition to studying cross-modal interactions between audition and touch, we also included visual events, to confirm and replicate previously observed cross-modal interactions involving vision.

The Present Study

Single visual, auditory, or tactile stimuli were presented on the left or right side. Each was preceded by a central symbolic precue that instructs participants to attend covertly to one side in the relevant modality. In the audition-relevant condition, the task was to detect infrequently presented auditory target stimuli (17% "oddballs," which were a double-pulse rather than the usual single-pulse stimulus) at the cued side. In the touch-relevant condition, participants had to detect infrequent tactile targets (i.e., double pulses) at the cued side. Stimuli at uncued locations were to be ignored, as were all irrelevant modality stimuli regardless of their location (vision was irrelevant throughout).

To study preparatory states involved in the control of covert attentional shifts, we examined ERP waveforms in response to cues directing attention to the left or right side, separately for the audition- and touch-relevant conditions. In order to measure ERP correlates of attentional shifts, it is important that the direction of the attentional shift (left vs. right) is not confounded with sensory differences in the cue. Therefore, the present central cues were designed to be physically equivalent across the different conditions (see also Hopfinger,

Buonocore, & Mangun, 2000; Nobre et al., 2000, for similar procedures in unimodal visual studies). Two small triangles (one red, one blue) were presented near central fixation to produce the symbolic cue, one to the immediate left and one to the immediate right of fixation. To obtain a symmetrical cue display, triangles always pointed in opposite directions ("◁▷" or "▷◁"). The direction to be attended for the task-relevant modality was indicated by the direction of pointing for the triangle in one particular color (red or blue). This relevant color was counterbalanced across subjects.

To investigate effects of cross-modal interactions in spatial attention on the processing of stimuli at attended and unattended locations, we measured ERPs to auditory, tactile, and visual nontarget stimuli. This was done at cued and uncued locations, separately for the audition- and vision-relevant conditions. Because visual stimuli were always irrelevant, any attentional modulations of visual ERPs would provide additional evidence for the existence of cross-modal interactions in endogenous spatial attention, either audio-visual (as in Teder-Sälejärvi et al., 1999; Eimer & Schröger, 1998; Hillyard et al., 1984) or tactile–visual (as in Eimer & Driver, 2000). More importantly, by examining tactile ERPs in the audition-relevant condition, and auditory ERPs in the tactile-relevant condition, we could investigate auditory–tactile and tactile–auditory interactions for the first time. Attentional modulation of auditory ERPs in the touch-relevant blocks (where auditory stimuli were irrelevant) would reveal tactile–auditory interactions in spatial attention. A similar logic applies to tactile ERPs in the audition-relevant blocks.

RESULTS

Behavioral Performance

Vocal responses were faster to tactile double-pulse targets in the touch-relevant condition than to auditory double-pulse targets in the audition-relevant condition [548 vs. 598 msec; $F(1,15) = 15.6, p < .001$]. Responses were also somewhat faster to target stimuli presented on the right versus left side [568 vs. 579 msec; $F(1,15) = 12.6, p < .003$]. Participants missed more auditory targets than tactile targets (4.3% vs. 2.7%), but this difference was not significant. False alarms to nontargets occurred on less than 0.3% of all trials.

ERPs in the Interval Between Central Cue and Peripheral Stimulus: Preparatory States

Figure 1 shows ERPs elicited in the interval between cue onset to 100 msec after the onset of the subsequent peripheral stimulus. These are shown for electrodes over the left and right hemisphere, in response to cues directing attention to the left versus right side. They are displayed separately for the audition- (A) and
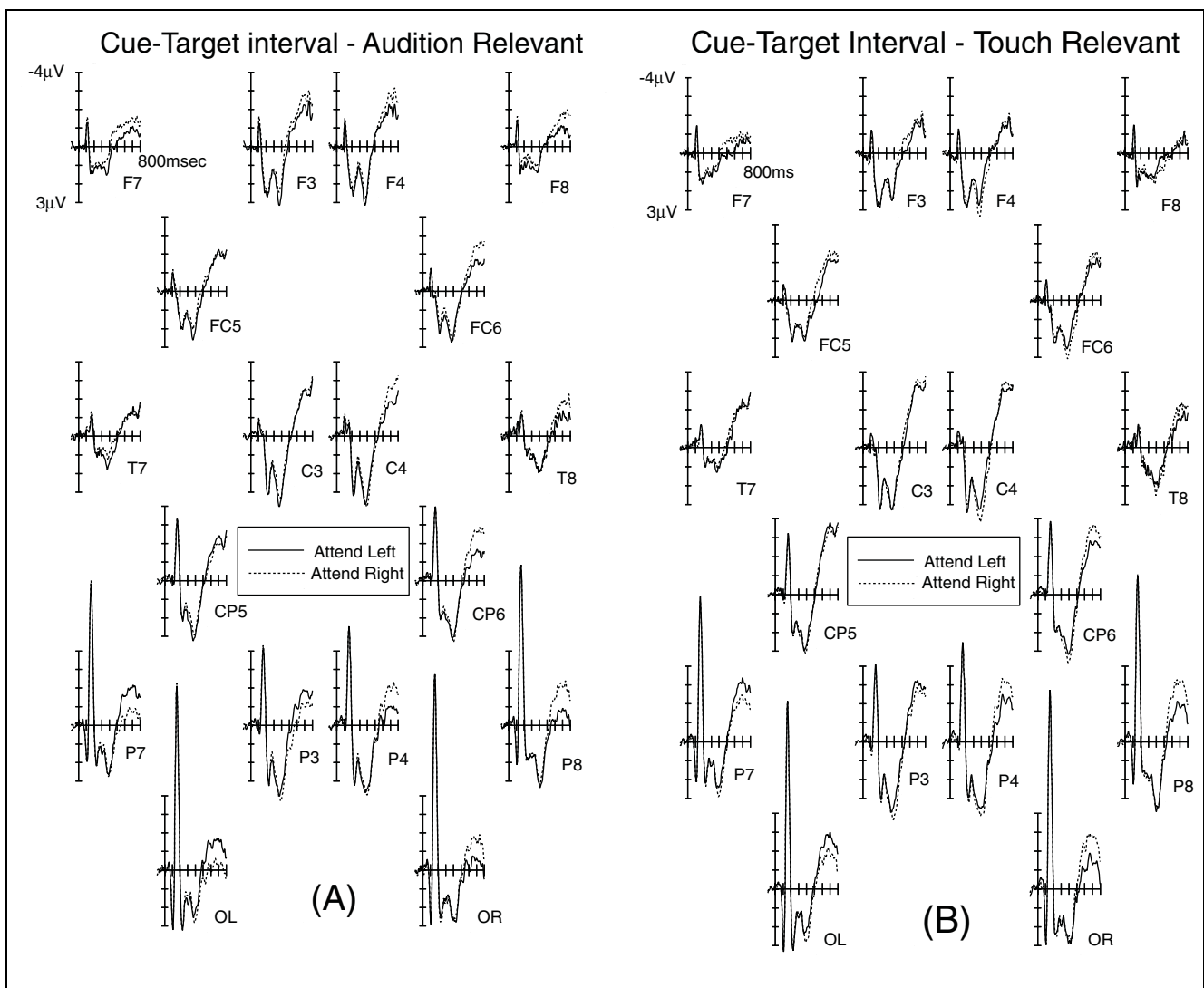
Figure 1. Grand-averaged ERPs elicited at lateral electrodes in the interval between cue onset and 800 msec after cue onset (100 msec after the onset of a peripheral stimulus), relative to a 100-msec baseline, in response to central cues directing attention to the left side (solid lines) or cues directing attention to the right side (dashed lines). (A) ERPs elicited in the audition-relevant condition. (B) ERPs elicited in the touch-relevant condition.

the touch-relevant conditions (B). The presence of ERP lateralizations sensitive to the direction of attentional shifts can be seen more clearly in the difference waveforms shown in Figure 2. These difference waves were generated in two stages. First, we subtracted ERPs recorded during attentional shifts to the right from ERPs elicited during leftward attentional shifts. Second, we subtracted the resulting difference waveforms at right electrodes from the difference waveforms emerging at corresponding electrodes over the left hemisphere. These double subtractions were conducted solely to simplify graphical presentation, not for formal statistics (see below). A net negativity contralateral to the direction of attentional shifts is reflected by positive amplitude values (downward-going deflections), while a net positivity at contralateral sites is reflected by negative values (upward deflections). Figures 1 and 2

suggest that the direction of cued attentional shifts (i.e., indicating the left or right hemifield as relevant in audition or touch) had systematic effects on ERPs elicited in the interval between central cue and subsequent peripheral stimulus. Critically, as regards our multimodal concerns, these effects were remarkably similar regardless of whether audition or touch was task-relevant. Between about 350 and 500 msec after cue onset, frontocentral ERPs were more negative at contralateral electrodes (ADAN), while no such effect was present at posterior sites. Starting about 500 msec after cue onset, posterior ERPs became more positive at contralateral sites (LDAP), whereas no such effect was visible at anterior electrodes (Figure 2).

Statistical analyses were used to confirm that the ADAN and LDAP effects apparent in Figure 2 were indeed related to systematically different ERP patterns over the

Figure 2. Difference waveforms obtained at lateral anterior, central, and posterior electrodes in the interval between cue onset and 800 msec after cue onset (100 msec after the onset of a peripheral stimulus) in the audition- (solid lines) and touch-relevant conditions (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 from ERPs in response to cues directing attention to the left, 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, and larger positivities at contralateral sites are reflected by negative values (see text). An ADAN at frontocentral contralateral sites was followed by an LDAP at posterior contralateral electrodes for both task conditions.
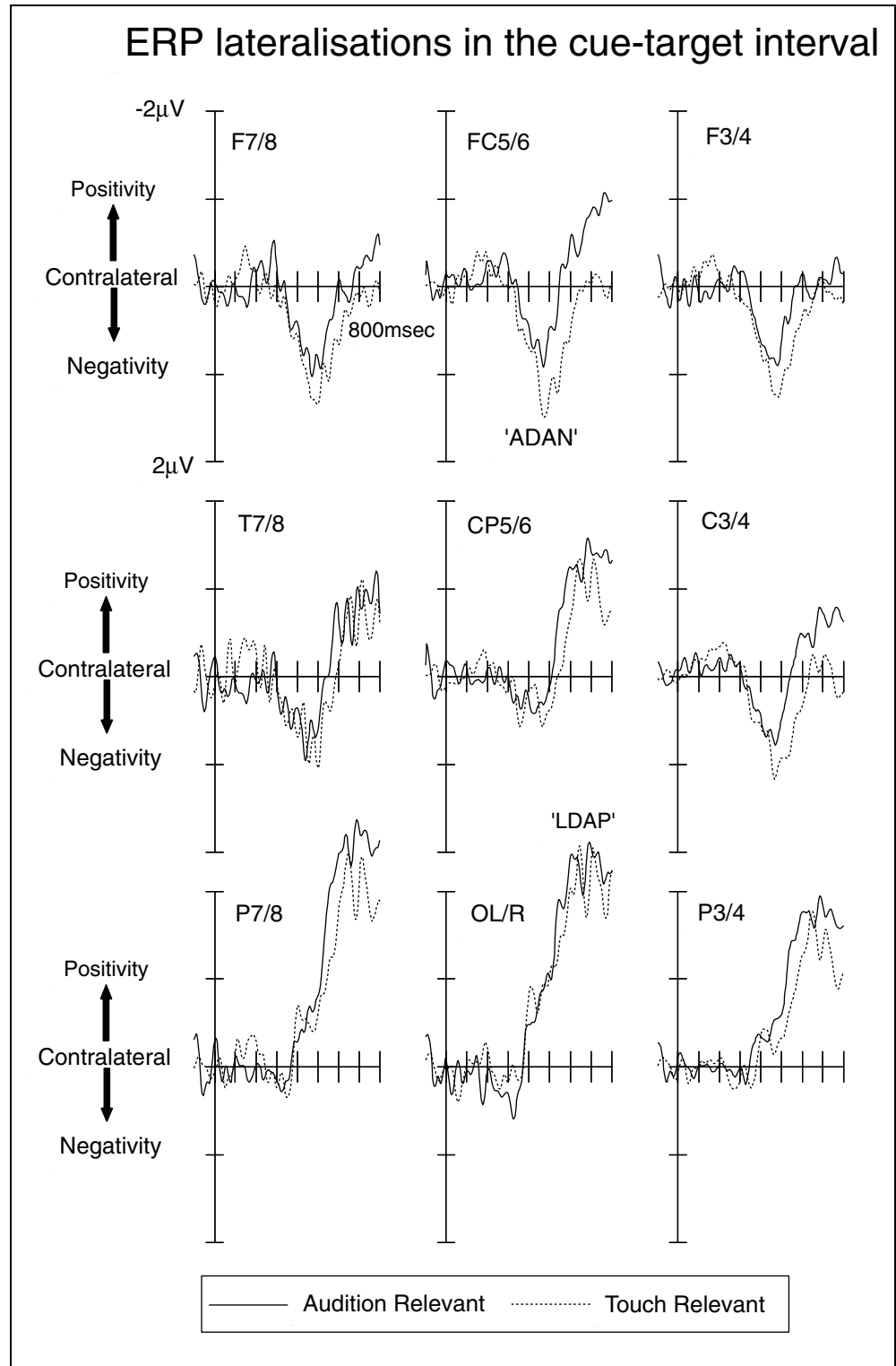
left and right hemisphere during leftward and rightward attentional shifts. In an initial analysis, ERPs elicited during leftward versus rightward attentional shifts were compared using unpaired *t* tests for each electrode site and sampling point, throughout the cue–target interval. This was done separately for the audition- and touch-relevant conditions. These analyses revealed no system-atic ERP modulations related to the direction of attentional shifts within the first 350 msec after cue onset (see Figures 1 and 2). In other words, there was no evidence whatsoever for the presence of a posterior EDAN.

Repeated measure ANOVAs were then conducted on ERP mean amplitudes elicited at lateral recording sites in the later cue–target intervals, from 350 to 500 msec and

from 500 to 700 msec, with the factors of cued direction (left vs. right), recording side (left vs. right), and task condition (audition- vs. touch-relevant). This was implemented separately for anterior, central, and posterior electrode pairs. In the 350–500-msec interval, an anterior negativity contralateral to the direction of attentional shifts (ADAN) was reflected in highly significant Recording Side × Cued Direction interactions at anterior sites [$F(1,15) = 56.9, p < .001$]. Further analyses revealed significant Recording Side × Cued Direction interactions in the audition- and touch-relevant condition at all anterior sites, as well as at C3/4 and T7/8, but not at CP5/6 or any posterior site. To assess whether an ADAN was elicited over both hemispheres, the effects of cue direction were analyzed separately for left and for right frontocentral electrodes. A reliable main effect of cued direction was present over the left hemisphere [$F(1,15) = 6.1, p < .026$], and this effect was nearly significant over the right hemisphere [$F(1,15) = 4.3, p < .055$]. Importantly, no three-way interactions (task condition by recording side by cued direction) were obtained, indicating that the ADAN was elicited similarly in the tactile- and audition-relevant conditions (see Figure 2). This was confirmed by the fact that reliable Frontal Recording Side × Cued Direction interactions were present for both task conditions when considered separately [both $F(1,15) > 27.4$, both $p < .001$].

In the 500–700-msec interval, the LDAP was reflected in a highly significant Recording Side × Cued Direction interaction at posterior sites [$F(1,15) = 23.6, p < .001$]. When analyzed separately for left and right posterior electrodes, main effects of cued direction were found in both analyses [both $F(1,15) > 10.8$, both $p < .005$]. This indicates that an LDAP was present over the left as well as over the right hemisphere. Subsequent analyses revealed highly significant Recording Side × Cued Direction interactions for both the audition- and the touch-relevant conditions [both $F(1,15) > 20.1$, both $p < .001$]. This demonstrates that an LDAP was elicited both when the relevant side was cued for audition and when it was cued for touch, with a very similar pattern being apparent for both modalities (see Figure 2). A reliable LDAP was also elicited at CP5/6 [$F(1,15) = 8.0, p < .013$], but not at T7/8 and C3/4 or at any frontal electrode.

ERPs in Response to Subsequent Peripheral Stimuli: Attentional Modulation of Sensory Responses

Auditory ERPs

Figure 3 shows ERPs elicited by auditory stimuli at cued and uncued locations when audition was task-relevant (A) or when touch was relevant instead (B). The corresponding cued-minus-uncued difference waveforms at frontal, central, and parietal sites are shown in Figure 5

(left). As expected, spatial attention resulted in enhanced negativities for auditory stimuli presented at cued relative to uncued locations. This effect started about 160 msec poststimulus, overlapping with the descending flank of the auditory N1 component. Consequently, no effects of spatial attention were obtained in an analysis window centered on the peak latency of the N1 (120–160 msec poststimulus). Between 160 and 200 msec, the main effects of spatial attention were present at lateral anterior, central, and posterior electrodes as well as at midline sites [all $F(1,15) > 5.3$, all $p < .037$]. Most importantly, there was no sign of any spatial attention by relevant modality interactions (all $Fs < 1$), indicating that attentional negativities for auditory ERPs were elicited not only in the audition-relevant condition, but also for the touch-relevant condition (see Figure 3B and Figure 5, left). That is, modulation of auditory ERPs by spatial attention were found even when audition was entirely task-irrelevant, with the central cue indicating which side should be attended for a tactile task instead. In analyses conducted separately for just the touch-relevant condition, effects of spatial attention on auditory ERPs were obtained at lateral central and posterior sites, as well as at midline electrodes [all $F(1,15) > 5.5$, all $p < .033$], and this effect approached significance at anterior electrodes [$F(1,15) = 4.0, p < .064$]. Thus, attentional negativities were elicited for auditory ERPs even when attention was cued to one side for touch, thus revealing cross-modal tactile–auditory interactions in spatial attention.

In a later time window, between 200 and 280 msec poststimulus, attentional negativities were present at lateral frontal and central electrodes as well as at midline sites [all $F(1,15) > 7.2$, all $p < .017$], but not at posterior electrodes. At lateral central electrodes plus Fz and Cz, spatial attention affected auditory ERPs in the audition-relevant condition [all $Fs(1,15) > 4.7$, all $p < .045$], but not in the tactile-relevant condition ($F < 1$). At anterior electrodes, reliable attentional negativities were elicited in the audition-relevant condition [$F(1,15) = 6.5, p < .022$]. This effect approached significance in the touch-relevant condition [$F(1,15) = 3.9, p < .067$].

As the difference waveforms in Figure 5 (left) suggest that additional attentional negativities were elicited at frontal electrodes beyond 300 msec poststimulus, further analyses were carried out on ERP mean amplitudes measured between 300 and 380 msec after auditory stimulus onset. Effects of spatial attention were found at frontal recording sites in the audition-relevant as well as in the touch-relevant condition [both $F(1,15) > 5.0$, both $p < .041$].

Tactile ERPs

Figure 4 shows ERPs elicited at lateral electrodes contralateral and ipsilateral to the stimulated hand (as well as at midline electrodes), by tactile stimuli at cued and

Figure 3. Grand-averaged
ERPs elicited by auditory
nontarget stimuli at cued loca-
tions (solid lines) and uncued
locations (dashed lines) in the
500-msec interval following sti-
mulus onset. (A) Audition-rele-
vant condition. (B) Touch-
relevant condition.
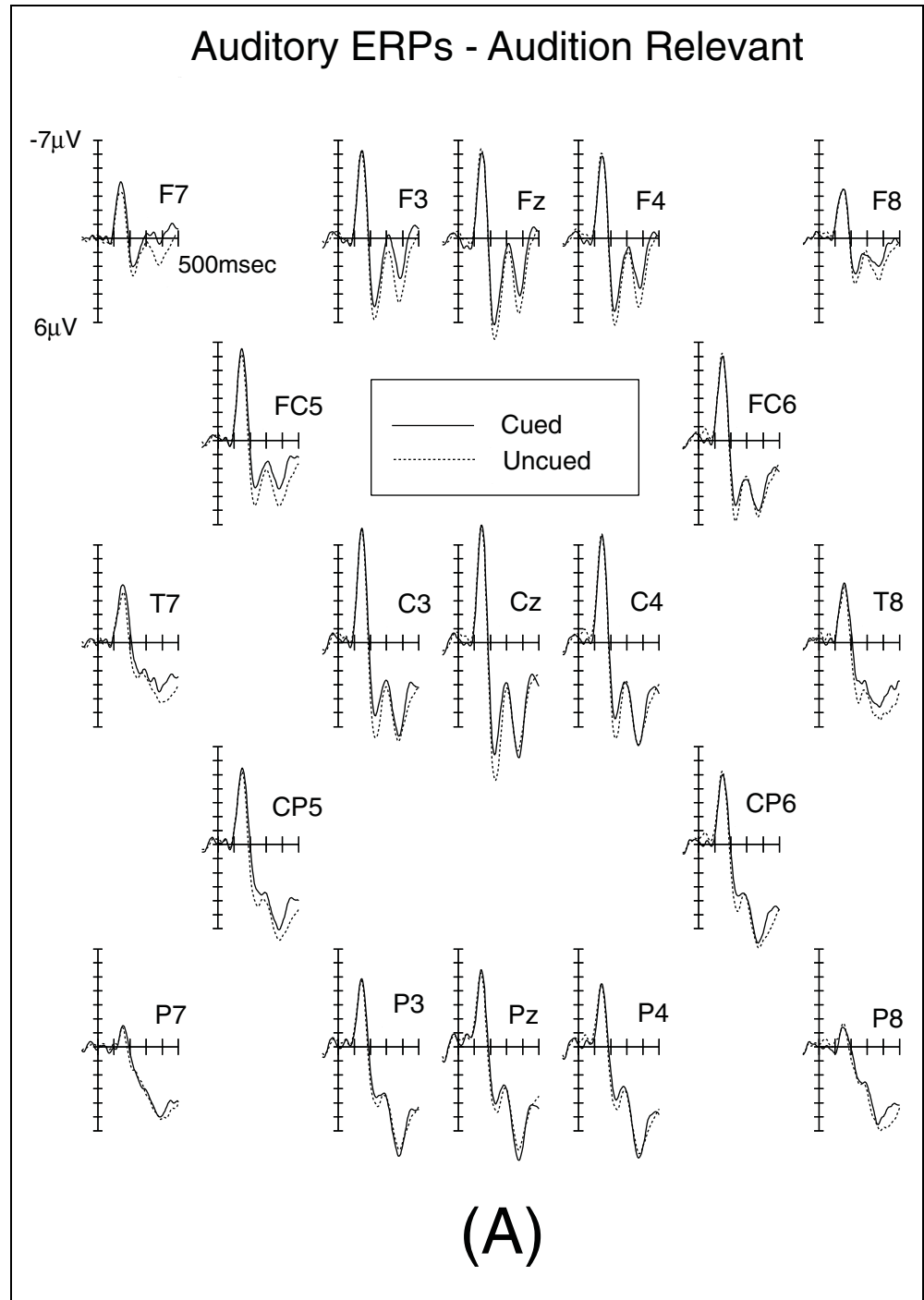
uncued locations. These are shown separately for the touch- (A) and the audition-relevant conditions (B). The resulting cued-minus-uncued difference waveforms at frontal, central, and parietal sites are shown in Figure 5 (right). Similarly to the attentional modulations of auditory ERPs, effects of spatial attention on somatosensory ERPs started around 160 msec poststimulus. When touch was relevant, enhanced negativities were elicited by tactile stimuli at cued versus uncued locations, and these effects tended to be largest at sites close to somatosensory areas (electrodes Cz and C3/4; see Figure 5, right). In contrast, attentional effects on tactile ERPs appear to be absent in the audition-relevant condition.

Statistical comparisons confirmed this pattern. Between 160 and 200 msec, effects of spatial attention on tactile ERPs were present at lateral central electrodes in the touch-relevant condition [$F(1,15) = 9.8, p < .007$], but not for the audition-relevant condition ($F < 1$). This difference was reflected in a Spatial Attention × Relevant Modality interaction [$F(1,15) = 8.5, p < .011$]. Between
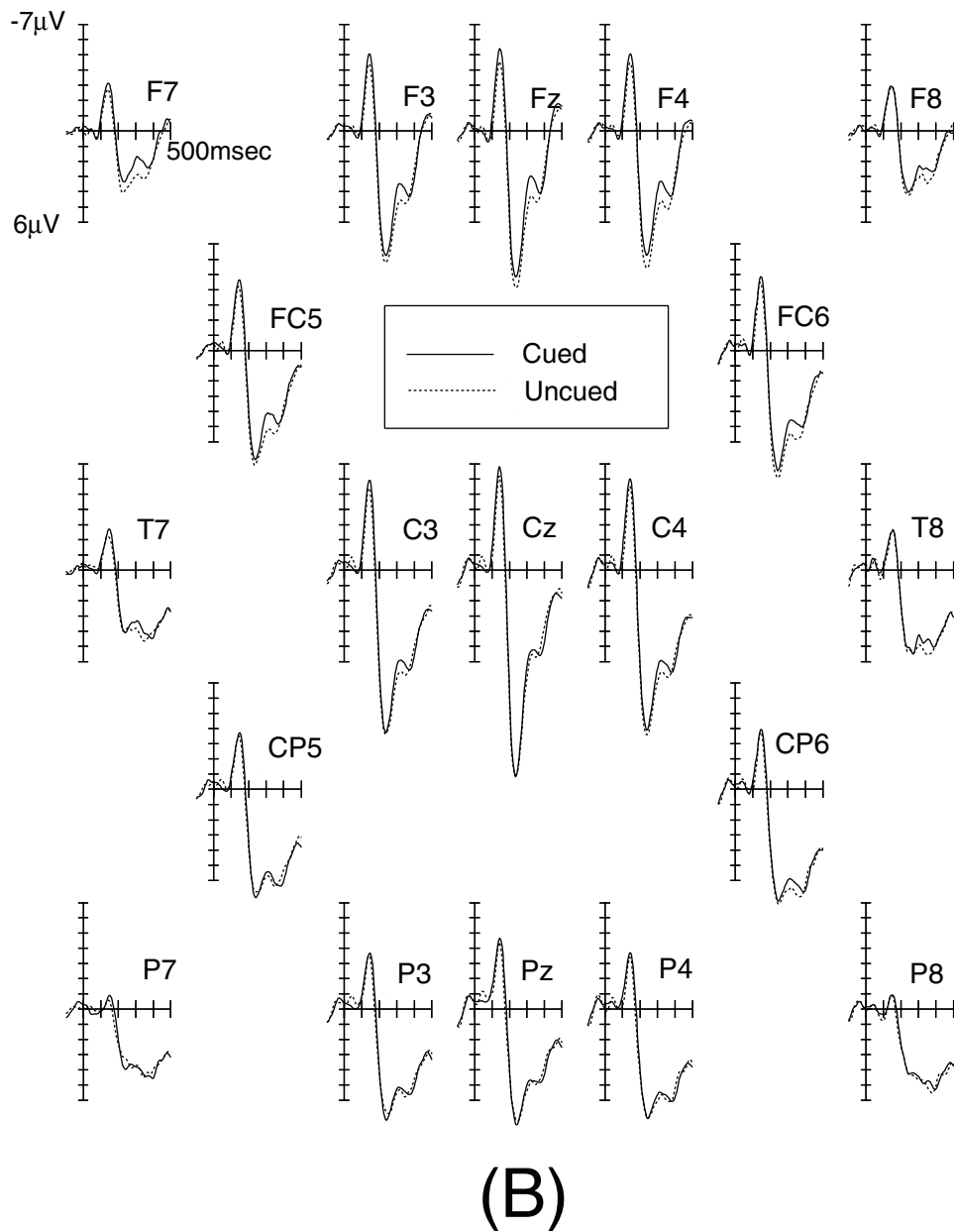
**Auditory ERPs - Touch Relevant**

Figure 3. (continued)

200 and 280 msec poststimulus, attentional negativities were present at midline electrodes and at lateral anterior and central sites when touch was relevant [all $F(1,15) > 5.6$, all $p < .032$], but not when audition was task-relevant instead (all $F < 1$). Again, this difference was reflected in significant Spatial Attention × Relevant Modality interactions [all $F(1,15) > 7.7$, all $p < .014$].

As the difference waveforms in Figure 5 (right) indicate that tactile stimuli at cued versus uncued locations elicited an additional negativity beyond 300 msec poststimulus, again in the touch-relevant conditions only, further analyses were carried out on ERP mean

amplitudes measured between 300 and 380 msec after tactile stimulus onset. Effects of spatial attention were found for all recording sites in the touch-relevant condition [all $F(1,15) > 10.8$, all $p < .005$], whereas no such effects were present for the audition-relevant condition (all $F < 1$).

Thus, while auditory ERPs had shown spatial attention effects for cued versus uncued locations regardless of whether audition or touch was the task-relevant modality, by contrast, tactile ERPs showed effects of spatial attention only when touch was task-relevant. The fact that attending to one side versus the other for audition

Figure 4. Grand-averaged ERPs elicited by tactile nontarget stimuli at cued locations (solid lines) and uncued locations (dashed lines) in the 500-msec interval following stimulus onset. (A) Touch-relevant condition. (B) Audition-relevant condition. ERPs elicited at electrodes contralateral to the stimulated hand are shown on the left, ERPs elicited at ipsilateral electrodes are shown on the right.

Somatosensory ERPs - Touch Relevant

CONTRALATERAL (A) IPSILATERAL
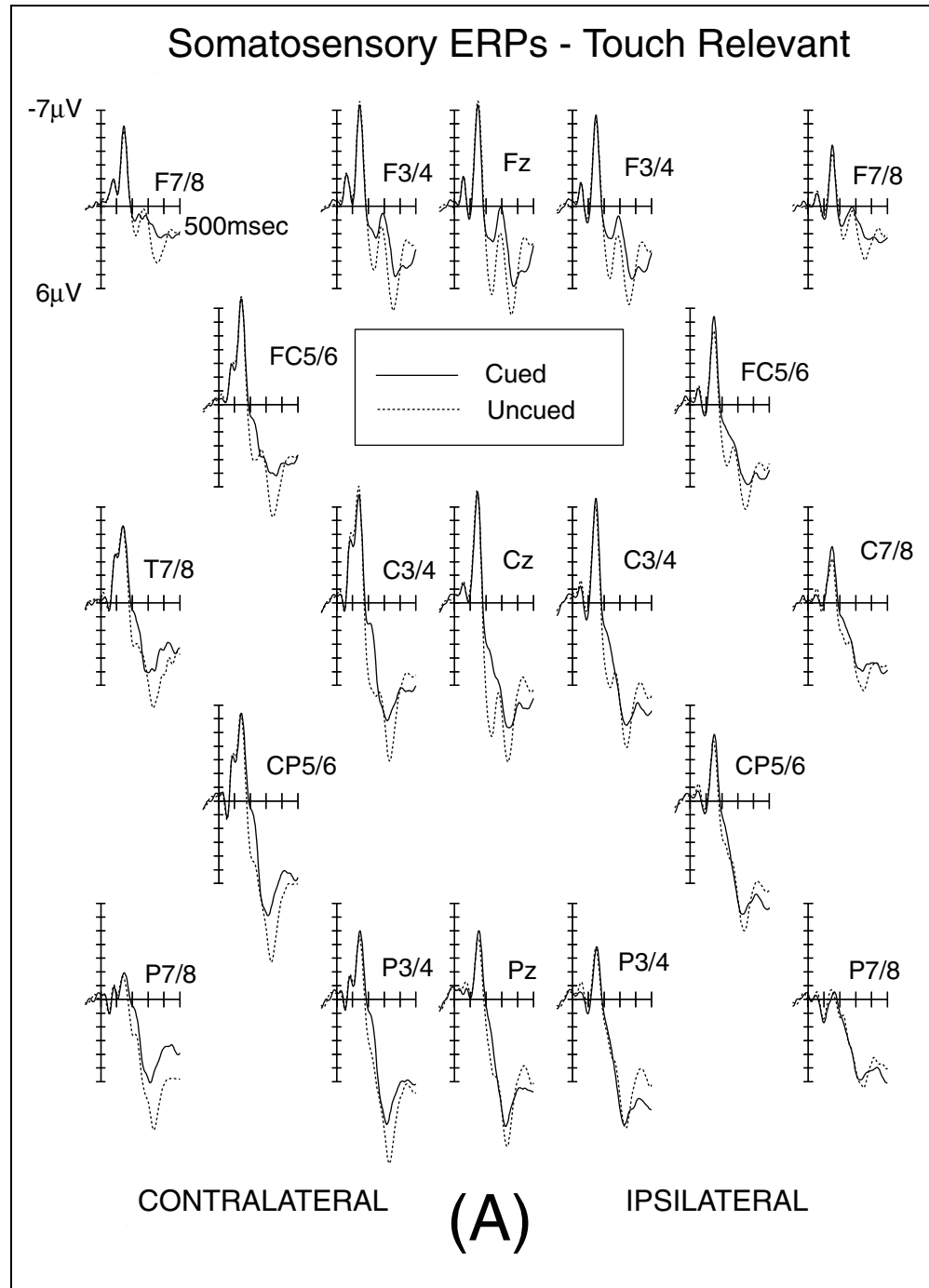
did not affect tactile ERPs is reminiscent of Eimer and Driver's (2000) finding that touch can be "decoupled" from spatial attention in another modality (vision in their study, but audition here) provided that touch is task-irrelevant throughout an entire block of trials. We discuss this point later.

Visual ERPs

Visual events were always irrelevant to the prescribed auditory or tactile tasks. The results obtained for visual ERPs in the audition- and touch-relevant conditions confirm previous cross-modal observations (Eimer & Schröger, 1998; Eimer & Driver, 2000; Hillyard et al., 1984). Accordingly, they will be summarized only briefly here. Figure 6 shows visual ERPs at lateral posterior electrodes contralateral to the side of visual stimulus presentation (P3/4 and OL/R), and at midline electrodes Cz and Pz, for visual stimuli at cued versus uncued locations in the audition- (left) and touch-relevant conditions (right). There were strong cross-modal influences of spatial attention in both cases, demonstrating

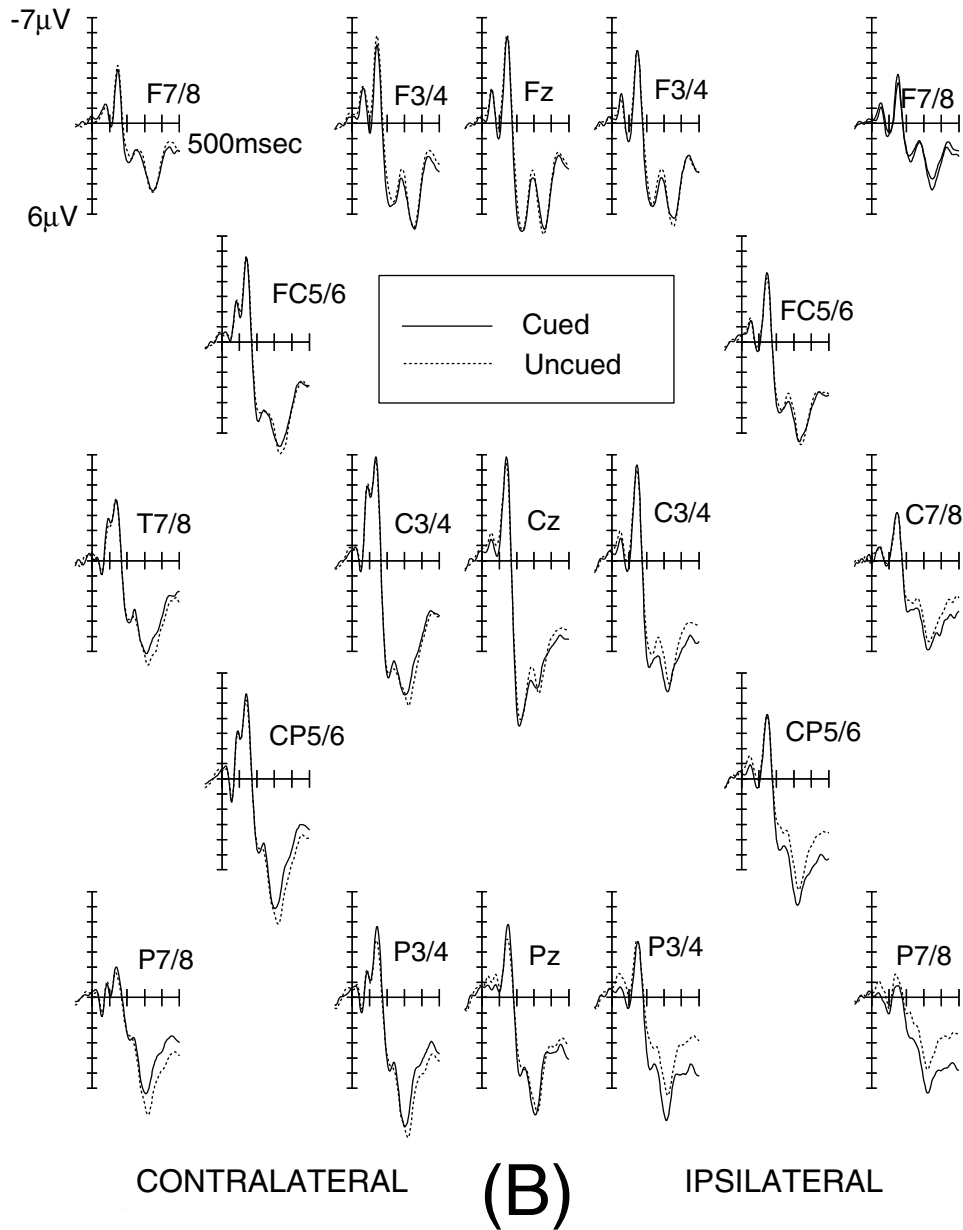## Somatosensory ERPs - Audition Relevant


Figure 4. (continued)

audio-visual and tactile–visual interactions, respectively. A reliable enhancement of the occipital P1 (90–130-msec time window) by spatial attention was present in the audition-relevant condition ($p < .048$), but not for the touch-relevant condition. However, modulations of posterior N1 components (160–200-msec time window) were found at all posterior electrodes in the touch-relevant condition (all $ps < .001$) and at P3/P4 in the audition-relevant condition also ($p < .024$). As in previous cross-modal studies, significant attentional negativities were also present in the N1 time range for visual ERPs at midline electrodes (all $ps < .036$), when atten-

tion was cued to one side for audition (as in Eimer & Schröger, 1998) or touch (as in Eimer & Driver, 2000) (see Figure 6).

DISCUSSION

The aim of the present ERP study was to investigate cross-modal interactions in endogenous spatial attention, both in terms of the control processes involved and their effects on stimulus processing. To identify ERP correlates of preparatory attentional control processes, we measured ERPs in response to central

Figure 5. Difference waveforms obtained at frontal, central, and parietal electrodes by subtracting ERPs to stimuli at uncued locations from ERPs to stimuli at cued locations. Left: Difference waveforms obtained for auditory stimuli in the audition- (solid lines) and touch-relevant conditions (dashed lines). Right: Difference waveforms obtained for tactile stimuli in the touch- (solid lines) and audition-relevant condition (dashed lines) at midline electrode, plus at electrodes contralateral (left side) or ipsilateral (right side) to the side of the stimulated hand.
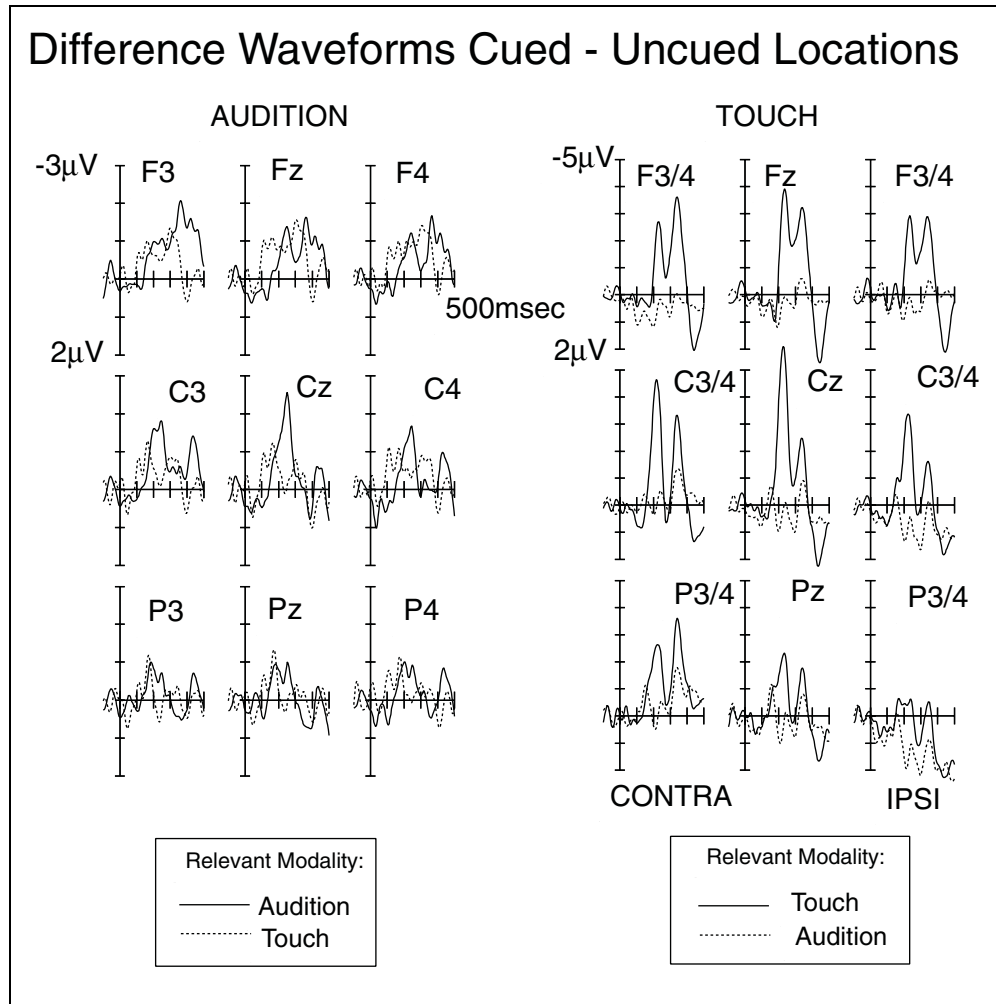

symbolic cues that signaled the relevant location for an auditory or a tactile task. In this way, we could study whether ERPs in the cue–target interval were similar or different when shifting attention to the location of relevant auditory versus tactile stimuli. Any close similarity for these two cases would implicate multimodal mechanisms in the control of endogenous spatial attention, as would any similarity to previously studied visual cases. To measure the effects of cross-modal interactions in spatial attention on processing within currently irrelevant modalities, we measured ERPs in response to auditory, tactile, and visual nontarget stimuli at locations that were attended or unattended for an auditory or tactile task. Any ERP effects of spatial attention within currently irrelevant modalities should reflect the impact of attentional interactions between sensory modalities. Previous ERP experiments with this general logic had reported audio-visual (e.g., Teder et al., 1999; Eimer & Schröger, 1998; Hillyard et al., 1984) and visual–tactile interactions (Eimer & Driver, 2000). Here, we examined possible audio-tactile interactions.

Our results provide the first evidence on the multimodal nature of preparatory attentional control mechanisms in the cue–target interval. They also confirm and extend previous ERP observations related to the effects of cross-modal interactions in spatial attention on processing within currently irrelevant modalities.

ERP Evidence on Preparatory Attentional Control Processes in the Cue–Target Interval

To investigate processes involved in the control of spatial attention, we compared ERPs elicited in the cue–target interval for cues directing attention to the left versus right side, separately for the audition- and touch-relevant conditions. Several previous studies have examined the ERP correlates of such preparatory attentional states, but only for visual–spatial orienting (e.g., Nobre et al., 2000; Mangun, 1994; Yamaguchi et al., 1994, 1995; Harter et al., 1989). If attentional shifts in different sensory modalities are controlled by a supramodal system, ERP correlates of covert attention shifts in the cue–target interval should be similar regardless of whether attention is directed to one side for a visual, auditory, or

Figure 6. Grand-averaged ERPs elicited at midline electrodes Cz and Pz and at lateral parietal (P3/4) and occipital (OL/R) electrodes contralateral to the side of presentation for visual non-target stimuli, at cued (solid lines) and uncued locations (dashed lines), in the 500-msec interval following stimulus onset. Left: Audition-relevant condition. Right: Touch-relevant condition.
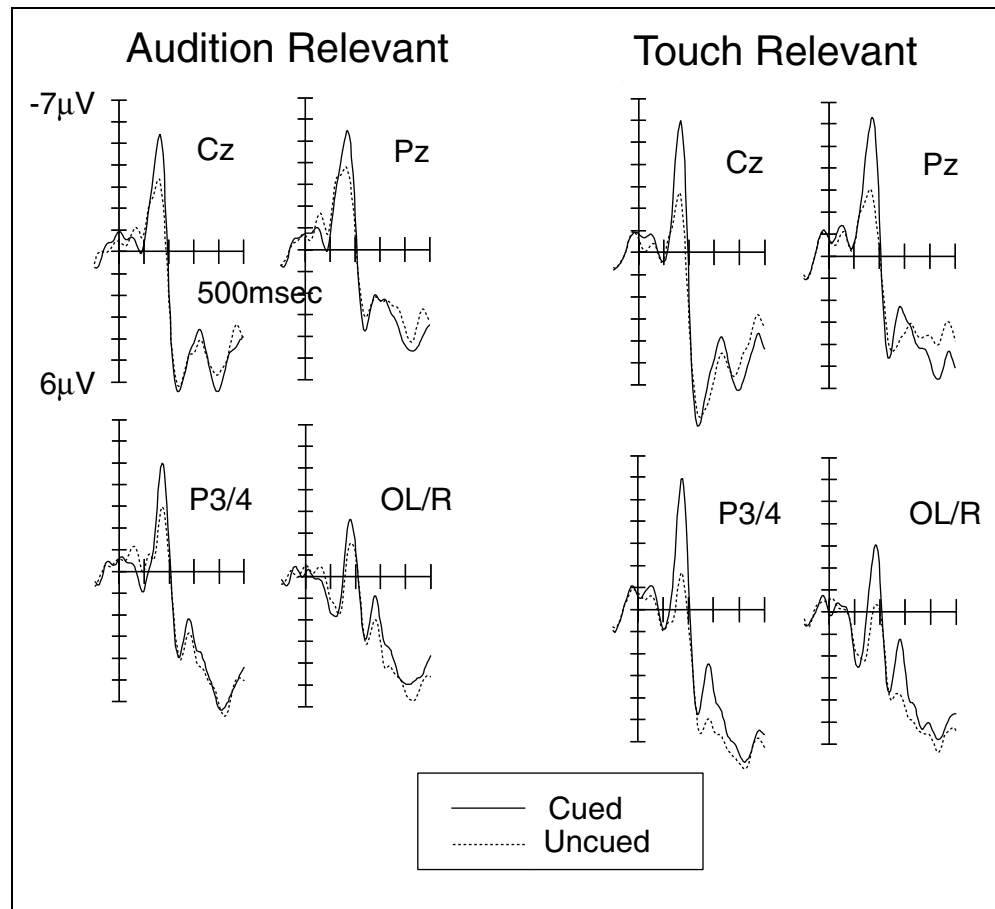
tactile task. By contrast, if separate modality-specific control systems were involved, there should be systematic differences between ERPs recorded during shifts of attention for vision, audition, or touch.

ERP modulations sensitive to the cued direction of a covert attentional shift were strikingly similar in the audition- and touch-relevant conditions. Moreover, these modulations also resembled those previously found in unimodal visual studies.[1] Between 350 and 500 msec after onset of the central cue, a frontocentral negativity was elicited contralateral to the direction of the attentional shift.[2] This ADAN was relatively small (but highly reliable), so it can be seen most clearly in the difference waveforms of Figure 2. Lateralized ERP effects that are similar to the ADAN in terms of their latency and scalp distribution have previously been reported in unimodal studies of visual–spatial attention (e.g., Nobre et al., 2000; Mangun, 1994). In those studies, they were tentatively interpreted as reflecting activation of frontal areas involved in the control of visual–spatial attention. The fact that an ADAN was elicited here in both the audition- and touch-relevant conditions, in a similar manner to previous visual studies, suggests that the processes responsible for this effect are not modality-specific. The ADAN may thus reflect supramodal control processes, possibly within an ''anterior attention system'' (Posner & Petersen, 1990) that controls spatial

parameters of attentional shifts regardless of sensory modality. In line with such an interpretation, physiological studies have identified cell populations in several areas of frontal cortex that have a multimodal representation of space (e.g., Graziano, Yap, & Gross, 1994).

Between 500 and 700 msec after cue onset, a posterior positivity was elicited contralateral to the direction of attentional shifts, in both the audition- and the touch-relevant conditions (Figure 1). This LDAP appears as negative-going deflections at lateral posterior sites in the difference waveforms of Figure 2. Given the striking similarity in terms of latencies and scalp distributions, the LDAP observed in the present study almost certainly reflects the same phenomenon as the LDAP observed in previous unimodal studies of visual–spatial orienting (e.g., Harter et al., 1989). This similarity of the LDAP for auditory, tactile, and visual cases during later phases of the cue–target interval is illustrated in Figure 7. Scalp distribution maps of ERP lateralizations are shown for the 500–700-msec interval after cue onset. These were obtained by subtracting ERPs in response to cues directing attention to the right side from ERPs to cues directing attention to the left. Enhanced positivities at electrodes contralateral to an attentional shift are indicated by negative amplitude values over the left hemisphere and positive values over the right hemisphere. Results obtained for the audition- and touch-relevant
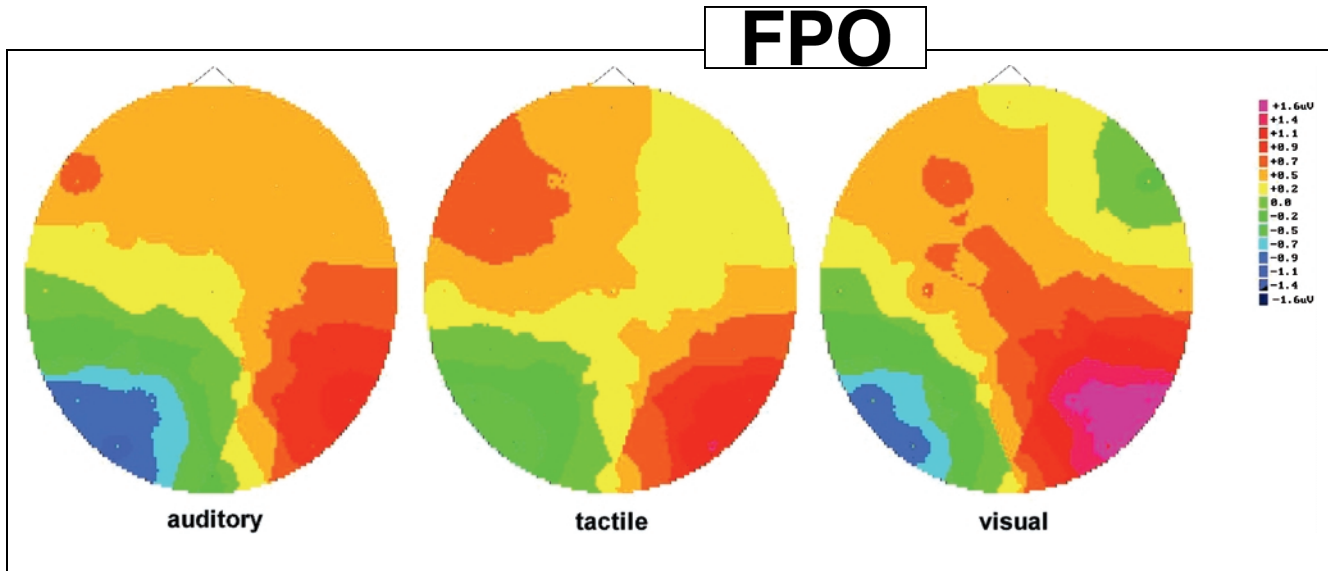
Figure 7. Scalp topography maps of mean difference amplitudes obtained in the 500–700-msec interval (relative to cue onset) by subtracting ERPs elicited in response to cues directing attention to the right side from ERPs to cues directing attention to the left side. An enhanced positivity at posterior electrodes contralateral to the direction of an attentional shift is reflected by negative amplitude values over the left hemisphere and positive amplitude values over the right hemisphere. Results obtained in the audition- (left map) and touch-relevant conditions (middle map) of the present study are presented, together with results obtained in an unpublished study from our laboratory, where an identical cueing procedure was employed to direct attention to the left or right side for a visual task (right map).

condition of the present experiment are shown. In addition, results from an unpublished follow-up study in our laboratory are also presented. Exactly the same cueing procedure was used in this study to direct attention to the left or right side in a visual task (i.e., participants now had to detect visual gap targets on the cued side). As can be seen in Figure 7, the overall distribution pattern of the LDAP is strikingly similar for attentional shifts cued for each of the three modalities.

The fact that an LDAP is elicited during cued shifts of spatial attention for an auditory task, and also for a tactile task, may seem surprising given previous suggestions that this component is related to the spatially selective activation of modality-specific visual areas (Harter et al., 1989). One possibility is that instead of reflecting visual activations, the LDAP may reflect supramodal attentional control processes (as suggested above for the ADAN). Given the distinctive posterior scalp distribution of the LDAP, it could conceivably reflect activity in posterior parietal areas, although a more ventral source remains possible. The posterior parietal cortex is involved in the control of visual–spatial attention (e.g., LaBerge, 1995), as well as in the integration of information from different sense modalities (e.g., Andersen, Snyder, Bradley, & Young, 1997). The fact that the frontal ADAN precedes the posterior LDAP could accord with Posner and Petersen's (1990) proposals that anterior circuits control more posterior spatial attention circuits (see also Hopfinger, Buonocore, et al., 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Rosen et al., 1999, for recent evidence on this from functional imaging, albeit only in unimodal visual studies).

A second possibility is that the LDAP may indeed reflect preparatory activation of modality-specific visual areas (as originally proposed by Harter et al., 1989), but that this can arise even for auditory or tactile tasks. Multimodal spatial attention may be dominated by visual representations of location, perhaps because vision typically has better spatial acuity than audition or touch (see Ward, 1994). Moreover, the present experimental situation provided many visible sources of information about the possible stimulus locations (e.g., the central fixation cross, visual cues, the visible position of the arms on the table, the visible locations of loudspeakers, and tactile stimulators on the left and right side). Such visual information may have played a role in directing attention to the left or right side even for hearing or touch. That is, visual information may have been used to anchor spatial selection by supramodal attentional control processes, even when relevant locations were selected for tactile or auditory tasks. This possibility could be studied in further experiments, by manipulating whether or not spatial information is available in vision (e.g., by repeating the study in complete darkness). In a similar vein, one could examine whether using nonvisual central cues would change the pattern of ERPs elicited in the cue–target interval.

Attentional Modulations of ERPs to Peripheral Nontarget Stimuli

Modulations of ERPs elicited by irrelevant visual stimuli confirmed previous findings (e.g., Eimer & Schröger, 1998; Eimer & Driver, 2000) that directing attention to one side for audition or touch can affect modality-

specific visual ERPs (with such effects arising as early as the P1 and/or N1; see Figure 6). More importantly, the present study provides new ERP evidence concerning the presence of similar tactile–auditory interactions in spatial attention. Directing attention to the location of relevant tactile events affected subsequent auditory as well as tactile ERPs on the cued versus uncued side (with modulation for auditory stimuli apparent within 160–200 msec of their onset). This observation provides the first demonstration of tactile–auditory interactions in endogenous spatial attention. The cross-modal influence on auditory ERPs in the touch-relevant condition was similar to that previously observed by Eimer and Schröger (1998) in their vision-relevant condition, in terms of the timing and distribution of the auditory modulation.

The present ERP evidence for an influence of cued tactile side on auditory responses may initially appear inconsistent with recent unpublished work by Lloyd, Spence, Merat, and McGlone (submitted). Using behavioral rather than ERP measures, they found no evidence for tactile–auditory interactions in endogenous spatial attention. However, it should be noted that auditory and tactile stimuli appeared at very different locations in their study (in terms of stimulus elevation), unlike the closely matched stimulus locations that were used across all modalities here, which revealed tactile–auditory interactions for the first time.

In marked contrast to the effects of spatial attention on auditory ERPs in the touch-relevant condition, directing attention in the audition-relevant condition did not influence tactile ERPs. While reliable attentional modulations of somatosensory ERPs were observed when touch was relevant (similar to previous ERP studies of tactile spatial attention; see Eimer & Driver, 2000; García-Larrea, Lukaszewicz, & Maugiere, 1995; Michie, Bearpark, Crawford, & Glue, 1987), no such effects were present in the audition-relevant condition, even though clear cross-modal effects on visual ERPs were present in the same auditory task. This corroborates and extends Eimer and Driver's (2000) proposal that the tactile modality may be unique, in that touch alone can be "decoupled" from an influence of which side is cued for another modality (provided that tactile events are entirely irrelevant throughout a block of trials). Touch may be different in this respect because it inherently relates to stimulation at the body surface rather than from external space, whereas audition and vision are both more distal senses. Whatever the reason for touch behaving differently, the present results indicate that touch can indeed be "decoupled" when task-irrelevant, not only from the spatial direction of attention for a visual task (as in Eimer & Driver, 2000), but also from spatial attention for an auditory task as here.

One striking feature of the multimodal interactions observed for ERPs to peripheral stimuli is that they typically affected early components that are traditionally considered to reflect "unimodal" sensory–perceptual processing. Thus, the visual N1 was affected by spatial attention when either audition or touch was relevant and likewise for the descending flank of the auditory N1 when touch was relevant. By contrast, some later modality-unspecific ERP components showed attentional modulations only when a particular modality was task-relevant. Thus, the present study is consistent with previous suggestions (e.g., McDonald & Ward, 2000; Eimer & Schröger, 1998; Eimer & Driver, 2000) that multimodal influences of spatial attention may affect modality-specific perceptual processing stages. In contrast, attentional effects on later, postperceptual stages seem to be largely restricted to currently task-relevant modalities (see Eimer, in press, for review).

Is Spatial Selection Supramodal?

As mentioned in the Introduction, two different ways of thinking about cross-modal interactions in spatial attention have emerged in the recent literature. One approach (e.g., Farah et al., 1989) suggests that attentional control mechanisms may be entirely supramodal, with cross-modal interactions in spatial attention reflecting this directly. Another approach (e.g., Spence & Driver, 1996) argues that spatial selection may arise primarily within the task-relevant modality, but then spread (in attenuated fashion) to affect other modalities (a "separable-but-linked" view). The results from the present study suggest that some hybrid account may be needed to provide a full explanation.

The ERP evidence obtained here in the cue–target interval is strikingly consistent with the notion of supramodal spatial selection of a cued location, regardless of whether attention is directed to the relevant location of tactile, auditory, or visual events (e.g., see Figure 7). As noted above, such selection could in principle operate primarily within the medium of visual space, yet still remain "supramodal" in the sense that the same processes are involved in selecting a particular location, regardless of whether the task involves auditory, tactile, or visual judgements at that location.

On the other hand, further aspects of our data (and of previous findings) may seem more consistent with a "separable-but-linked" view, than with an entirely supramodal account. First, effects of spatial attention on sensory processing are typically larger in amplitude for the primary task-relevant modality than for irrelevant secondary modalities (e.g., see Eimer & Schröger, 1998; Hillyard et al., 1984). Second, as discussed above, later ERP effects of spatial attention subsequent to the sensory components are typically found only for task-relevant modalities (Eimer, in press). Third, touch can apparently be "decoupled" from spatial attention in other modalities (audition here, vision in Eimer & Driver, 2000) when entirely task-irrelevant.

The present ERP data from the cue–target interval suggest that the same supramodal attentional control

processes were activated during attentional shifts, regardless of which modality (audition or touch) was task-relevant. On the other hand, the subsequent effects of spatial attention on the ERPs elicited by peripheral auditory, tactile, or visual stimuli depended to some extent on which modality was task-relevant. This apparent discrepancy implies that some aspect of preparatory state must have differed between the audition- and touch-relevant conditions, even though the ERP data obtained during attentional orienting were indistinguishable for these two conditions. The fact that the relevant modality remained constant for a series of blocks (while spatial attention was cued on a trial-by-trial basis) may have resulted in systematic tonic differences in the overall activation level between the tactile- and audition-relevant conditions. For example, a "decoupling" of touch from multimodal spatial attention might in principle be achieved simply by reducing overall activity levels for touch during blocks where tactile stimuli are irrelevant. Such "baseline shifts" in overall activity have recently been uncovered in several functional imaging studies of unimodal visual attention (e.g., Kastner et al., 1999; see Driver and Frith, 2000, for review). Applying functional imaging measures, such as fMRI, to the present design could shed further light on this issue, as some shifts in baseline activity for one modality versus another might be found between blocks.

Such considerations lead us to proposed a "hybrid" account of cross-modal interactions in spatial attention, which combines supramodal attentional control processes with others that depend on the current task relevance of each modality. The phasic selection of relevant locations may typically operate in a supramodal manner (as the present ERP data from the cue–target interval strongly suggest), so that selecting a particular side for a task in one modality can influence processing in other modalities. But the influence from such supramodal spatial selection on stimulus processing within a particular modality will also depend on the tonic state of activity in that modality, which can vary with task relevance. Note that this proposal combines aspects of two contrasting approaches to multimodal interactions in spatial attention, which are usually considered as mutually exclusive (i.e., a strictly supramodal attentional control system vs. some degree of modality-independence in the control of spatially selective processing). On our present account, spatial selection would operate supramodally, but its consequences for stimulus processing may also depend on baseline shifts related to the task relevance of one modality versus another.

In conclusion, the present ERP data from the cue–target interval strongly suggest that directing attention to the location of task-relevant stimuli is based on similar control processes regardless of the modality of these stimuli. This implies a multimodal process of spatial selection, which would, in turn, explain why selecting a particular side for one modality could affect modality-specific ERPs for stimuli in other currently irrelevant modalities. On the other hand, while such multimodal influences on sensory responses are indeed observed, ERP effects (and behavioral effects) of spatial attention are usually maximal for the task-relevant modality. A hybrid account of cross-modal interactions in spatial attention, which includes supramodal control of phasic attentional shifts, plus tonic and modality-specific "baseline shifts," may accommodate all of these findings.

METHODS

Participants

Nineteen paid volunteers participated in the experiment. Two had to be excluded because of poor eye fixation control in the cue–target interval, one further participant was excluded because of a large number of eye blinks during trials. Thus, 16 participants (nine females), aged 19–30 years (mean of 24 years) remained in the sample. Thirteen participants were right-handed, three were left-handed, and all had normal or corrected vision by self-report.

Stimuli and Apparatus

Participants sat in a dimly lit experimental chamber, with a head-mounted microphone positioned about 2 cm in front of the mouth. A computer monitor was placed in front of the participant at a viewing distance of 55 cm. Ensembles comprising two adjacent triangles were employed as central cue stimuli. Together, these two triangles covered a visual angle of about 3.5° × 2.5° and were presented at the center of the computer screen at an angle of about 30° below eye level. One of the triangles was red, the other blue, and they always pointed in opposite directions ("▷◁" or "◁▷"). These different cue arrangements were equiprobable and randomly distributed in each block. A central fixation cross, located in the space between the two triangles, was continuously present on the computer screen throughout the experimental blocks. Tactile stimuli were presented via one of two solenoids, on left and right side, which drove a metal rod with a blunt conical tip through a hole to contact the outside of either index finger. Each rod thus made contact with the outer side of the terminal segment of an index finger whenever a current was passed through the solenoid. The rods and the index fingers were occluded, so that participants could not see any rod movements. Continuous white noise was presented from a central loudspeaker at 65 dB SPL, as measured from the participant's head, throughout the experimental blocks in order to mask any sounds made by the operation of the tactile stimulators. Peripheral auditory stimuli were louder bursts of white noise (200-msec duration, including 5-msec rise and 5-msec fall times; amplitude 80 dB SPL) presented from one of

two loudspeakers located on the left and right side, near either hand. Visual stimuli were 200-msec illuminations of one of two ensembles of green LEDs on the left and right side, consisting of six segments arranged in a circle plus one central segment, with each ensemble located near one hand. The angular size of each LED was 0.65°, the diameter of the circle was 2.4°. The two tactile stimulators, the two peripheral loudspeakers, and the two LED ensembles were placed on a table 25° to the left or right of the central fixation cross, in close spatial register, and at a viewing distance of about 45 cm.

Tactile nontarget stimuli consisted of one rod tip contacting the participants' index finger for 200 msec. Tactile target stimuli had a gap, where this continuous contact was interrupted for 10 msec after a duration of 95 msec. Auditory nontarget stimuli consisted of a continuous white noise burst from either of the peripheral loudspeakers. For auditory target stimuli, the noise was interrupted after 90 msec by a 20-msec silent interval, after which the noise was turned on again for 90 msec. The gap was twice as long for auditory targets than for tactile targets because results from pilot studies indicated that otherwise it was much easier to detect tactile gap targets than auditory gap targets. All visual stimuli consisted of a continuous 200-msec illumination of one LED ensemble (no visual targets were required, as there was no visual task). Vocal response onset times were measured with a voice key.

Procedure

The experiment consisted of 16 experimental blocks with 72 trials per block. Each trial started with the presentation of a central cue (100-msec duration), which was followed after an interval of 600 msec by an auditory, tactile, or visual peripheral stimulus (200-msec duration). Intertrial interval was 1000 msec. Two task conditions were delivered, each consisting of eight successive blocks. In the audition-relevant condition, the task was to respond vocally (by saying ''yes'') whenever an auditory gap target was presented at the location (left or right) indicated by the central cue on that trial. Auditory events on the uncued side (including those with gaps) were to be ignored, as were any tactile or visual events on either side. In the touch-relevant condition, the task was to respond vocally whenever a tactile gap target was presented at a cued location, with all the tactile events on the other side to be ignored, as for all visual and auditory events on either side. The relevant location for audition or touch was cued by the direction of either the red or the blue central triangle. For half of the participants, blue triangles indicated the attended location, while red triangles were relevant for the other half of the participants. Relevant left- and right-pointing triangles were presented with equal probability to the left or right of fixation.

In 60 trials per block, auditory, tactile, or visual nontargets were presented with equal probability and in random order on the left or right side at cued or uncued locations. In the remaining randomly intermingled 12 trials, gap targets within the relevant modality were presented on the left or right side. Eight of these targets were presented on the cued side (and thus required a response), while the remaining four were presented on the uncued side (requiring no response). The order in which the audition- and touch-relevant conditions were delivered was balanced across participants. Instructions specifying the relevant modality were displayed on a computer screen prior to the start of each block. Participants were instructed to direct their attention to the cued location in just the relevant modality, in order to respond as quickly and accurately as possible to auditory (or tactile, depending on block) target stimuli presented at this location, while withholding responses to all other stimuli. They were explicitly encouraged to maintain central eye fixation throughout the trials. Several training blocks were run prior to the beginning each of the two task conditions. Eye movements were closely monitored during these training blocks. Whenever the horizontal EOG revealed that participants did not maintain central eye fixation, they were reminded again of the necessity of continuously fixating the central cross throughout an experimental block. Additional training blocks were run until fixation control was regarded as satisfactory.

Recording and Data Analysis

EEG was recorded with Ag–AgCl electrodes and linked-earlobe reference from F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, and P8 (according to the 10–20 system) and from OL and OR (located halfway between O1 and P7, and O2 and P8, respectively). Horizontal EOG was recorded bipolarly from the outer canthi of both eyes. The impedance for the EOG electrodes was kept below 10 kΩ and for all other electrodes below 5 kΩ. The amplifier bandpass was 0.1 to 40 Hz. EEG and EOG were sampled with a digitization rate of 200 Hz and stored on disk. Voice onset times were measured for each vocal response.

EEG and EOG were epoched off-line into 1400-msec periods, starting 100 msec prior to cue onset and ending 600 msec after the onset of the peripheral stimulus. Separate averages were computed for ERPs recorded in the cue–target interval (relative to a 100-msec baseline preceding cue onset) and for ERPs in response to subsequent peripheral stimuli (relative to a 100-msec baseline preceding the onset of these stimuli). Trials with eyeblinks (Fpz exceeding ±60 μV relative to baseline), horizontal eye movements (HEOG exceeding ±30 μV relative to baseline), or other artifacts (a voltage exceeding ±60 μV at any electrode location relative to baseline) were excluded from analysis. Averaged HEOG waveforms in response to cues directing attention to the left versus right side, obtained in both task conditions,

were scored for systematic deviations of eye position, indicating residual tendencies to move the eyes towards the cued location. A residual HEOG deviation exceeding ±2 μV led to the disqualification of two participants.

The EEG obtained in the cue–target interval was averaged for all combinations of task condition (audition- vs. touch-relevant) and cued direction (left vs. right). Mean amplitude values were computed at lateral anterior sites (F7/8, F3/4, FC5/6), lateral central sites (T7/8, C3/4, CP5/6), and lateral posterior sites (P7/8, P3/4, OL/R) within different latency windows relative to cue onset, and these values were analyzed separately for anterior, central, and posterior electrodes by repeated measures ANOVAs for the factors of task condition, cued direction, and recording side (left vs. right hemisphere). The EEG obtained in response to peripheral stimuli was averaged for nontarget (i.e., single pulse) trials only, to avoid contamination by vocal responses to double-pulse targets. Trials where false-positive vocal responses were recorded on nontarget trials were excluded from analysis.

Separate averages were computed for auditory, tactile, and visual nontarget stimuli for all combinations of task condition, cued direction, and stimulus side (left vs. right). Mean amplitude values were computed for auditory, somatosensory, and visual ERPs within different latency windows measured relative to onset of the peripheral stimulus. Mean amplitude values obtained at lateral anterior sites, lateral central sites, lateral posterior sites, and at midline electrodes (Fz, Cz, Pz) were submitted to separate ANOVAs. For the analyses of visual ERPs, electrode Oz was included in the set of midline electrodes. Analyses of auditory and somatosensory ERPs in response to peripheral stimuli included the factors of electrode site, recording side (for lateral electrodes only), task condition, spatial attention (stimulus at cued location vs. uncued location), and stimulus side. Visual ERPs were analyzed separately for the audition- and touch-relevant conditions, omitting the factor of task condition. When appropriate, Greenhouse–Geisser adjustments to the degrees of freedom were performed, and the adjusted p values are reported. Nonsignificant terms and results due trivially to stimulus and anatomical laterality are not reported. Whenever interactions between attention and electrode site were found (for brevity, these are not all reported in full), additional analyses were conducted for single electrode sites. For vocal responses, repeated measures ANOVAs were performed on response latencies and on arc sin-transformed error rates for the factors of task condition and target location (left vs. right).

Notes

1. The only difference between the present results and previous ERP patterns observed in the cue–target interval for visual–spatial attention was that no posterior EDAN was found at electrodes contralateral to the direction of an attentional shift. The absence of an EDAN in the present study may reflect functional differences between attentional orienting processes in vision versus audition and touch. Alternatively, the EDAN observed in some previous unimodal visual studies may at least partially result from physical dissimilarities between cues directing attention to the left versus right. With one notable exception (Nobre et al., 2000), all previous ERP studies reporting EDAN-like effects in the cue–target interval compared left- and right-pointing arrow cues that differed physically.

2. It is unlikely that the ADAN is an artifact of undetected eye movements in the direction indicated by the cue. Trials with eye movements were excluded from analysis, and the residual HEOG deviation in the cue–target interval in response to left and right cues was below ±1 μV. Inspection of Figure 2 shows that ADAN amplitudes were of comparable size at frontal electrode pairs (F7/8, F3/4) and at C3/4, and tended to be largest at FC5/6. This distribution is inconsistent with the idea that the ADAN is caused by eye movement contamination, which should be most pronounced at frontal sites.

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