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Crossmodal links in spatial attention between vision, audition, and touch: evidence from event-related brain potentials

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Abstract

Results from event-related potential (ERP) studies are reviewed that investigated crossmodal links in spatial attention between vision, audition and touch to find out which stages in the processing of sensory stimuli are affected by such crossmodal links. ERPs were recorded in response to visual, auditory, and tactile stimuli under conditions where attention was directed to a specific location within one (primary) modality, while stimuli in another (secondary) modality were to be ignored regardless of their position. Systematic ERP effects of spatial attention were observed not only in the primary modality, but also for secondary modality stimuli, thus revealing crossmodal links in spatial attention. These links affected relatively early sensory-specific ERP components between 100 and 200 ms post-stimulus. Beyond 200 ms, ERPs to secondary modality stimuli were little affected by the current focus of attention within another modality. This pattern of results suggests that crossmodal links in spatial attention may affect sensory-perceptual processes within modality-specific cortical regions, but have little impact on later post-perceptual processing stages.

Keywords: Visual-spatial attention; Auditory-spatial attention; Tactile-spatial attention; Crossmodal attention; Event-related brain potentials

1. Introduction

Research on spatial attention has traditionally focused on spatially selective processing within single sensory modalities. However, in everyday life, attention often needs to be directed to information delivered by different input systems, but from the same location in space. For example, when trying to follow a conversation in a noisy party, attending to relevant lip movements may be as important as attending to the speaker's voice coming from the same location. Spatial synergies in the processing of information across sensory modalities could facilitate the crossmodal co-ordination and integration of attentional processing, and thus the selection of relevant objects and events. Whether there are crossmodal links in spatial attention between vision, audition, and touch, and how such links affect performance, has only recently been addressed systematically (see [6] for an overview).

Several behavioural studies (eg, [2,29,30]) have found evidence for cross-modal links in endogenous (voluntary) spatial attention between vision, audition, and touch. In these studies, attention was covertly directed to the expected location of target stimuli within one (primary) modality. On some trials, stimuli of a different (secondary) modality were presented, but these stimuli were equally likely (or even somewhat more likely) to be presented on the side opposite to the expected location in the primary modality. Superior performance for stimuli at the expected location in the primary modality was observed not only for that primary modality, but also for secondary modality stimuli, suggesting that the focus of attention within one modality influences the processing of information in other modalities.

While these results demonstrate crossmodal links in spatial attention, they do not allow any firm conclusions as to which stages in the processing of visual, auditory, and somatosensory processing are affected by crossmodal links in spatial attention. Performance benefits for secondary modality stimuli at attended locations could result from effects of crossmodal attention on perceptual processes, or from attentional modulations of later, post-perceptual stages. In addition, such crossmodal effects may reflect the activity of a

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single supramodal system that controls covert attentional orienting processes in different modalities [13], or may result from spatial synergies between independent modality-specific attentional control systems [29].

Because of their excellent temporal resolution, event-related brain potentials (ERPs) provide a useful tool to identify processing stages affected by attentional selectivity, as well as to investigate control processes involved in directing spatial attention. Effects of spatial attention can be investigated by measuring ERPs to stimuli presented at attended and unattended locations. ERP waveforms consist of successive components, which reflect different stages in the processing of external events. Short-latency ERP components are sensory-specific, elicited maximally over modality-specific brain regions, and sensitive to variations in basic physical stimulus parameters. These 'exogenous' components reflect modality-specific perceptual processes in the visual, auditory, or somatosensory system [4]. Longer-latency ERP components are not sensory-specific, have a broader, modality-unspecific scalp distribution, and are not directly affected by variations in physical stimulus attributes. These 'endogenous' components are generally linked to post-perceptual processing stages involved in stimulus identification and categorisation, and in response selection and activation [4]. If early ERP components reflect sensory-perceptual processing, while later components are related to post-perceptual processing stages, studying how these components are affected by spatial attention can help to distinguish perceptual from post-perceptual effects of attentional selectivity.

Effects of unimodal spatial attention on ERP waveforms have been investigated in vision (eg, [7,8,23]), audition (eg, [1,16,27]), and touch (eg, [15,25,26]). Both modality-specific and unspecific effects were observed (see below for more details), suggesting that spatial attention affects sensory-specific perceptual stages as well as post-perceptual processes. Because ERPs are systematically affected by unimodal spatial attention, ERP measures can also be useful to study links in spatial attention across sensory modalities. If there are such links, systematic differences between ERPs to visual, auditory, or tactile stimuli at attended versus unattended locations should be observed under conditions where attention is currently directed within another sensory modality. Effects of crossmodal links in spatial attention on sensory-specific ERP components would indicate that such links modulate perceptual processes in modality-specific brain areas. If crossmodal effects were only found for later sensory-unspecific components, this would suggest that crossmodal links affect stages beyond the initial perceptual processing of stimuli.

2. Experimental procedures

We have employed ERP measures to investigate effects of crossmodal links in spatial attention between vision, audition, and touch on the processing of visual, auditory, and tactile information, in a series of studies which used variations of one basic experimental procedure (see Fig. 1). Visual stimuli were brief flashes of peripheral LEDs, auditory stimuli were presented via loudspeakers, and tactile stimuli were delivered by punctators driven by solenoids which were attached to the left and right index finger. All stimuli were presented on the left or right side (about 25° to the left or right of fixation) at closely aligned locations for the different modalities (see Fig. 1). White noise was continuously presented throughout the experimental blocks to mask sounds made by the tactile stimulators. In most experiments, two sensory modalities were involved (vision and audition, or vision and touch, or touch and audition). One modality was task-relevant (primary modality), the other was entirely task-irrelevant (secondary modality). These assignments were reversed in the second half of the experiment, and the order of the task-relevant modality was counterbalanced across participants. On each trial, a single stimulus was presented on the left or right side. Participants had to maintain central fixation, and to direct their attention to the left or right side within the primary modality in order to detect and respond vocally (by saying 'yes') to occasional 'oddball' target stimuli in the primary modality at the attended location. Participants were told to ignore primary modality stimuli at unattended locations as well as all secondary modality stimuli (regardless of their position). Targets were infrequent and were either slightly longer than non-targets [9,11], or contained a 'gap', where the continuous stimulation was briefly interrupted by an empty interval [10,12]. In some experiments [11,12], attended locations were indicated on a trial-by-trial basis by arrow precues presented centrally on a computer screen (as shown in Fig. 1). In other experiments [9,10], no cues were presented, and the attended location was specified via verbal instructions at the beginning of each block, and remained constant throughout a block of trials.

EEG was recorded with Ag-AgCl electrodes relative to a linked-earlobe reference (amplifier bandpass 0.1 to 40 Hz, digitisation rate 200 Hz). Trials with vocal responses to non-target stimuli, eyeblinks, horizontal eye movements, or other movement artefacts were excluded from analysis. ERPs were computed for non-target stimuli only, to avoid any contamination with potentials caused by response selection and execution. ERPs measured in response to stimuli at attended and unattended locations were computed separately for the primary and secondary modality. Mean amplitude values were computed for auditory, somatosensory, and visual ERPs within different time windows centered on the latencies of successive ERP components. These values were then submitted to repeated measures analyses of variance, including the factors electrode site, stimulus side, primary versus secondary modality, and attended versus unattended location. The α level criterion was set at $P < 0.05$, and only significant effects will be reported below.

Because covert spatial attention was directed to the relevant location within the primary modality, attentional effects on ERPs elicited by primary modality stimuli should be similar to the effects reported in previous unimodal studies. Because participants were instructed to ignore secondary modality stimuli regardless of their location, there was no need for any additional attentional shift within this modality. The critical question was whether ERPs obtained for secondary modality stimuli would nevertheless be affected by the current focus of attention within the primary modality. The presence of ERP effects of spatial attention for the secondary modality would demonstrate that the locus of spatial attention in the primary modality modulates the processing of secondary modality stimuli, and thus provide evidence for the existence of crossmodal links in spatial attention.

3. Crossmodal links in spatial attention between vision and audition

In an initial study [11], we used this procedure to investigate crossmodal links in spatial attention between vision and audition. In one experimental half (Vision Primary), participants were instructed to re-

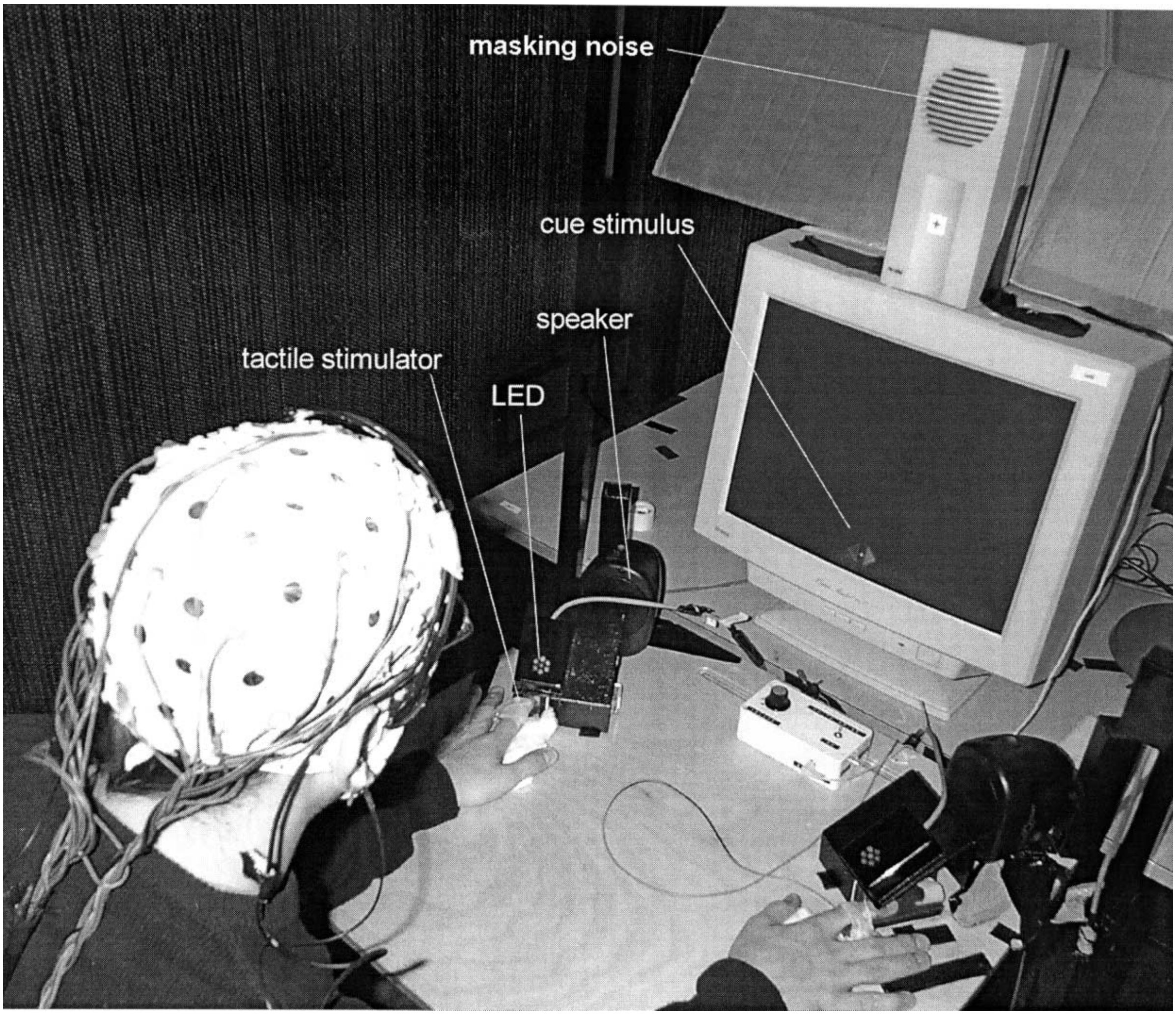

Fig. 1. The basic experimental setup used in the ERP studies reviewed in this paper. EEG was recorded while single stimuli were presented on the left or right side. Visual stimuli were brief flashes of LEDs, auditory stimuli were presented via loudspeakers, and tactile stimuli were delivered by stimulators attached to the left and right index finger. Participants had to direct attention to one side in order to detect occasional target stimuli in one modality at that location. In the experiment shown here, the attended side for the relevant modality is indicated at the beginning of each trial by a symbolic precue presented on a computer screen. In other experiments, no precues were shown, and the attended location was constant for a block of trials.

spond to visual targets at attended locations and to ignore all auditory stimuli. In the other half (Audition Primary), auditory targets at attended locations had to be detected, and visual stimuli were to be ignored. Relevant locations were indicated by symbolic precues (left-pointing and right-pointing arrows) at the beginning of each trial. That is, participants had to frequently shift their attention from the left to the right, or vice versa, on successive trials (transient attention).

Fig. 2 shows ERPs elicited at occipital electrodes contralateral to the visual field of stimulus presentation in response to visual non-target stimuli at attended and unattended locations when vision was primary (top) and in the Audition Primary condition (bottom). When vision was primary, enhanced visual P1 and N1 components were elicited by visual stimuli at attended locations, confirming findings from previous unimodal visual ERP studies [7,8,23]. P1 and N1 are modality-specific components thought to be generated in ventrolateral extrastriate occipital cortex (P1), or in lateral occipito-temporal areas (occipito-temporal N1) [22,24]. Attentional modulations of these components reflect effects of spatial attention on relatively early stages of visual-perceptual processing. P1 modulations have been attributed to 'sensory gating' mechanisms in extrastriate visual cortex, while the N1 effect may indicate attentional modulations of visual feature discrimination processes [22]. In the Audition Primary condition, the P1 component elicited by visual stimuli was not affected by attention. In contrast, spatial attention clearly modulated the subsequent N1 component. As can be seen in Fig. 2 (bottom), the N1 was larger in response to visual stimuli at locations attended within audition. This finding not only reflects the existence of crossmodal links in spatial attention from audition to vision, but also suggests that such links may affect sensory-perceptual stages of visual processing. Fig. 2 also shows that N1 components were larger when vision was relevant (top) than when visual stimuli could be entirely ignored (bottom). This difference reflects the impact of *intermodal attention* (attention to one input modality versus another) on visual ERPs (see [3,37], for similar ERP effects of intermodal attention).

Fig. 3 illustrates the findings for the auditory modality obtained in the same study. It shows ERPs elicited at the vertex electrode (Cz) in response to auditory stimuli at attended and unattended locations in the Audition Primary (top) and Vision Primary (bottom) conditions. Similar to previous unimodal auditory ERP studies [1,27], auditory-spatial attention was reflected in an enhanced negativity for attended-location stimuli

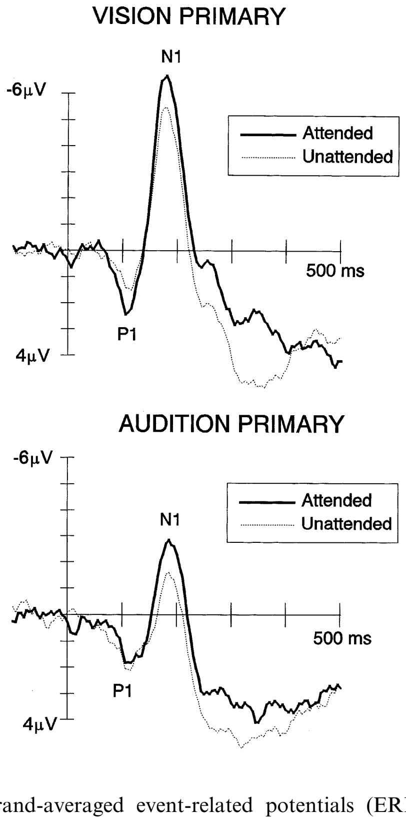

Fig. 2. Grand-averaged event-related potentials (ERPs) elicited at occipital electrodes contralateral to the visual field of stimulus presentation in response to visual stimuli at attended locations (thick solid lines) and unattended locations (thin dashed lines) under conditions where attention was directed to one side within vision (Vision Primary, top) or within audition (Audition Primary, bottom).

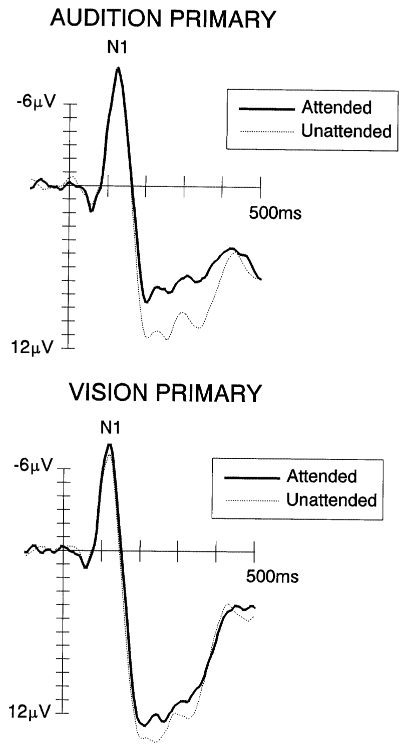

Fig. 3. Grand-averaged event-related potentials (ERPs) elicited at Cz in response to auditory stimuli at attended locations (thick solid lines) and unattended locations (thin dashed lines) under conditions where attention was directed to one side within audition (Audition Primary, top) or within vision (Vision Primary, bottom).

that started on the descending flank of the auditory N1 component, and remained present for several hundred milliseconds. The early phase of this negative difference ('Nd') between attended and unattended auditory stimuli has been thought to originate from auditory cortex in the superior temporal lobe, while the 'late Nd' beyond 200 ms post-stimulus has been linked to subsequent processing stages like the maintenance of stimuli in auditory memory [27,36]. As can be seen from Fig. 3, an 'early Nd' was present not only when audition was primary, but also in the Vision Primary condition (bottom), revealing the existence of crossmodal links in spatial attention from vision to audition, and suggesting that visual-spatial attention may have an effect on sensory-specific auditory processing. However, the 'late Nd' beyond 200 ms post-stimulus was considerably attenuated when vision was primary (see also [18,33] for analogous findings). Similar to the results obtained for vision, auditory N1 components were larger when auditory stimuli were relevant (top) than under conditions where they could be ignored (bottom), again due to the influence of intermodal selective attention.

Overall, the ERP results obtained in this visual/auditory study [11] demonstrate that there are crossmodal links in spatial attention between vision and audition, and vice-versa, thus supporting and extending previous behavioural evidence for such links [29]. The fact that crossmodal attention had an effect on sensory-specific components in the secondary modality suggests that these crossmodal links may affect sensory-perceptual processing stages. Directing attention within audition modulates the sensory processing of visual stimuli, and directing attention within vision modulates the modality-specific processing of auditory stimuli.

4. Crossmodal links in spatial attention between vision and touch

Behavioural evidence has also suggested that there are symmetrical crossmodal links in spatial attention between vision and touch [32]. We investigated whether such links are reflected in visual and somatosensory ERPs in an experiment [10] that employed a procedure similar to the visual/auditory study [11], except that attention had to be maintained at one specific location for an entire experimental block (sustained attention). Participants were instructed at the beginning of each block to direct their attention to the left or right side within just the primary modality in order to detect infrequent targets at that location in that modality only. They had to respond to visual 'oddball' targets at attended locations in the Vision Primary condition, and to tactile 'oddball' targets at attended locations in the Touch Primary condition, while ignoring all secondary modality stimuli, regardless of location.

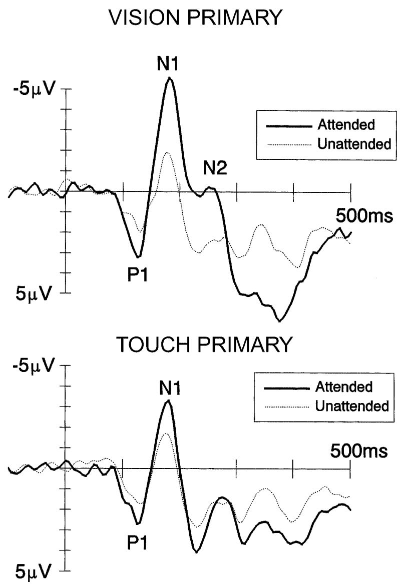

Fig. 4. Grand-averaged event-related potentials (ERPs) elicited at occipital electrodes contralateral to the visual field of stimulus presentation in response to visual stimuli at attended locations (thick solid lines) and unattended locations (thin dashed lines) under conditions where attention was directed to one side within vision (Vision Primary, top) or within touch (Touch Primary, bottom).

Attentional modulations of visual ERPs were similar to the effects observed in the visual/auditory study. Fig. 4 shows visual ERPs at occipital electrodes contralateral to the visual field of stimulus presentation for visual non-targets at attended and unattended location when vision was primary (top) and when touch was primary (bottom). In both conditions, visual stimuli at attended locations elicited larger P1 and N1 components relative to visual stimuli at unattended locations. The observation that crossmodal attentional effects on visual ERPs in the Touch Primary condition started about 100 ms post-stimulus (Fig. 4, bottom), and the fact that larger P1 and N1 components were elicited in response to visual stimuli at locations attended within touch, provide strong evidence that crossmodal links in spatial attention from touch to vision can affect relatively early perceptual stages of visual processing. In contrast, later attentional modulations of visual ERPs were only observed in the Vision Primary condition. Fig. 4 shows that the N2 component was enhanced for visual stimuli at attended locations when vision was primary (top), but was unaffected by spatial attention when touch was primary (bottom). This finding suggests that crossmodal links in spatial attention from touch to vision may have little effect on post-perceptual stages in the processing of visual information.

Additional support for this conclusion is provided by the pattern of attentional ERP modulations obtained at midline electrodes. Fig. 5 shows ERPs elicited by visual stimuli at attended and unattended locations in the Vision Primary and Touch Primary conditions at electrodes Cz (top) and Pz (bottom) together with the resulting attended-location minus unattended-location difference waveforms. While effects of spatial attention were similar for both task conditions up to about 200 ms post-stimulus, subsequent attentional ERP modulations in the N2 and P3 time range were restricted to the Vision Primary condition. The fact that crossmodal links in spatial attention from touch to vision had a strong impact on relatively early portions of visual ERP waveforms, but not on longer-latency ERP components, indicates that crossmodal links from touch to vision may affect sensory-perceptual stages rather than later stages in the processing of visual information.

An unexpectedly different pattern of results was obtained for tactile stimuli. Fig. 6 shows somatosensory ERPs at central electrodes located over the primary somatosensory cortex contralateral to the stimulated hand, in response to tactile non-targets at attended and unattended locations when touch was primary (top) versus when vision was primary (bottom). In the Touch Primary condition, tactile stimuli at attended locations elicited an enhanced negativity relative to unattended tactile stimuli which overlapped with the modality-specific somatosensory N140 and the subsequent N2 component. This result is in line with observations from previous unimodal tactile ERP studies [15,25,26]. As the N140 component is thought to be generated in secondary somatosensory cortex (SII; [14]), the attentional modulation of this component indicates that tactile-spatial attention can modulate sensory-specific

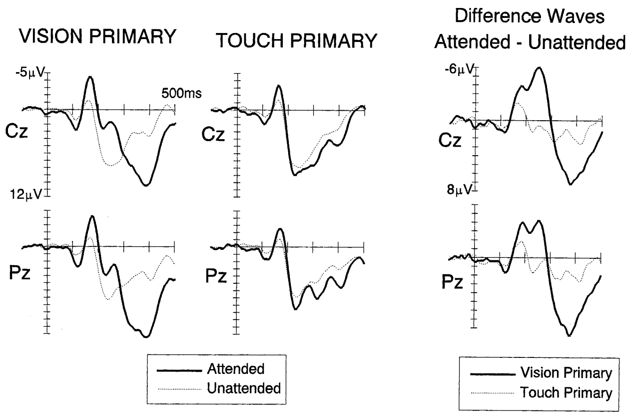

Fig. 5. Left and middle panel: Grand-averaged event-related potentials (ERPs) elicited at midline electrodes Cz and Pz in response to visual stimuli at attended locations (thick solid lines) and unattended locations (thin dashed lines) under conditions where attention was directed to one side within vision (Vision Primary, left) or within touch (Touch Primary, middle). Right panel: Difference waveforms obtained at Cz and Pz by subtracting ERPs to visual stimuli at unattended locations from ERPs to visual stimuli at attended locations in the Vision Primary condition (thick solid lines) and in the Touch Primary condition (thin dashed lines).

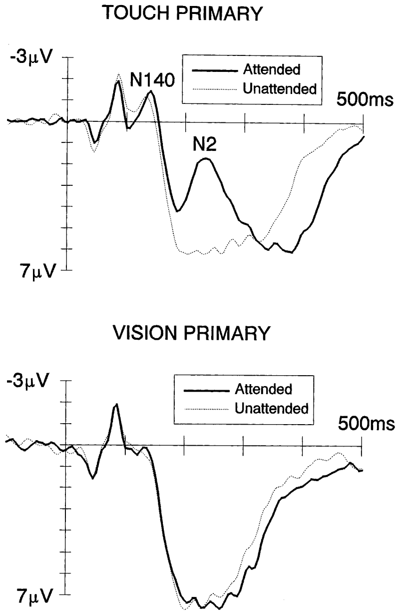

Fig. 6. Grand-averaged event-related potentials (ERPs) elicited at central electrodes contralateral to the stimulated hand in response to tactile stimuli at attended locations (thick solid lines) and unattended locations (thin dashed lines) under conditions where attention was directed to one side within touch (Touch Primary, top) or within vision (Vision Primary, bottom).

stages of somatosensory processing. Most importantly, however, no statistically reliable effects of spatial attention on somatosensory ERPs were obtained when vision was primary and tactile stimuli were irrelevant (Fig. 6, bottom). In other words, there was no indication of any differential effect of visual-spatial attention on the processing of tactile stimuli at attended and unattended locations.

This pattern of results could suggest that there are asymmetrical links in spatial attention between vision and touch, with visual processing being affected by tactile-spatial attention, but not vice-versa. However, this conclusion is inconsistent with the fact that Spence et al. [32] obtained clear-cut *behavioural* evidence for the existence of symmetrical cross-modal links between vision and touch. This discrepancy may be linked to an important methodological difference in the procedures used in our visual/tactile ERP experiment and in the behavioural study by Spence et al. In order to measure effects of crossmodal attention on behavioural performance, participants have to respond to stimuli in the secondary modality. As a consequence, these stimuli cannot be completely ignored. In contrast, tactile stimuli were entirely task-irrelevant in the Vision Primary condition of the visual/tactile ERP experiment (as for all secondary modality stimuli in the present ERP studies), and participants were instructed to ignore them. It is possible that somatosensory processing can be decoupled from spatial attention within other sensory modalities when tactile stimuli can be completely ignored, but not when they remain potentially relevant for responding (as in previous behavioural work, eg, [32]).

To test whether tactile stimuli have to be potentially task-relevant in order to be affected by visual-spatial attention, we measured ERPs to tactile stimuli in another experimental condition that was identical to the Vision Primary condition, except that participants now also had to respond to rare tactile target stimuli regardless of their location [10]. Thus, while participants still had no reason to focus tactile attention on just the side that was relevant for vision, they could no longer entirely ignore touch, as they occasionally had to response to tactile targets on either side. The results obtained in this condition are shown in Fig. 7 for electrodes located over the somatosensory cortex contralateral and ipsilateral to the stimulated hand. Visual-spatial attention now had a clear impact on somatosensory ERPs, as tactile stimuli at visually attended locations elicited an enhanced negativity relative to tactile stimuli at unattended locations. Similar to the results obtained for the Touch Primary condition (Fig. 6, top), this effect overlapped with the somatosensory N140 component and extended, albeit in an attenuated fashion, up to about 300 ms post-stimulus. This pattern of results suggests that while the distribution of spatial attention within vision leaves tactile processing unaffected when tactile stimuli can be entirely ignored, the

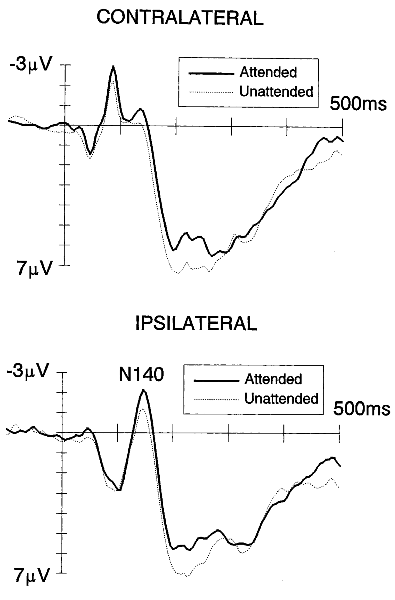

Fig. 7. Grand-averaged event-related potentials (ERPs) elicited at central electrodes contralateral (top) and ipsilateral (bottom) to the stimulated hand in response to tactile stimuli at attended locations (thick solid lines) and unattended locations (thin dashed lines) under conditions where attention was directed to one side within vision, but occasional tactile targets required a response regardless of their location.

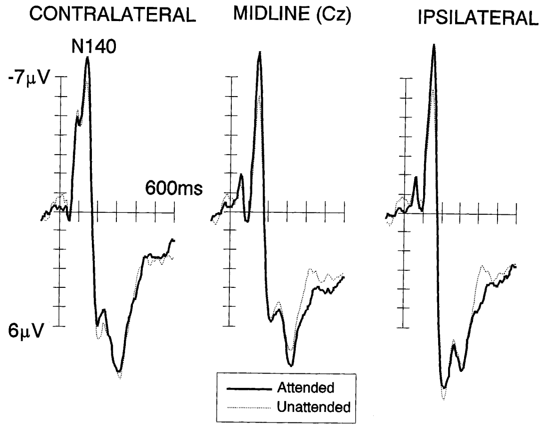

Fig. 8. Grand-averaged event-related potentials (ERPs) elicited at Cz (middle) and at central electrodes contralateral (left) and ipsilateral (right) to the stimulated hand in response to tactile stimuli at attended locations (thick solid lines) and unattended locations (thin dashed lines) under conditions where visual-spatial attention was cued to one side on a trial-by trial basis, and tactile stimuli could be ignored.

modalities become linked when touch is potentially response-relevant. The fact that these insights could not have been obtained exclusively on the basis of behavioural measures underlines the value of ERPs for the study of attentional mechanisms. In contrast to measures of overt performance, ERPs can be recorded under conditions of fully focused attention when unattended stimuli are entirely response-irrelevant.

In our initial visual/tactile ERP study ([10]; see Figs. 4–7), attended locations remained constant for an entire block of trials (sustained attention), whereas these locations were cued on a trial-by-trial basis (transient attention) in the visual/auditory ERP experiment [11]. To investigate any effects of transient visual-spatial attention on tactile processing, we recorded somatosensory ERPs in a recent unpublished experiment. In this study, responses were required to visual target stimuli at attended locations, and tactile stimuli could be completely ignored. In contrast to the Vision Primary condition of the visual/tactile ERP study described above [10], the focus of visual-spatial attention was now manipulated on a trial-by-trial basis by central symbolic precues (as in Fig. 1). Fig. 8 shows ERP waveforms obtained at Cz and at central electrodes contralateral and ipsilateral to the stimulated hand in response to tactile stimuli at visually attended and unattended locations. While no crossmodal effect on tactile ERPs had been found in the earlier study with sustained visual-spatial attention when touch was completely task-irrelevant (Fig. 6, bottom), clear attentional modulations of the somatosensory N140 component were obtained for transient visual-spatial attention. These effects were restricted to the N140 latency range (see Fig. 8), and were maximal at electrodes close to primary somatosensory cortex. This result indicates that transient visual-spatial attention modulates sensory-specific stages of somatosensory processing even when tactile stimuli can be completely ignored.

Overall, the pattern of results obtained in the ERP studies discussed in this section suggests that there are strong crossmodal links in spatial attention between vision and touch, that these links affect early perceptual stages of visual and somatosensory processing. There may however be one exception to this general rule. Somatosensory processing can be decoupled from spatially selective processes within vision when tactile stimuli are task-irrelevant and the focus of visual attention remains constant for an extended period of time.

5. Crossmodal links in spatial attention between audition and touch

Crossmodal links between audition and touch have not yet been investigated systematically. Initial results from the only behavioural study to date [21] suggest that attentional spatial synergies between audition and touch may be considerably weaker than crossmodal links between vision and audition, and between vision and touch. We have recently studied ERP correlates of crossmodal links between audition and touch in a study [12] where the attended location was cued on a trial-by-trial basis, primary versus secondary modalities (audition or touch) were blocked in successive experimental halves, and all secondary modality stimuli were task-irrelevant. When audition or touch were primary modalities, attentional ERP modulations within these modalities were similar to the results reported earlier (see Figs. 3 and 6). Again, the important crossmodal question was whether similar effects would be observed when the respective modalities were secondary and task-irrelevant. Fig. 9 shows ERPs elicited by auditory

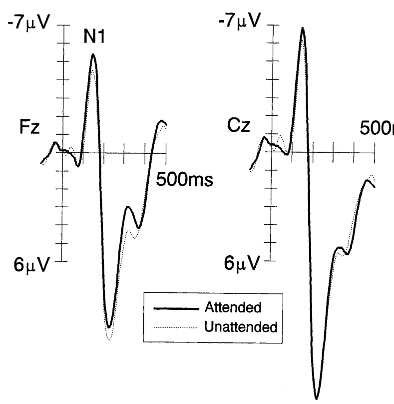

Fig. 9. Grand-averaged event-related potentials (ERPs) elicited at Fz (left) and Cz (right) in response to auditory stimuli at attended locations (thick solid lines) and unattended locations (thin dashed lines) when attention was directed to one side within touch.

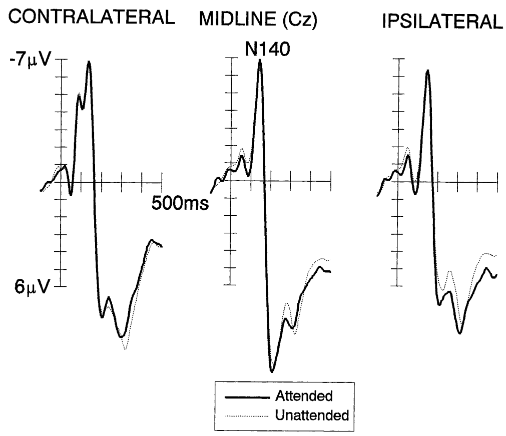

Fig. 10. Grand-averaged event-related potentials (ERPs) elicited at Cz (middle) and at central electrodes contralateral (left) and ipsilateral (right) to the stimulated hand in response to tactile stimuli at attended locations (thick solid lines) and unattended locations (thin dashed lines) under conditions where attention was directed to one side within audition.

stimuli at midline electrodes Fz and Cz in the Touch Primary condition at tactually attended versus unattended locations. Similar to the results observed in the visual/auditory study [11] (Fig. 3), an enhanced negativity was elicited for auditory stimuli at tactually attended locations, which overlapped with the auditory N1 component. Fig. 10 shows somatosensory ERPs elicited at Cz and at central electrodes contralateral and ipsilateral to the stimulated hand by tactile stimuli at auditorily attended versus unattended locations in the Audition Primary condition. In contrast to the effects of tactile-spatial attention on auditory ERPs, auditory-spatial attention did not have any statistically reliable impact on somatosensory ERP waveforms.

Effects of tactile-spatial attention on auditory ERPs were remarkably similar to the auditory ERP modulations produced by visual-spatial attention [11]. This suggests that there are crossmodal links in spatial attention from touch to audition, and that attentional orienting within vision and within touch have similar effects on auditory processing. The absence of any influence of auditory-spatial attention on somatosensory ERPs may indicate that there are no crossmodal links from audition to touch, or that such links are considerably weaker than the links observed for other combinations of modalities. It would however be premature to draw any firm conclusions with respect to this issue from the results of a single study. As described in the previous section, crossmodal links from vision to touch are sensitive to factors like the difference between transient and sustained attention and the task-relevance of tactile stimuli. Further research is required to find out whether these or other factors also affect crossmodal links between audition and touch.

6. Can attention be directed to opposite locations in different modalities?

The research reviewed in the previous sections has found electrophysiological evidence for crossmodal links in covert spatial attention between vision and audition, vision and touch, and to some extent between touch and audition. Directing attention to a specific location within one modality can influence sensory processing within other, currently irrelevant modalities. While such crossmodal links may usually facilitate the integration of information delivered by different sensory modalities, they might cause problems in cases when attention has to be simultaneously directed to different locations in different modalities [5,29]. The existence of synergies in spatial attention between vision and audition should make it difficult to bias the sensory processing of visual information in favour of one side of visual space, while simultaneously biasing auditory-perceptual processes in favour of input arriving from the opposite hemifield. If this is correct, effects of spatial attention on early sensory-specific ERP components should be eliminated or reduced when attention has to be directed to opposite locations in vision and audition. However, since crossmodal links were found to have less impact on post-perceptual processing (as reflected by longer-latency ERP components), attentional ERP modulations beyond 200 ms post-stimulus might still be observed under such opposite-location divided attention conditions.

These predictions were tested in an experiment [9] where single visual or auditory stimuli were presented on the left or right side in an unpredictable sequence, and participants had to detect visual as well as auditory 'oddball' target stimuli among standards at particular, prespecified locations, which applied throughout a block (sustained attention). In the Attend Same Side condition, the relevant location (left or right) was identical for both modalities. In the Attend Opposite Sides condition, participants had to detect visual targets on the left side, and auditory targets on the right, or vice versa. These instructions were varied between blocks. Fig. 11 shows ERPs elicited by visual stimuli at visually attended and unattended locations for posterior parietal electrodes contralateral to the visual field of stimulus presentation. As expected, spatial attention resulted in a modulation of sensory-specific P1 and N1 components in the Attend Same Side condition (top). In contrast, no attentional P1 and N1 effects were present under Attend Opposite Sides instructions (bottom). However, an enhanced negativity for visual stimuli at attended locations was elicited in this condition beyond 200 ms in the N2 time range. A similar pattern of results was observed for auditory stimuli. Fig. 12 shows auditory ERPs at Cz under Attend Same Side (top) and Attend Opposite Sides (bottom) instructions. While an attentional negativity overlapping with the auditory N1 was elicited when attention was directed to identical locations in both modalities during Attend Same Side blocks (top), this effect was absent in the Attend Opposite Sides condition, where enhanced negativities for auditory stimuli at attended locations only emerged about 200 ms after stimulus onset (bottom).

Similar results were also found for somatosensory ERPs in an unpublished experiment which used the same procedure, except that auditory stimuli were now replaced by tactile stimuli. Fig. 13 shows somatosensory ERPs recorded at Cz to tactile stimuli at attended and unattended locations in the Attend Same Side condition (top) and in the Attend Opposite Sides condition (bottom). When attention was directed to identical locations within vision and touch, an attentional modulation of the somatosensory N140 component was followed by an enhanced negativity for attended tactile stimuli beyond 200 ms post-stimulus. Under Attend Opposite Sides instructions, the N140 effect was eliminated, whereas longer-latency attentional negativities remained present.

Overall, the ERP results observed when attention had to be divided between locations across modalities confirm and extend the findings from the crossmodal attention studies reviewed earlier, which has used the primary/secondary modality paradigm. If crossmodal synergies in spatial attention affect early perceptual

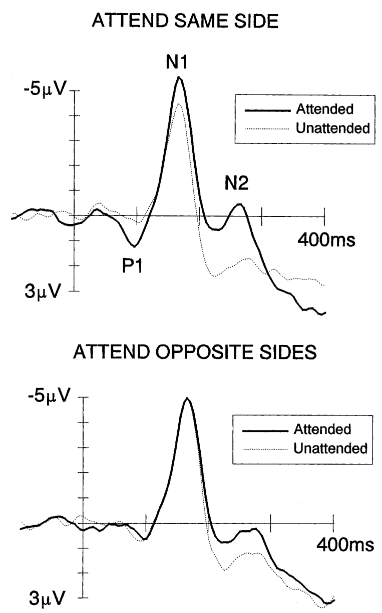

Fig. 11. Grand-averaged event-related potentials (ERPs) elicited at parietal electrodes contralateral to the visual field of stimulus presentation in response to visual stimuli at attended locations (thick solid lines) and unattended locations (thin dashed lines) under conditions where attention had to be directed to identical locations within vision and audition (Attend Same Side, top), versus under conditions where attention had to be directed to opposite sides within vision and audition (Attend Opposite Sides, bottom).

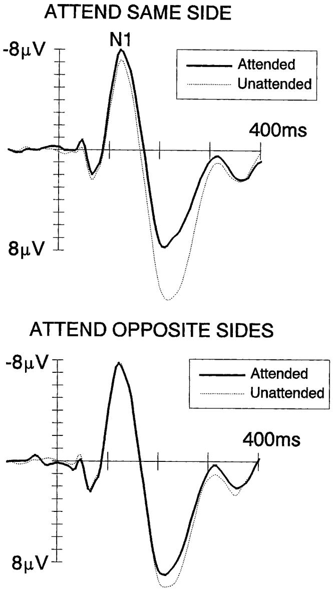

Fig. 12. Grand-averaged event-related potentials (ERPs) elicited at Cz in response to auditory stimuli at attended locations (solid lines) and unattended locations (dashed lines) under conditions where attention had to be directed to identical locations within vision and audition (Attend Same Side, top), versus under conditions where attention had to be directed to opposite sides within vision and audition (Attend Opposite Sides, bottom).

processes, attentional modulations of these processes should be eliminated or reduced when opposite spatial biases are simultaneously active in different modalities. In line with this prediction, early attentional modulations of sensory-specific ERP components were found when attention was directed to a common location within two modalities, but not when attention had to be directed to opposite locations. In contrast, attentional ERP effects beyond 200 ms post-stimulus were observed for both conditions, reflecting the fact that crossmodal links in spatial attention have less impact on post-perceptual processing.

7. Summary and conclusions

In most of the experiments reviewed in this paper, event-related brain potentials were recorded in response to visual, auditory, and tactile stimuli on either side, while attention had to be directed to a specific side within one primary modality, and while secondary modality stimuli were task-irrelevant regardless of their position. The aims were to find out whether there are crossmodal links in spatial attention between vision, audition, and touch; and to investigate which stages in the processing of sensory stimuli are affected by such links. The results found in these studies were highly consistent, and thus allow some general conclusions with respect to both issues. First, we obtained clear-cut electrophysiological evidence for symmetrical crossmodal links between vision and audition, and between vision and touch, thereby confirming and extending results from behavioural studies [29,32]. ERP effects of spatial attention were not only observed within the currently relevant primary modality, but also for secondary modality stimuli, even when the latter could be completely ignored (with the possible exception of touch, which may be decoupled from sustained spatial attention in other modalities when entirely task-irrelevant). Similar crossmodal links may also exist between audition and touch, although this needs to be systematically investigated in future studies. It should be noted that these crossmodal ERP effects were consistently found even within just the first half of each experiment; that is, before participants were ever required to attend and respond to stimuli in the currently irrelevant modality. This shows that these effects cannot be accounted for by a residual attentional bias from a previous task condition.

Second, the latencies and scalp distributions of attentional ERP modulations observed for the secondary modality allow further conclusions with respect to the locus of these crossmodal effects. Crossmodal links in spatial attention affected relatively early sensory-specific ERP components between 100 and 200 ms post-stimulus. In vision, occipital P1 and/or N1 components

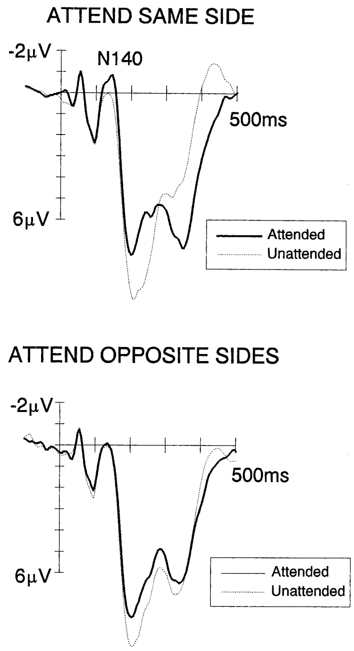

Fig. 13. Grand-averaged event-related potentials (ERPs) elicited at Cz in response to tactile stimuli at attended locations (thick solid lines) and unattended locations (thin dashed lines) under conditions where attention had to be directed to identical locations within vision and touch (Attend Same Side, top), versus under conditions where attention had to be directed to opposite sides within vision and touch (Attend Opposite Sides, bottom).

were modulated when attention was directed within audition or within touch. Likewise, the auditory N1 and the somatosensory N140 were affected by visual-spatial attention. In contrast, ERP effects due to crossmodal links beyond 200 ms post-stimulus were generally small or entirely absent. This pattern of results suggests that crossmodal links in spatial attention affect sensory-perceptual processes within modality-specific cortical regions, but have less impact on later post-perceptual stages. The observation that early attentional ERP modulations were eliminated when attention had to be directed to opposite locations within different modalities, while longer-latency effects remained present, provides additional support for the conclusion that synergies in spatially selective processing across modalities manifest themselves primarily at the sensory-perceptual level.

In conventional stage models of information processing, sensory-perceptual processing is based on separate modality-specific modules which operate in parallel, but in a strictly independent fashion. Because they are assumed to be informationally encapsulated, these perceptual modules should not be not affected by crossmodal interactions. On such accounts, any crossmodal effects should be confined to subsequent central modality-unspecific stages. Viewed from this perspective, the observation that crossmodal links in spatial attention can modulate processes within sensory-specific brain regions, but appear to have little effect on post-perceptual processes may seem almost paradoxical. It shows that modality-specific perceptual processes are not completely modular, but can be affected by spatially selective processes within other sensory modalities.

The study of crossmodal links in spatial attention has only just begun, and there are important issues that need to be addressed in future research. Crossmodal links in spatial attention may reflect increased activation of the contralateral hemisphere when attention is directed to the left or right within one modality [20], with this activation then spreading to affect representations of other modalities within the same activated hemisphere. Alternatively, such links may be based on a reference frame which specifies the relative locations of stimuli from different modalities within external space [32]. While the experiments reviewed in this paper investigated effects of crossmodal links in endogenous (voluntary) spatial attention, there is behavioural [30,31,34,35] as well as initial electrophysiological [19] evidence for the existence of crossmodal links in exogenous (involuntary) spatial attention. Further research is needed to find out whether crossmodal links in exogenous spatial attention are functionally similar to the links in endogenous attention discussed in this paper. In addition to studying the effects of crossmodal links in spatial attention on the processing of visual, auditory, and tactile information, ERPs can also be used to investigate control structures involved in directing spatial attention to specific locations within different sensory modalities. Crossmodal links in spatial attention may reflect the activity of a single supramodal attentional control system [13], or be caused by synergies between independent modality-specific control processes [29]. Since ERP studies of attentional control processes have so far been confined to the visual modality [eg, [17] [28]], we have recently begun to study ERP correlates of attentional shifts in audition and somatosensation [12]. ERP modulations observed during spatial shifts of auditory, tactile, and visual attention were very similar, thus implicating supramodal mechanisms in the control of spatial attention. A combination of converging methods (ERPs, functional brain imaging, behavioural measures) will be needed to gain further insights into the control of attentional shifts within and across different sensory modalities, to identify coordinate systems involved in the control of intramodal and crossmodal spatial attention, and to find out whether attentional orienting processes are mediated by modality-specific or supramodal control systems.

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References

[1] Alho K. Selective attention in auditory processing as revealed by event-related brain potentials. Psychophysiology 1992;29:247–63.

[2] Butter CM, Buchtel HA, Santucci R. Spatial attentional shifts: further evidence for the role of polysensory mechanisms using visual and tactile stimuli. Neuropsychologia 1989;27:1231–40.

[3] De Ruiter MB, Kok A, van der Schoot M. Effects of inter- and intramodal selective attention to non-spatial visual stimuli: an event-related potential analysis. Biological Psychology 1998;49: 269–94.

[4] Donchin E, Ritter W, McCallum C. Cognitive psychophysiology: the endogenous components of the ERP. In: Callaway E, Tueting P, Koslow SH, editors. Event-related Brain Potentials in Man. New York: Academic Press, 1978:349–411.

[5] Driver J, Spence C. Spatial synergies between auditory and visual attention. In: Umiltà C, Moscovitch M, editors. Attention and Performance, vol. XV. Cambridge, MA: MIT Press, 1994:311–31.

[6] Driver J, Spence C. Attention and the crossmodal construction of space. Trends in Cognitive Sciences 1998;2:254–62.

[7] Eason RG. Visual evoked potential correlates of early neural filtering during selective attention. Bulletin of the Psychonomic Society 1981;18:203–6.

[8] Eimer M. Sensory gating' as a mechanism for visual-spatial orienting: electrophysiological evidence from trial-by-trial cueing experiments. Perception & Psychophysics 1994;55:667–75.

[9] Eimer M. Can attention be directed to opposite locations in different modalities? An ERP study. Clinical Neurophysiology 1999;110:1252–9.
[10] Eimer M, Driver J. An event-related brain potential study of cross-modal links in spatial attention between vision and touch. Psychophysiology 2000;37:697–705.
[11] Eimer M, Schröger E. ERP effects of intermodal attention and cross-modal links in spatial attention. Psychophysiology 1998;35:313–27.
[12] Eimer M., Van Velzen J., Driver J. Crossmodal interactions between audition, touch and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. Journal of Cognitive Neuroscience (in press).
[13] Farah MJ, Wong AB, Monheit MA, Morrow LA. Parietal lobe mechanisms of spatial attention: Modality-specific or supramodal? Neuropsychologia 1989;27:461–70.
[14] Frot M, Rambaud L, Guénot M, Maugière F. Intracortical recordings of early pain-related CO_2-laser evoked potentials in human second somatosensory (SII) are. Clinical Neurophysiology 1999;110:133–45.
[15] García-Larrea L, Lukaszewicz AC, Mauguière F. Somatosensory responses during selective spatial attention: The N120-to-N140 transition. Psychophysiology 1995;32:526–37.
[16] Giard MH, Perrin F, Pernier J, Perronet F. Several attention-related wave forms in auditory areas: a topographic study. Electroencephalography and Clinical Neurophysiology 1988;69: 371–84.
[17] Harter MR, Miller SL, Price NJ, LaLonde ME, Keyes AL. Neural processes involved in directing attention. Journal of Cognitive Neuroscience 1989;1:223–37.
[18] Hillyard SA, Simpson GV, Woods DL, Van Voorhis S, Münte TF. Event-related brain potentials and selective attention to different modalities. In: Reinoso-Suarez F, Ajmone-Marsan C, editors. Cortical Integration. New York: Raven Press, 1984:395–414.
[19] Kennett S., Eimer M., Spence C., Driver J. Tactile-visual links in exogenous spatial attention under different postures: convergent evidence from psychophysics and ERPs. Journal of Cognitive Neuroscience 2001;13:462–78.
[20] Kinsbourne M. Orientational model of unilateral neglect: evidence from attentional gradients within hemispace. In: Robertson IH, Marshall JC, editors. Unilateral Neglect: Clinical and Experimental Studies. Hillsdale, NJ: Erlbaum, 1993:63–86.
[21] Lloyd D.M., Spence C., Merat N., McGlone F. Crossmodal links in covert endogenous spatial attention between audition and touch. Perception & Psychophysics (submitted).
[22] Mangun GR. The neural mechanisms of visual selective attention. Psychophysiology 1995;32:4–18.
[23] Mangun GR, Hillyard SA. Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. Journal of Experimental Psychology: Human Perception and Performance 1991;17:1057–74.
[24] Mangun GR, Hillyard SA, Luck SJ. Electrocortical substrates of visual selective attention. In: Meyer DE, Kornblum S, editors. Attention and Performance, vol. XIV. Cambridge, MA: MIT Press, 1993:219–43.
[25] Michie PT. Selective attention effects on somatosensory event-related potentials. Annals of the New York Academy of Sciences 1984;425:250–5.
[26] Michie PT, Bearpark HM, Crawford JM, Glue LCT. The effects of spatial selective attention on the somatosensory event-related potential. Psychophysiology 1987;24:449–63.
[27] Näätänen R. Processing negativity: an evoked-potential reflection of selective attention. Psychological Bulletin 1982;92:605–40.
[28] Nobre AC, Sebestyen GN, Miniussi C. The dynamics of shifting visuospatial attention revealed by event-related brain potentials. Neuropsychologia 2000;38:964–74.
[29] Spence C, Driver J. Audiovisual links in endogenous covert spatial attention. Journal of Experimental Psychology: Human Perception and Performance 1996;22:1005–30.
[30] Spence C, Driver J. Audiovisual links in exogenous covert spatial attention. Perception and Psychophysics 1997;59:1–22.
[31] Spence C, Nicholls MER, Gillespie N, Driver J. Cross-modal links in exogenous covert spatial orienting between touch, audition, and vision. Perception & Psychophysics 1998;60:544–57.
[32] Spence C, Pavani F, Driver J. Crossmodal links between vision and touch in covert endogenous spatial attention. Journal of Experimental Psychology: Human Perception and Performance 2000;26:1298–319.
[33] Teder-Sälejärvi WA, Münte TF, Sperlich FJ, Hillyard SA. Intramodal and cross-modal spatial attention to auditory and visual stimuli: an event-related brain potential (ERP) study. Cognitive Brain Research 1999;8:327–43.
[34] Ward LM. Supramodal and modality-specific mechanisms for stimulus-driven shifts of auditory and visual attention. Canadian Journal of Experimental Psychology 1994;48:242–59.
[35] Ward LM, McDonald JJ, Lin D. On asymmetries in cross-modal spatial attention orienting. Perception & Psychophysics 2000;62:1258–64.
[36] Woldorff MG, Gallen CC, Hampson SR, Hillyard SA, Pantev C, Sobel D, Bloom FE. Modulation of early sensory processing in human auditory cortex during auditory selective attention. Proc Natl Acad Sci USA 1992;90:8722–6.
[37] Woods DL, Alho K, Algazi A. Intermodal selective attention. I. Effects on event-related potentials to lateralized auditory and visual stimuli. Electroencephalography and clinical Neurophysiology 1992;82:341–55.