PERGAMON

Neuroscience and Biobehavioral Reviews 25 (2001) 497–511

NEUROSCIENCE AND BIOBEHAVIORAL REVIEWS

www.elsevier.com/locate/neubiorev

Crossmodal links in endogenous and exogenous spatial attention: evidence from event-related brain potential studies

Martin Eimer[a,*], Jon Driver[b]

[a]School of Psychology, Birkbeck College, University of London, Malet Street, London WC1E 7HX, UK
[b]Institute of Cognitive Neuroscience, University College London, London WC1N 3AR, UK

Abstract

The adaptive control of behaviour in response to relevant external objects and events often requires the selection of information delivered by different sensory systems, but from the same region in external space. This can be facilitated by crossmodal links in the attentional processing of information across sensory modalities. Results from recent event-related potential (ERP) studies are reviewed that investigated mechanisms underlying such crossmodal links in spatial attention between vision, audition and touch. Crossmodal attention effects were observed for early modality-specific visual, auditory, and somatosensory ERP components, indicating that crossmodal links in spatial attention affect sensory-perceptual processes within modality-specific cortical regions. ERP modulations prior to target events but sensitive to the direction of an attentional shift were remarkably similar during anticipatory covert shifts of visual, auditory, or tactile attention. These results suggest that such attentional shifts are mediated by supramodal frontoparietal control mechanisms. Finally, ERP evidence is reviewed suggesting that effects of crossmodal links in endogenous (voluntary) as well as exogenous (involuntary) spatial attention are mediated by a representations of external space which are updated across postural changes.

Keywords: Visual-spatial attention; Auditory-spatial attention; Tactile-spatial attention; Crossmodal attention; Event-related brain potentials; Cognitive control; Exogenous attention; Endogenous attention

1. Background

In everyday life, the adaptive control of behaviour requires the integration and coordination of information originating from different input modalities, but from overlapping positions in external space. When trying to follow a conversation in a noisy room with distracting sounds, attending to relevant lip movements may be as important as attending to the speaker's voice coming from the same location. Here, attention is directed to information delivered by different input systems, but from the same spatial location. Attending to relevant external objects often requires spatial attention to be coordinated across different input modalities, in order to select visual, auditory, and tactile information originating from the same object or event. This fact may have important implications for mechanisms of attentional selectivity, which could involve spatial synergies (crossmodal links) in the attentional processing of information across sensory modalities. Until recently, most experimental investigations of spatial attention have focused on spatially selective processing within single sensory modalities, with little contact between research on visual-spatial attention, auditory-spatial attention, or tactile-spatial attention. Because of this focus on unimodal attention, the questions of whether there are crossmodal links in spatial attention between vision, audition, and touch; which mechanisms are involved in such links; and how these links affect the processing of information at attended and unattended locations have only now begun to be addressed systematically (see Ref. [7] for an overview).

Several behavioural studies (e.g. Refs. [3,42,44]) have found evidence for cross-modal links in endogenous (voluntary) spatial attention between vision, audition, and touch. In these experiments, participants had to direct their attention to the expected location of target stimuli within one (primary) modality. On a small number of trials, stimuli of a different (secondary) modality were presented, but these stimuli were equally likely (or even more likely) to be presented on the side opposite to the expected location in the primary modality. Superior performance for stimuli at the location attended in the primary modality was observed not only for that primary modality, but also for secondary modality stimuli. This demonstrates that the focus of attention within one modality (that is, a spatial expectancy

* Corresponding author. Fax: +44-20-7631-6312.
E-mail address: m.eimer@bbk.ac.uk (M. Eimer).

0149-7634/01/$ - see front matter
PII: S0149-7634(01)00029-X

specific to a particular modality) can influence the processing of information in other modalities.

While these results demonstrate crossmodal links in spatial attention between vision, audition, and touch, they do not provide any direct insight into the neural processes underlying such links. Several important questions related to the presence of crossmodal links in spatial attention cannot be resolved exclusively on the basis of behavioural measures. For example, the fact that performance benefits can be observed 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. Because of their excellent temporal resolution, event-related brain potentials (ERPs) provide a useful tool to determine which stages in the processing of visual, auditory, or somatosensory stimuli can be affected by crossmodal attention. 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 parameters of stimuli such as their intensity. These 'exogenous' components reflect modality-specific perceptual processes in the visual, auditory, or somatosensory systems. Longer-latency ERP components are not sensory-specific, have a 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/or in response selection and activation [6]. 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 crossmodal links in spatial attention should help to distinguish any perceptual effects from any post-perceptual effects of such links.

In addition to investigating effects of crossmodal links in spatial attention on the perceptual and/or post-perceptual processing of visual, auditory, or somatosensory information, an equally important question concerns the nature of the attentional control mechanisms responsible for the existence of such links. Attentional control processes are involved in directing covert spatial attention, and are activated in anticipation of and preparation for stimuli expected at specific locations. Two different ways of thinking about the control of spatial attention have emerged in the recent literature. One approach (e.g. Ref. [15]) suggests that attentional orienting processes are controlled by a single supramodal system, which directs spatial attention to the location of relevant external stimuli, regardless of their modality. Another approach (e.g. Ref. [42]) argues that shifts of spatial attention are primarily controlled by modality-specific mechanisms, although the effects of such attentional shifts may then spread (in attenuated fashion) to other sensory modalities. Again, this controversy is hard to resolve on the basis of behavioural measures alone. However, as described below, recent ERP studies have provided new insights into the nature of attentional control processes and their implications for crossmodal links in spatial attention.

The present article reviews electrophysiological evidence from ERP studies that investigated crossmodal links in spatial attention between vision, audition, and touch. In Section 2, effects of such links in endogenous attention on the processing of visual, auditory, and tactile stimuli at currently attended or unattended locations will be discussed, in order to find out whether these links primarily affect perceptual or post-perceptual processes. In Section 3, ERP studies investigating attentional control processes will be reviewed. Here, one central question is whether these control processes are supramodal or modality-specific. Section 4 discusses the spatial coordinates of crossmodal links in spatial attention, and the final section reviews recent behavioural and ERP evidence for the existence of crossmodal links in exogenous (involuntary) spatial attention in response to salient but spatially nonpredictive events.

2. Effects of crossmodal links in endogenous spatial attention on visual, auditory, and somatosensory processing

Most ERP studies investigating effects of crossmodal links in spatial attention have studied how links between vision and audition affect the processing of visual and auditory stimuli at currently attended vs. unattended locations. In a pioneering crossmodal ERP study, Hillyard et al. [19] presented a stream of brief flashes and tone bursts at an eccentricity of 30° to the left or right of fixation. Separate groups of participants were instructed to attend either to the tones or to the flashes, and to press a button whenever a target (a tone of slightly longer duration for one group, a longer flash for the other group) was presented at the relevant location (left vs. right side) that was specified at the beginning of each block. For the group attending to auditory stimuli, visual stimuli at relevant locations elicited an enhanced negativity between 150 and 200 ms as compared to visual stimuli at irrelevant locations. However, this spatial attention effect on visual ERPs was considerably larger for the participant group that attended to visual stimuli. Auditory spatial attention resulted in a broad negativity elicited by sounds at attended locations beyond 100 ms. This effect was also present, although somewhat smaller, when attention was directed to relevant locations of visual stimuli. This pattern of results provided some initial electrophysiological evidence for the existence of crossmodal links in spatial attention between vision and audition, since ERP effects of spatial attention were found not only within the currently relevant modality, but also for the other task-irrelevant modality.

A more recent study ERP correlates of crossmodal visual/

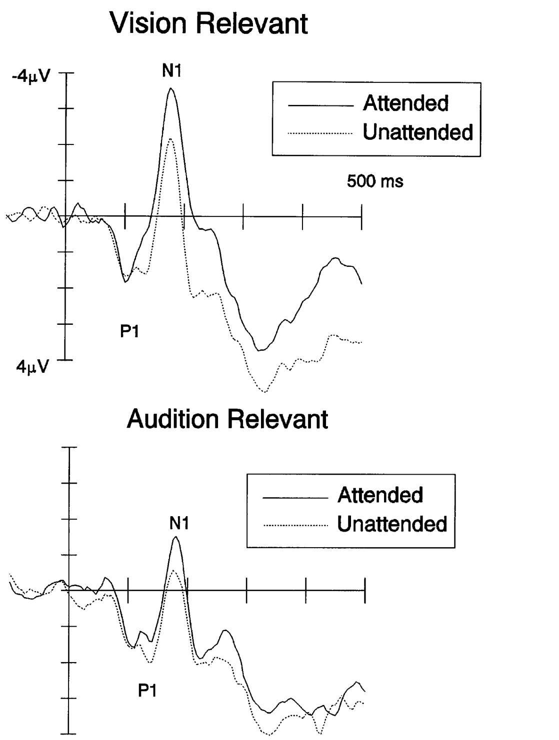

Fig. 1. Grand-averaged event-related potentials (ERPs) elicited at occipital electrodes (OL, OR) contralateral to the visual field of stimulus presentation in response to visual non-target stimuli at attended locations (solid lines) and unattended locations (dashed lines) under conditions where attention was directed to one side within vision (Vision Relevant, top), or within audition (Audition Relevant, bottom). Data from Ref. [13].

auditory links was conducted by Eimer and Schröger [13]. The overall design of this study was similar to the previous Hillyard et al. experiment [19], except that the direction of spatial attention was now manipulated on a trial-by-trial basis via central symbolic cues (left-pointing or right-pointing arrows presented at the beginning of each trial), rather than being sustained throughout a block of trials. That is, participants had to frequently shift their attention from the left to the right, or vice versa, on successive trials (transient attention). All participants had to attend to either the auditory or visual modality in different halves of the experiment. In one experimental half (Vision Relevant), participants were instructed to respond to infrequent visual targets on the side specified by the central cue, and to ignore all auditory stimuli. In the other half (Audition Relevant), infrequent auditory targets at cued locations had to be detected, and visual stimuli were to be ignored. Visual stimuli were brief flashes of peripheral LEDs, auditory stimuli were presented via loudspeakers, and visual and auditory targets were slightly longer than non-targets. All stimuli were presented on the left or right side (25° to the left or right of fixation) at closely aligned locations for the two different modalities. Participants had to maintain central fixation, and to direct their attention covertly to the left or right side within the primary modality in order to detect and respond vocally (by saying 'yes') to infrequent target stimuli in only the currently relevant modality at the cued location. They were instructed to ignore relevant modality stimuli at unattended locations as well as all irrelevant modality stimuli (regardless of their position). As in all other studies described in detail below, trials with eye movements towards the attended location detected in the horizontal electrooculogram (HEOG) were discarded from analysis.

Fig. 1 shows visual ERPs observed in this study ([13], Exp. 2) at occipital electrodes contralateral to the visual field of stimulus presentation, in response to visual non-target stimuli at attended and unattended locations. Separate ERP waveforms are shown for the Vision Relevant condition (top) and for the Audition Relevant condition where visual stimuli could be entirely ignored (bottom). When vision was relevant, enhanced visual N1 components were elicited by visual stimuli at attended locations, thus confirming findings from many previous unimodal ERP studies on visual-spatial attention (e.g. Refs. [8,9,31]). There was no reliable attentional modulation of the earlier occipital P1. 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) [32]. Attentional modulations of these components thus 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 [30]. Most importantly, attentional modulations of the occipital N1 elicited by visual stimuli were also found when audition was task-relevant and all visual stimuli could simply be ignored. The N1 was significantly larger in response to visual stimuli at cued locations (Fig. 1, bottom). 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 relatively early perceptual stages of visual processing. Finally, Fig. 1 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 nonspatial impact of *intermodal attention* (attention to one input modality vs. another) on visual ERPs (see Refs. [5,50], for further ERP studies of intermodal attention).

Fig. 2 illustrates ERP effects of crossmodal links in spatial attention between vision and audition obtained in the same experiment [13] at midline electrodes Fz and Cz. On the left side, ERPs elicited in response to visual stimuli at attended and unattended locations are shown, separately for the Vision Relevant and Audition Relevant conditions. Enhanced negativities for attended-location stimuli were elicited in both task conditions. Although the onset of these ERP effects was comparable in these two conditions, attentional modulations beyond 200 ms post-stimulus were clearly attenuated when audition was relevant and visual stimuli could be entirely ignored. Fig. 2 (right) shows

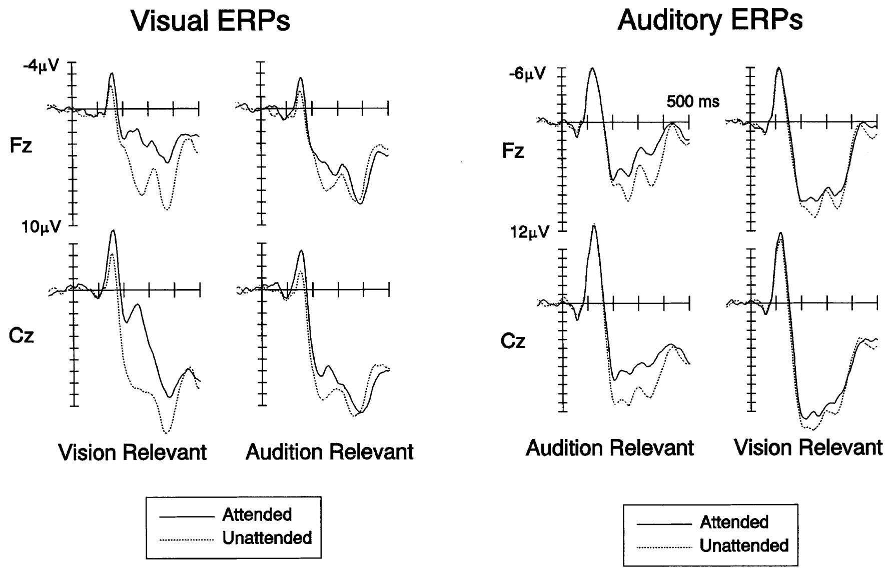

Fig. 2. Left panel: Grand-averaged event-related potentials (ERPs) elicited at midline electrodes Fz and Cz in response to visual non-target stimuli at attended locations (solid lines) and unattended locations (dashed lines) under conditions where attention was directed to one side within vision (Vision Relevant, left), or within audition (Audition Relevant, right). Right panel: Grand-averaged event-related potentials (ERPs) elicited at midline electrodes Fz and Cz in response to auditory non-target stimuli at attended locations (solid lines) and unattended locations (dashed lines) under conditions where attention was directed to one side within audition (Audition Relevant, left), or within vision (Vision Relevant, right). Data from Ref. [13].

ERPs elicited by auditory stimuli at attended and unattended locations, separately for the Audition Relevant and Vision Relevant conditions. Similar to previous unimodal auditory ERP studies (e.g. Refs. [1,37]), auditory-spatial attention was reflected in an enhanced negativity for sounds at cued locations 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 ('early Nd') between attended and unattended auditory stimuli is thought to originate from auditory cortex in the superior temporal lobe, while later portions of this effect have been linked to subsequent processing stages like the maintenance of stimuli in auditory memory [37,49]. As can be seen from Fig. 2 (right), an 'early Nd' was present not only when audition was task-relevant, but also in the Vision Relevant condition where auditory stimuli could be completely ignored. This finding suggests crossmodal links in spatial attention from vision to audition, and indicates that the current focus of visual-spatial attention can modulate sensory-specific auditory processing. Fig. 2 (right) also shows that attentional effects beyond 200 ms post-stimulus were considerably attenuated when vision rather than audition was task-relevant (see also Ref. [45] 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.

The effects obtained in this ERP experiment [13] are very similar to the results of other ERP studies investigating crossmodal links in spatial attention between vision and audition under comparable experimental circumstances [19,45]. Together, these findings demonstrate electrophysiological effects of such crossmodal links, thus supporting and extending previous behavioural evidence [42]. The fact that crossmodal attention has an effect on sensory-specific components in the currently irrelevant modality suggests that crossmodal links can affect modality-specific 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. However, it should also be noted that attentional ERP modulations tended to be larger for the currently relevant modality than for the modality that could be entirely ignored (see also Ref. [19]). This fact indicates that task relevance does play some role in the spatially selective processing of stimuli within different modalities (see Section 3 for a further discussion of this issue).

In a recent ERP study [12], we employed ERP measures to investigate effects of crossmodal links of spatial attention between vision and *touch*. Because behavioural evidence [44] has suggested that there are symmetrical crossmodal links between these two modalities, we expected to find effects analogous to those observed in previous visual/auditory studies [13,19,45] for ERPs elicited by visual and tactile stimuli. We used experimental procedures similar to our visual/auditory study [13], except that attention had to be maintained at one specific location for an entire experimental block (sustained attention), and that auditory stimuli were replaced by tactile stimuli. Participants were instructed at the beginning of each block to direct their attention to the left or right side within the currently relevant modality (vision or touch) in order to detect infrequent targets at

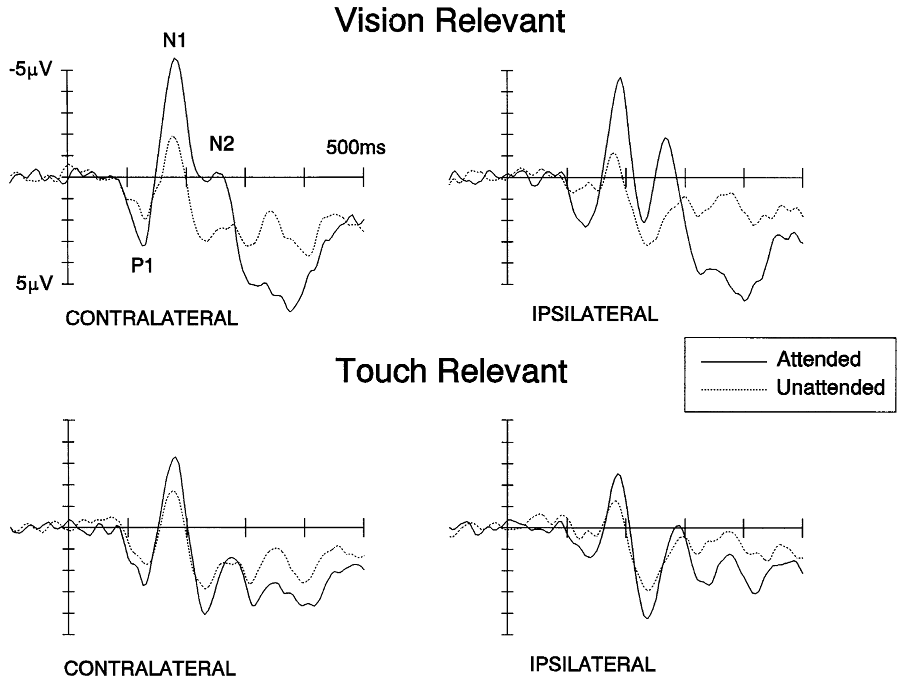

Fig. 3. Grand-averaged event-related potentials (ERPs) elicited at occipital electrodes (OL, OR) contralateral (left) and ipsilateral (right) to the visual field of stimulus presentation in response to visual non-target stimuli at attended locations (solid lines) and unattended locations (dashed lines) under conditions where attention was directed to one side within vision (Vision Relevant, top), or within touch (Touch Relevant, bottom). Data from Ref. [12].

the attended location in that modality only. Thus, they had to respond to only visual targets at attended locations in the Vision Relevant condition, and to only tactile targets at attended locations in the Touch Relevant condition, while ignoring all irrelevant modality stimuli, regardless of their location. Visual stimuli were again delivered via LEDs, while tactile stimuli were delivered by punctators driven by solenoids which were attached to the left and right index finger, close to the location of the LED on the same side. Visual and tactile target stimuli contained a 'gap', where the continuous stimulation was briefly interrupted by an empty interval. White noise was continuously presented throughout the experimental blocks to mask any sounds made by the tactile stimulators.

Attentional modulations of visual ERPs at occipital electrodes contralateral and ipsilateral to the visual field of stimulus presentation are shown in Fig. 3, separately for the Vision Relevant condition (top) and the Touch Relevant condition (bottom). Visual stimuli at attended locations elicited larger P1 and N1 components relative to visual stimuli at unattended locations, and these effects were present not only when vision was relevant (Fig. 3, top), but also when touch was relevant and visual stimuli could be entirely ignored (Fig. 3, bottom). The observation that crossmodal attentional effects on visual ERPs in the Touch Relevant condition started about 100 ms post-stimulus provides strong evidence that crossmodal links in spatial attention from touch to vision can affect early perceptual stages of visual processing. In contrast, later attentional modulations of visual ERPs were only observed in the Vision Relevant condition. Fig. 3 shows that the N2 component was enhanced for visual stimuli at attended locations when vision was relevant (top), but was unaffected by spatial attention when touch was task-relevant and visual stimuli could be ignored (bottom). This observation again suggests that crossmodal links in spatial attention seem to have little effect on post-perceptual processing stages.

An unexpectedly different result was initially obtained for the somatosensory modality. Under standard experimental conditions, where tactile stimuli could be entirely ignored when vision was relevant, no attentional modulations of somatosensory ERPs were elicited at all [12]. In other words, there was no indication of any differential effect of visual attention on the processing of tactile stimuli at attended and unattended locations. This finding is clearly inconsistent with the fact that Spence et al. [44] obtained *behavioural* evidence for crossmodal attentional links from vision to touch, as well as from touch to vision. This apparent discrepancy may be linked to an important methodological difference in the procedures used in our ERP experiment [12] and in the previous behavioural study [44]. In order to measure behavioural effects of crossmodal attention, participants need to respond not only to primary modality stimuli, but also to stimuli within the secondary modality. As a consequence of this fact, these stimuli cannot be completely ignored. In contrast, tactile stimuli were entirely task-irrelevant in the Vision Relevant condition of our ERP experiment [12]. It is possible that somatosensory processing can be decoupled from spatial attention within other sensory modalities when tactile stimuli can be

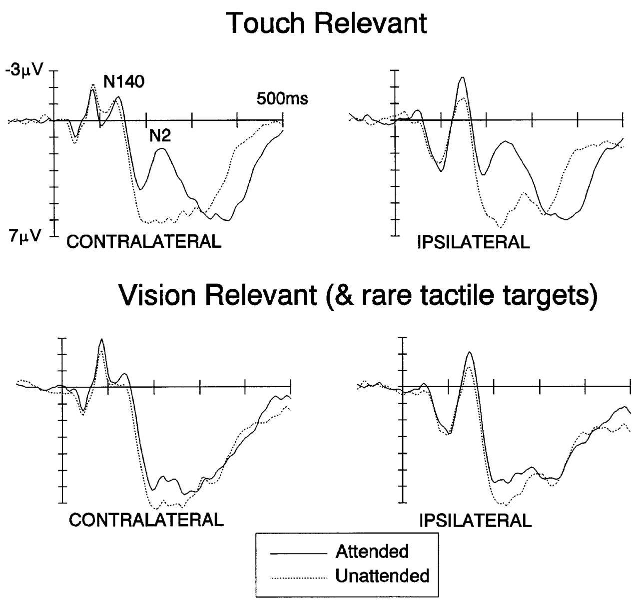

Fig. 4. Grand-averaged event-related potentials (ERPs) elicited at central electrodes (C3, C4) contralateral (left) and ipsilateral (right) to the stimulated hand in response to tactile non-target stimuli at attended locations (solid lines) and unattended locations (dashed lines) under conditions where attention was directed to one side within touch (Touch Relevant, top), or within vision (Vision Relevant, bottom). In the Vision Relevant condition, rare tactile targets were delivered with equal probability to the left and right hand (see text for further details). Data from Ref. [12].

completely ignored (see Ref. [48] for similar considerations with respect to auditory stimuli and exogenous spatial attention), but not when they remain potentially relevant for responding, as in previous behavioural studies.

To investigate whether tactile stimuli have to be potentially task-relevant to be affected by crossmodal links in spatial attention, we measured ERPs to tactile stimuli in another experimental condition which was identical to the Vision Relevant condition, except that participants now also had to respond to rare tactile targets (delivered only on six out of 96 trials per block) *regardless of their location* [12]. Thus, while participants still had no reason to focus tactile attention on the side relevant for vision, they could no longer entirely ignore touch. Fig. 4 (bottom) shows attentional modulations observed in this condition at electrodes located over somatosensory areas contralateral and ipsilateral to the stimulated hand. Fig. 4 (top) shows the corresponding effects obtained in the Touch Relevant condition where attention had to be directed to the location of potentially relevant tactile stimuli, while vision could be ignored. When touch was relevant, tactile stimuli at attended locations elicited an enhanced negativity which overlapped with the modality-specific somatosensory N140 and the subsequent N2 component (Fig. 4, top). This result is in line with observations from previous unimodal ERP studies on tactile attention (e.g. Refs. [17,36]). As the N140 component is assumed to be generated in secondary somatosensory cortex (SII; [16]), the attentional modulation of this component indicates that tactile-spatial attention can modulate sensory-specific stages of somatosensory processing. A very similar pattern of attentional effects was observed when attention was to be directed to one side within vision, but tactile stimuli could not be entirely ignored (Fig. 4, bottom). Tactile stimuli at visually attended locations now elicited an enhanced negativity relative to tactile stimuli at unattended locations, and this effect overlapped with the somatosensory N140 component and extended, albeit in an attenuated fashion, up to about 300 ms post-stimulus.

Overall, the results obtained in this visual/tactile ERP study [12] suggest that there are crossmodal links in spatial attention between touch and vision, and to some extent vice versa, and that these links can affect relatively early perceptual stages of visual and somatosensory processing. However, somatosensory processing may be decoupled from spatially selective processes within vision when tactile stimuli are task-irrelevant throughout and thus can be entirely ignored.

Given that behavioural and electrophysiological effects of crossmodal links between vision and audition, and vision and touch have been demonstrated, one remaining issue to be investigated is whether similar crossmodal effects can also be observed between audition and touch. Initial results from a recent, still unpublished behavioural study [28] suggest that crossmodal links between audition and touch may be considerably weaker than the links between vision and audition, or between vision and touch. We have recently studied ERP correlates of crossmodal links between audition and touch in an experiment [14] where the attended location was cued on a trial-by-trial basis, task-relevant vs. irrelevant modalities (audition or touch) were blocked in successive experimental halves, and irrelevant modality stimuli could be entirely ignored. In other respects, the procedure was equivalent to the visual/auditory and visual/tactile ERP studies described previously [12,13].

When audition or touch were relevant, attentional ERP modulations within these modalities were similar to the results observed before (see Fig. 2, right, and Fig. 4, top). Fig. 5 shows ERPs elicited by auditory stimuli at midline electrodes Fz and Cz in the Touch Relevant condition, where all auditory stimuli could be ignored. Similar to the results observed in crossmodal visual/auditory ERP studies [13,19,45], an enhanced negativity was elicited for auditory stimuli at tactually attended locations, which overlapped with the auditory N1 component. This suggests that there are crossmodal links in spatial attention from touch to audition, and that the effects of covert tactile attention on the processing of auditory stimuli at attended vs. unattended location may be similar to the effects of visual attention upon audition. In contrast, there were no statistically reliable attentional modulations of somatosensory ERP waveforms in the Audition Relevant condition (not shown in Figs.). This absence of any influence of auditory-spatial attention on somatosensory ERPs may reflect the fact that tactile stimuli were task-irrelevant in the Audition Relevant

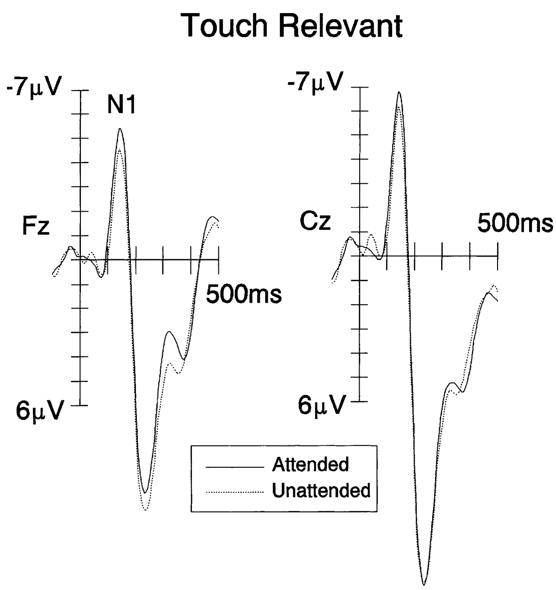

Fig. 5. Grand-averaged event-related potentials (ERPs) elicited at midline electrodes Fz (left) and Cz (right) in response to auditory stimuli at attended locations (solid lines) and unattended locations (dashed lines) when attention was directed to one side within touch. Data from Ref. [14].

condition, so that touch could again be decoupled from attentional orienting within another modality (see above).

Several conclusions can be drawn on the basis of the existing ERP experiments reviewed in this section. First, these studies provided electrophysiological evidence for crossmodal links in spatial attention between vision and audition, and between vision and touch, thereby confirming and extending results from behavioural studies [42,44], as well as initial evidence for crossmodal links from touch to audition. ERP effects of spatial attention were not only observed within a currently relevant modality, but also for other modalities even though these were task-irrelevant (with the possible exception of touch, which may be decoupled from spatial attention in other modalities when tactile stimuli can be entirely ignored). The latencies and scalp distributions of attentional ERP modulations observed for currently irrelevant modalities also allow some tentative conclusions with respect to the locus of these crossmodal effects. Crossmodal links in spatial attention affected the amplitudes of early sensory-specific ERP components between 100 and 200 ms post-stimulus. In vision, occipital P1 and/or N1 components 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. While such amplitude modulations of exogenous ERP components suggest an attentional gating of sensory-specific perceptual processing, some of these effects could also reflect the presence of attentional processing negativities, which may coincide with these early components. However, the overall pattern of results obtained clearly suggests that crossmodal links in spatial attention can affect sensory-perceptual processes within modality-specific cortical regions. In contrast, ERP effects due to crossmodal links beyond 200 ms post-stimulus were small or entirely absent, indicating that these links may have less impact on post-perceptual processing stages.

3. Crossmodal links in spatial attention and the control of covert attentional shifts

The studies reviewed in the previous section have investigated effects of crossmodal links in spatial attention on the processing of stimulus events at currently attended vs. unattended locations within different sensory modalities. In addition to studying such effects across modalities, research on crossmodal attention also needs to investigate covert attentional control processes, which are initiated in anticipation of upcoming relevant information at a specific location. In this section, ERP studies are reviewed that investigated whether anticipatory shifts of spatial attention are controlled by a supramodal mechanism or by separate modality-specific processes.

Attentional control processes might in principle be mediated by a single supramodal mechanism, which controls attentional shifts within different modalities [15]. In this view, the observed crossmodal attention effects are an immediate consequence of the supramodal control of attentional orienting. Alternatively, attention shifts in vision, audition, and touch may be controlled by separate modality-specific mechanisms. According to this view, the crossmodal effects reviewed in the previous section could be seen as reflecting spatial synergies between separate attentional control processes [42]. In the ERP studies discussed before, crossmodal spatial effects tended to be larger for the currently relevant modality than for the modality that could be ignored. This observation may seem more in line with the idea that attentional control processes within different modalities are 'separable-but-linked' than with a fully supramodal account. If attentional shifts were controlled by an entirely supramodal system, one might expect to find equivalent attentional effects within different modalities, regardless of whether a specific modality is currently relevant or irrelevant.

One way to investigate directly whether control processes involved in shifts of spatial attention are supramodal or modality-specific is to measure and compare ERP correlates of covert attentional shifts obtained while attention is directed to specific locations within different modalities in anticipation of expected target events. If shifts of spatial attention in vision, audition, and touch were controlled by a unitary supramodal system, one should find similar ERP patterns for preparatory attention shifts in all these modalities. In contrast, if separate modality-specific control systems were involved, this should be reflected in systematic differences in the ERPs recorded during anticipatory attentional shifts within different modalities.

Although several studies have investigated ERP correlates

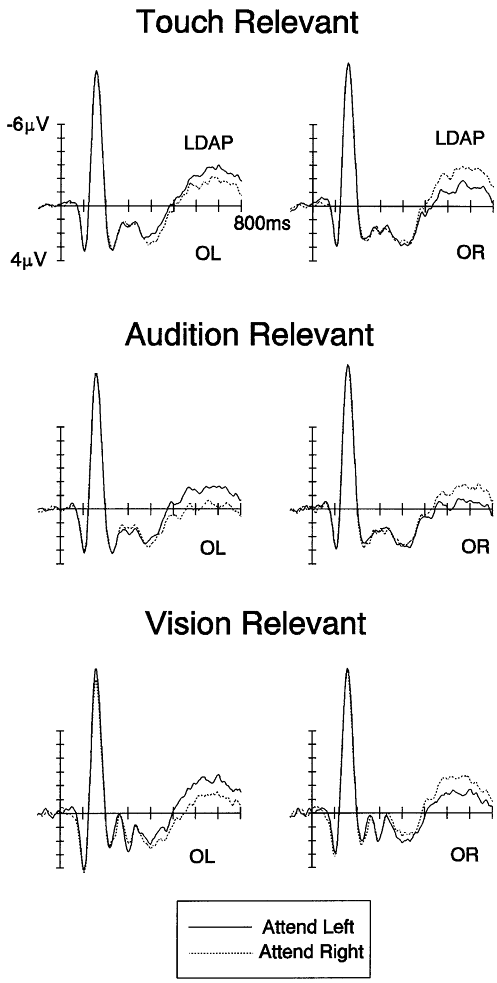

Fig. 6. Grand-averaged ERPs elicited at lateral occipital electrodes OL and OR in the 800 ms interval following the onset of a central symbolic cue directing attention to the left side (solid lines) or right side (dashed lines). Top panel: ERPs elicited when the cue indicated the relevant location of tactile events. Middle panel: ERPs elicited when the cue indicated the relevant location of auditory events. Data from Ref. [14]. Bottom panel: ERPs elicited when the cue indicated the relevant location of visual events. Unpublished data. For all three attention conditions, an enhanced positivity contralateral to the direction of an attentional shift ('Late Directing Attention Positivity', LDAP) was elicited. See text for details.

of attentional control in the interval between a cue stimulus indicating the direction of an attentional shift and a subsequent target stimulus, all these studies have been unimodal, focussing exclusively on visual-spatial orienting. For example, Harter et al. [18] measured ERPs during leftward vs rightward shifts of visual attention, triggered by central arrow cues which 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 Refs. [38,51,52]), and subsequently an enhanced contralateral positivity at posterior electrodes ('Late Directing Attention Positivity', LDAP) during later phases of the cue-target interval. In addition, Mangun and colleagues ([29]; see also Ref. [21]) and Nobre et al. [38] observed enhanced negativities at frontal electrodes contralateral to the direction of attentional shifts ('Anterior Directing Attention Negativity', ADAN). These effects were thought to reflect successive phases in the control of covert visual-spatial orienting. The EDAN has been linked to the encoding of spatial information provided by the cue and the initiation of an attentional shift [18]. The ADAN may reflect the activation of frontal structures involved in the control of attentional shifts ([38]; see also Refs. [4,39] for further discussion of frontal circuits for attentional control). The LDAP has been interpreted as indicating preparatory modulations in the excitability of visual sensory areas in anticipation of an expected visual stimulus on one or the other side [18].

Because these studies have focussed exclusively on processes underlying the control of visual-spatial attention, they do not allow any conclusions as to whether attentional shifts are controlled by supramodal or modality-specific mechanisms. To investigate whether similar ERP effects can be observed during anticipatory shifts of auditory or tactile attention (as predicted by the view that attentional orienting is controlled supramodally), we have recently recorded ERPs in response to centrally presented symbolic attentional cues which directed attention to the location of task-relevant auditory or tactile events. These data were obtained in the auditory/tactile study described in the previous section [14], where participants had to detect infrequent target stimuli at the cued location within just one currently relevant modality (either audition or touch in different experimental halves), while ignoring currently irrelevant modalities.

ERP modulations time-locked to the central cue, and sensitive to the direction of a covert attentional shift, were strikingly similar in the Audition Relevant and Touch Relevant conditions, and also closely resembled the effects previously found in unimodal visual studies, except for the fact that no early contralateral negativity (EDAN) was observed in either condition. Fig. 6 shows ERPs elicited at lateral occipital electrodes OL and OR in the 800 ms interval following the onset of a central attentional cue directing attention either to the left or to the right side. The top panel displays results obtained in the Touch Relevant condition, and the middle panel shows the results from the Audition Relevant condition. An occipital positivity contralateral to the direction of an attentional shift, starting about 500 ms after the onset of the attentional cue, was elicited during shifts of tactile attention as well as during shifts of auditory attention. This 'late directing attention positivity' (LDAP) was strikingly similar in terms of latencies and scalp distributions to the LDAP effect observed previous unimodal studies of visual-spatial orienting (e.g. Ref. [18]), and thus almost certainly reflects the same phenomenon. To illustrate the similarity of LDAP effects during shifts of tactile, auditory, and visual attention, Fig. 6 (lower panel) shows ERPs obtained in our lab in a recent, still unpublished study, in response to central precues specifying the relevant location of upcoming visual events. An LDAP is clearly present during shifts of visual attention, and this effect closely resembles the ERP pattern observed for attention shifts within touch and audition.

The fact that an LDAP is elicited not only when attention is directed in anticipation of relevant visual events on one side or the other, but also during shifts of tactile or auditory attention, may be somewhat surprising, given previous suggestions that this component is related to the preparatory activation of modality-specific visual areas [18]. It is not immediately obvious why visual areas should be selectively activated in anticipation of auditory or tactile events at specific locations. However, one could argue that multimodal spatial attention will often be dominated by visual representations of location, perhaps because vision typically has better spatial acuity than audition or touch [46]. Moreover, the experimental situation realised in our study [14] included visual cues and provided many other visible sources of information about relevant stimulus locations (e.g. central fixation cross; the visible position of the arms on the table, the visible locations of loudspeakers and tactile stimulators on the left and right side). Visual information may thus have been used to guide spatial selection, even though attention was to be directed within audition or touch. To address this important issue, we have recently run an experiment where attention had to be directed to the location of relevant tactile events while all visual stimuli had to be ignored, relevant locations were indicated by auditory rather than visual cues, and all stimuli were delivered in complete darkness (to eliminate continuously available visual sources of information about stimulus locations). Although results have not yet been fully analysed, the LDAP pattern observed in response to auditory cues directing tactile attention to the left or right side was similar to the results obtained in our previous study [14]. This suggests that the LDAP is elicited independently of the modality of an attentional cue, and regardless of whether additional visual sources of spatial information are present or not. Given these recent observations, it seems plausible to assume that the LDAP may reflect supramodal attentional control processes in posterior parietal areas. These areas are known to be involved in the control of visual-spatial attention (e.g. Ref. [27]), and also in the integration of information from different sense modalities (e.g. Ref. [2]).

In addition to the LDAP, our auditory/tactile ERP study [14] also revealed an earlier frontocentral negativity, which was elicited contralateral to the direction of an attentional shift, regardless of whether attention was directed to the location of relevant tactile or auditory events (not shown in Figs.; see Ref. [14] for details). This effect was very similar to the 'anterior directing attention negativity' (ADAN) reported in previous unimodal studies of visual-spatial attention [29,38]. The ADAN may reflect supramodal control processes within an 'anterior attention system' [39] which determine spatial parameters of attentional shifts, regardless of sensory modality. The fact that the frontal ADAN precedes the posterior LDAP is in line with Posner & Petersen's [39] proposal that anterior circuits may control more posterior spatial attention circuits (see also Refs. [20,23,40], for recent functional imaging evidence on this, albeit only from unimodal visual studies).

Overall, the observation that ERP modulations sensitive to the direction of anticipatory attentional shifts elicited in response to cues indicating the side of upcoming task-relevant visual, auditory, or tactile events are highly similar across modalities supports the hypothesis that shifts of spatial attention are controlled by supramodal processes. However, recall also that the studies reviewed in the previous section have shown that crossmodal attentional ERP effects are usually somewhat smaller for currently irrelevant modalities than for the relevant modality. This fact might initially seem more consistent with a 'separable-but-linked' view [42] than with the idea that attentional shifts are controlled in an entirely supramodal fashion [15]. The attenuation of spatial attentional effects for currently irrelevant modalities implies that some aspect of attentional control must have been affected by the task-relevance of one specific sensory modality, even though the ERP data obtained during anticipatory attentional orienting were virtually indistinguishable when attention was directed to the location of relevant auditory, tactile, or visual events. To account for these apparently inconsistent findings, one could propose that although the selection of relevant locations typically operates in a supramodal manner, the effects of spatial selection on stimulus processing within a particular modality may also depend on the tonic state of activity within that modality. Instructing participants to attend to a relevant modality, and to simultaneously ignore irrelevant modality stimuli for several successive blocks of trials may have resulted in systematic tonic differences in the overall activation level of modality-specific visual, auditory, or somatosensory areas. Attentional effects may be attenuated within currently irrelevant modalities as a result of such tonic baseline shifts of modality-specific activation levels, which are determined by the task-relevance of a modality (see Ref. [47] for earlier considerations along similar lines).

A different, and complementary way to investigate whether attentional control processes are supramodal or modality-specific is to study whether attention can be simultaneously directed into opposite directions within different modalities. If spatial selectivity was controlled by a supramodal system, visual, auditory, and tactile attention would necessarily shift together, and directing attention to opposite locations within different modalities should be impossible. If the control of spatial attention was modality-specific, it might be possible to 'split' attentional selectivity between modalities, in order to simultaneously attend to visual stimuli on the left, and auditory stimuli on the right, or vice versa. These alternatives have been investigated with behavioural measures in an experiment [42] where participants had to respond to visual and auditory targets when about 80% of all visual targets appeared on one side and

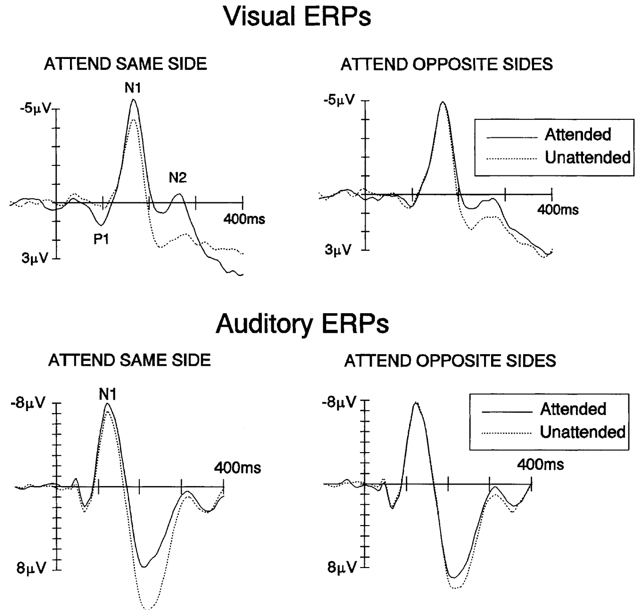

Fig. 7. Top panel: Grand-averaged event-related potentials (ERPs) elicited at parietal electrodes (PL, PR) contralateral to the visual field of stimulus presentation in response to visual stimuli at attended locations (solid lines) and unattended locations (dashed lines) under conditions where attention had to be directed to identical locations within vision and audition (Attend Same Side, left), and when attention had to be directed to opposite sides within vision and audition (Attend Opposite Sides, right). Bottom panel: Grand-averaged event-related potentials (ERPs) elicited at Cz in response to auditory stimuli at attended locations (solid lines) and unattended locations (dashed lines) when attention had to be directed to identical locations within vision and audition (Attend Same Side, left), or to opposite sides within vision and audition (Attend Opposite Sides, right). Data from Ref. [10].

about 80% of all auditory targets were presented on the opposite side. When the likely target side for each modality was constant for an entire block, small but reliable effects of spatial attention were obtained for both modalities. However, these effects were much larger under conditions where a common location was most likely for both modalities, so that visual and auditory attention could be directed to the same side. This pattern of results suggests that attentional orienting processes within one modality are not completely independent from attentional processes within another modality.

This issue was further investigated in an ERP experiment [10] where single visual or auditory stimuli were presented on the left or right side in an unpredictable sequence, and participants had to detect infrequent visual as well as auditory target stimuli among non-targets at one side which was specified prior to an experimental block. 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. If attentional shifts were controlled by a single supramodal system, ERP effects of spatial attention should be largely eliminated when attention has to be directed to opposite locations in vision and audition. In contrast, if such shifts were mediated by independent modality-specific control systems, having to attend to opposite locations within different modalities should have little or no effect on attentional ERP modulations observed for each modality.

Fig. 7 (top) shows ERPs elicited at posterior parietal electrodes contralateral to the visual field of stimulus presentation by visual non-target stimuli at visually attended and unattended locations. As expected, spatial attention resulted in a modulation of sensory-specific components in the Attend Same Side condition (left), with enhanced P1 and N1 amplitudes elicited by visual stimuli at attended locations. In contrast, attentional P1 and N1 effects were completely eliminated under Attend Opposite Sides instructions (right). However, an enhanced negativity for visual stimuli at attended locations which was elicited in the N2 time range in the Attend Same Side condition remained to be present, albeit in an attenuated fashion, in the Attend Opposite Sides condition. A similar pattern of results was observed for auditory stimuli. Fig. 7 (bottom) shows auditory ERPs at Cz under Attend Same Side (left) and Attend Opposite Sides (right) instructions. While an early attentional negativity overlapping with the auditory N1 was elicited when attention was directed to identical locations in both modalities during Attend Same Side blocks (left), this effect was completely absent in the Attend Opposite Sides condition (right). Here, enhanced negativities for auditory stimuli at attended locations only emerged about 200 ms after stimulus onset, and were considerably reduced relative to the Attend Same Side condition.

These ERP results thus confirm and extend the findings reviewed in the previous section. The observation that early sensory-specific effects of spatial attention on visual and auditory ERPs observed when visual and auditory attention could be directed to a common location were eliminated when opposite sides had to be attended in vision and audition is inconsistent with the view that spatial attention is controlled by strictly modality-specific sub-systems. Spatially selective modulations of perceptual processes in vision and audition are linked not only when directing attention to the same location in different modalities will not interfere with task performance (as in the relevant/irrelevant modality experiments reviewed in the previous section), but remain to be linked when task demands require the attentional focus to be 'split' between modalities. This may reflect one basic limitation of a supramodal attentional control system.

If crossmodal links in spatial attention affect early perceptual processes (as suggested in Section 2), attentional effects on these processes should be eliminated 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, presumably reflecting the fact that crossmodal links in spatial attention have less impact on post-perceptual processing.

4. Spatial coordinates of crossmodal links in spatial attention

Another issue relevant for the understanding of attentional control processes and their role for crossmodal interactions in spatial attention concerns the spatial coordinate systems involved in crossmodal attention. Integrating spatial information across modalities is a nontrivial problem, as spatial representations are initially highly modality-specific (retinotopic in vision, somatotopic in touch, tonotopic and then head-centred in audition). In addition, the eyes, head, and body move continuously and independently in daily life, so that the spatial mapping between sensory modalities has to be updated with each posture change. In the experiments reviewed so far, head and eyes were fixed straight ahead, and hands rested in their usual position, with the left hand on the left side, and the right hand on the right. Given this fixed posture, visual and tactile stimuli on the same side will project initially to the same hemisphere. Under such conditions, crossmodal links in spatial attention between vision and touch could be explained in terms of a simple 'hemispheric-activation' account. According to Kinsbourne [25,26], activation of appropriate control structures in the left hemisphere results in a rightward shift of spatial attention, while right-hemisphere activation results in an attentional shift to the left side. In other words, attentional shifts are controlled by the relative levels of activation of the two hemispheres. If directing attention to one side was achieved by activating control mechanisms in the contralateral hemisphere, crossmodal links in spatial attention may simply result from a spread of this activation to modality-specific areas within the same hemisphere. As an alternative to this hemispheric-activation account, one might argue that the crossmodal links in spatial attention are based on representations of common locations in external space across the modalities, regardless of initial hemispheric projections.

These two hypotheses can be distinguished by studying crossmodal links in spatial attention between vision and touch when hand posture is varied. With crossed hands, the left hand is located on the right side of visual space, but still projects to the contralateral (right) hemisphere. If directing attention to one hand was achieved by activating control structures in the contralateral hemisphere, attending to the hand located on the left should result in attentional benefits on the left side of visual space with uncrossed hands, but in benefits for the opposite visual field when hands are crossed. By contrast, if crossmodal links depend on common external locations rather than on initial hemispheric projections, the position of an attended hand and not its anatomical identity should determine crossmodal attentional effects on the processing of visual stimuli. Attending to the hand on the left side should result in processing benefits for the left side of visual space, regardless of hand posture.

We tested whether crossmodal links in spatial attention from touch to vision are determined by an external spatial reference frame, or merely by differences in hemispheric activation levels in an ERP study [11] where participants directed tactile attention to the left or right side in order to detect infrequent tactile 'gap' targets delivered to the currently attended hand. Tactile stimulation of the other hand, and visual stimuli on either side were to be ignored. The crucial additional manipulation concerned hand posture, as hands were either uncrossed or crossed in different experimental blocks. Fig. 8 shows ERPs elicited at occipital electrodes contralateral and ipsilateral to the side of visual stimulation by visual non-target stimuli presented on the tactually attended or unattended side of external space. ERPs are shown separately for blocks where hands were in their normal uncrossed position (left) and for blocks where hands were crossed (right). Fig. 9 shows visual ERPs elicited at midline electrodes by visual stimuli on the tactually attended vs. unattended side of external space, separately for both hand postures. Effects of spatial attention on ERPs elicited by irrelevant visual stimuli at tactually attended and unattended locations did not differ systematically between the two hand postures, when considered in terms of their external locations. At occipital sites, visual stimuli presented at the same external location as the attended hand elicited enhanced P1, N1, and P2 components, and this effect was present when hands were uncrossed as well as with crossed hands (Fig. 8). At midline sites, visual stimuli at tactually attended external locations elicited an enhanced negativity between 150 and 200 ms post-stimulus, and these ERP modulations were again present for both hand postures (Fig. 9). These findings are inconsistent with the hemispheric-activation account, which predicts that crossmodal attentional effects on ERPs elicited by visual stimuli at tactually attended and unattended positions within external space should have reversed when hand posture was changed. These data suggest that crossmodal links in endogenous spatial attention between touch and vision are mediated by the proximity of visual stimuli to the current location of an attended hand in external space, and not by fixed hemispheric projections.

5. Crossmodal links in exogenous (involuntary) spatial attention

The experiments reviewed in the previous sections have investigated various aspects of crossmodal interactions in endogenous (voluntary) spatial attention. However, attention can also be attracted reflexively and involuntarily

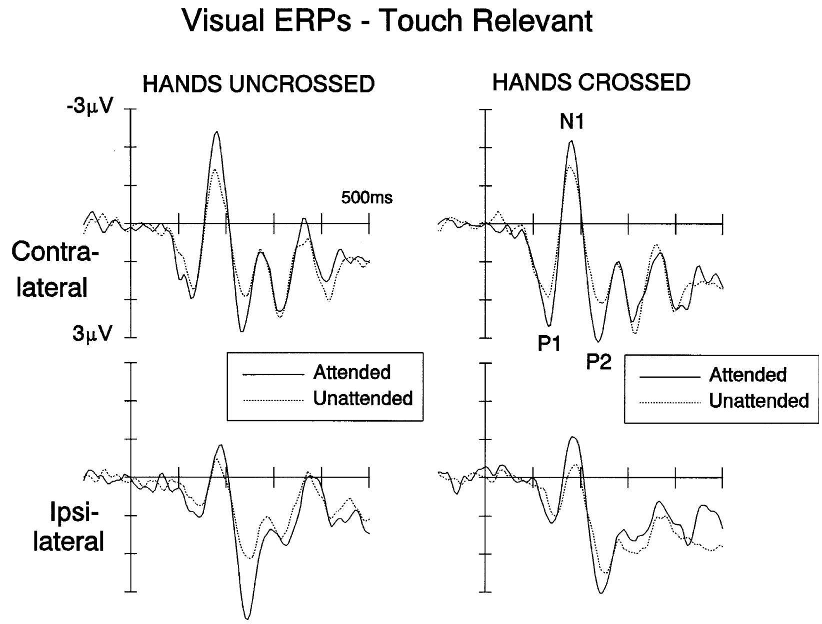

Fig. 8. Grand-averaged event-related potentials (ERPs) elicited at occipital electrodes (OL, OR) contralateral (top) and ipsilateral (bottom) to the visual field of stimulus presentation in response to visual non-target stimuli at the same external location as attended tactile events (solid lines) or at external locations contralateral to the side attended within touch (dashed lines). Attention was directed to one side within touch, and hands were either uncrossed (left) or crossed (right). Data from Ref. [11].

by salient external objects and events. Such exogenous attentional orienting processes are typically studied in tasks that use spatially uninformative but salient peripheral events as nonpredictive 'cues'. For example, visual stimuli that appear abruptly in the visual field will summon attention automatically to their location, resulting in superior performance in response to subsequent visual stimuli presented at or near that location (e.g. Ref. [22]). Similar behavioural effects of exogenous spatial attention have also been found with auditory stimuli [34,41]. Involuntary shifts of spatial attention triggered by stimuli in one modality can also affect performance in response to subsequently presented stimuli in a different modality, thereby reflecting crossmodal links in exogenous spatial attention. Responses to visual stimuli are faster and/or more accurate when these stimuli are presented on the same side as a previous uninformative auditory event [35,43], and responses to auditory stimuli can be facilitated by previous visual events at the same location [46,48]. Irrelevant auditory events not only influence the speed of responses to subsequent visual targets, but can also affect signal detection performance. Masked visual stimuli are detected more accurately when preceded by an auditory event at the same location [33], suggesting that involuntary attentional orienting processes elicited by sudden sounds can have crossmodal effects on the sensory processing of visual stimuli.

In a recent ERP study investigating crossmodal links in exogenous spatial attention from audition to vision [35], uninformative auditory events on the left or right side were followed with a stimulus onset asynchrony (SOA) of 100–300 ms by visual targets at the same or the opposite location. Responses to visual targets were faster when the appeared on the same side as the preceding auditory event. An attentional negativity (Nd) was elicited for visual ERPs recorded from contralateral occipital sites between 200 and 400 ms after stimulus onset when auditory and visual stimuli appeared at identical locations relative to visual ERPs in trials where auditory and visual stimuli were presented on opposite sides. While this observation provides electrophysiological evidence for crossmodal links in exogenous spatial attention, the fact that no attentional effects of P1 and N1 components were observed in this study [35] suggests that crossmodal effects of an auditory event on visual processes may be located after the initial sensory processing of visual information.

Along similar lines, we have recently investigated ERP correlates of crossmodal links in exogenous spatial attention from *touch* to vision in a study [24] where single visual stimuli presented on the left or right side were preceded by spatially nonpredictive brief tactile cue stimuli (10 ms duration). Visual stimuli were presented with equal probability on the same or the opposite side relative to the preceding tactile event. Participants had to ignore all tactile cues, and to respond to infrequent visual 'gap' targets regardless of their location. In separate experimental blocks, the SOA between tactile and visual stimuli was either very short (150 ms) or slightly longer (300 ms). In addition, hand posture was also varied in separate blocks (uncrossed hands vs. crossed hands), to investigate the spatial coordinate systems (see Section 4) involved in crossmodal links in exogenous spatial attention.

Fig. 10 shows ERPs elicited at lateral occipital electrodes

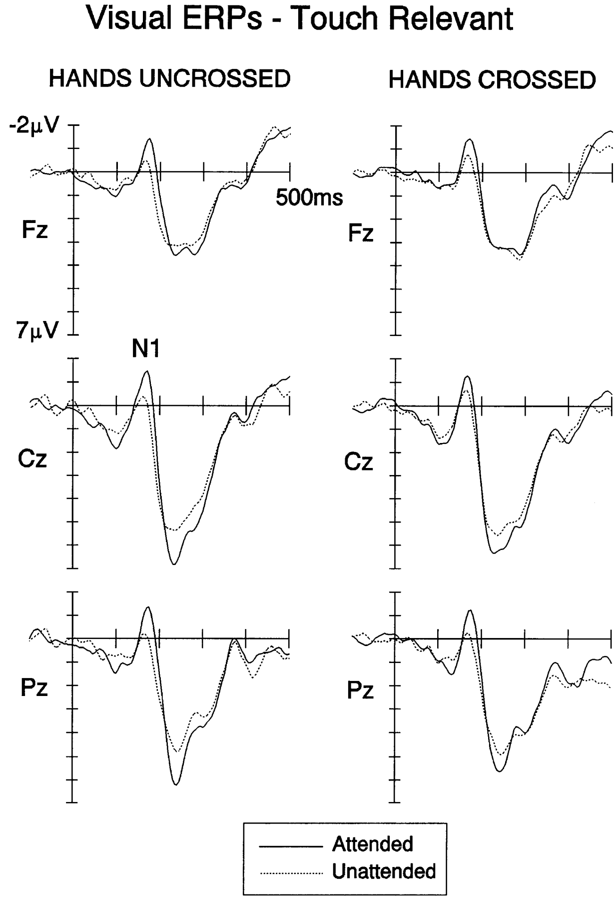

Fig. 9. Grand-averaged event-related potentials (ERPs) elicited at midline electrodes Fz, Cz, and Pz in response to visual non-target stimuli at the same external location as attended tactile events (solid lines) or at locations opposite to the side attended within touch (dashed lines). Attention was directed to one side within touch, and hands were either uncrossed (left) or crossed (right). Data from Ref. [11].

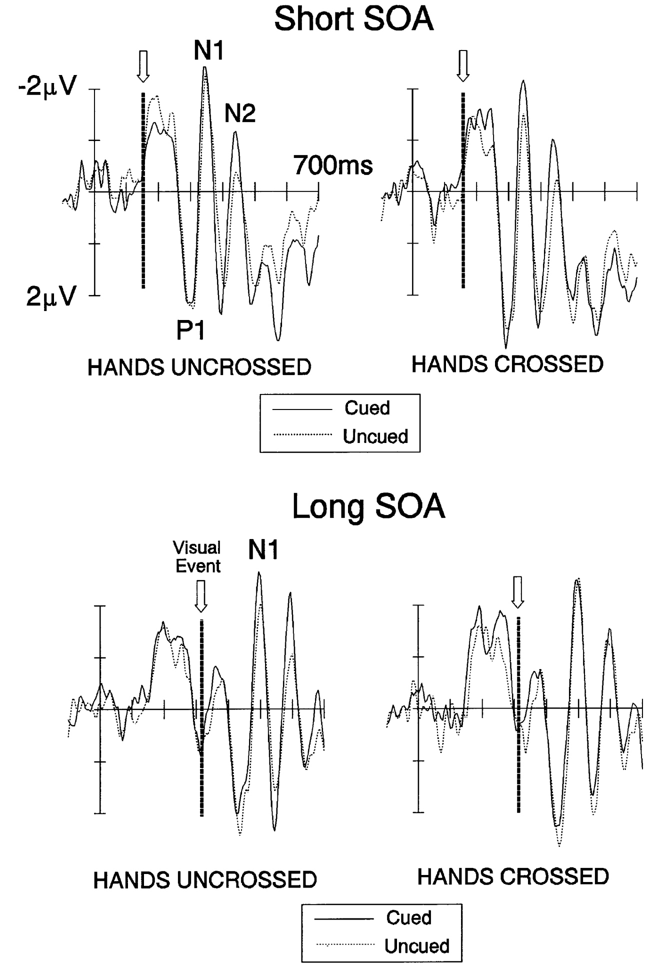

Fig. 10. Grand-averaged event-related potentials (ERPs) in response to visual non-target stimuli at tactually cued (sold lines) and uncued (dashed lines) locations. Tactile cues were uninformative with respect to the location of subsequent visual events. ERPs are plotted with the *y*-axes at the onset of the tactile cue. The onset of the subsequent visual stimulus is indicated by arrows and dashed vertical lines. ERP data were collapsed across right and left occipital electrodes (OL, OR) and visual stimulus positions. Waveforms are shown separately for uncrossed hands (left side) and crossed hands (right side), and for short (top) and long (bottom) cue-target SOAs. Data from Ref. [24].

in response to visual non-target stimuli at tactually cued and uncued locations, displayed separately for the short cue-target SOA (top) and the long cue-target SOA (bottom), and for uncrossed hands (left) as well as for crossed hands (right). ERP waveforms are time-locked to the onset of the tactile cue stimuli, and the onset of subsequent visual stimuli is indicated by arrows and dashed vertical lines. While no reliable effects of crossmodal attentional cueing were obtained for the P1 component, other visual ERP components were modulated by the location of the tactile cue. Most importantly, the N1 component was reliably enhanced in response to visual stimuli at tactually cued relative to uncued positions (see Fig. 10), presumably reflecting effects of crossmodal exogenous attention on the modality-specific processing of visual stimuli. The only exception to this general pattern was the crossed hands/long SOA condition, which failed to produce any significant effects of attentional cueing on the N1 and subsequent ERP components (Fig. 10, bottom right). These ERP effects of crossmodal exogenous spatial attention were perfectly mirrored by the results of a parallel behavioural experiment included in the same study [24]. Here, participants had to make elevation judgements with respect to visual stimuli presented near tactually cued or uncued locations. These judgments were generally better in response to visual stimuli on the cued side, and this effect was somewhat smaller with longer SOAs as well as with crossed hands, and was completely absent in the long SOA/crossed hands condition.

The results of our tactile/visual experiment [24] as well as the findings from the auditory/visual study [35] provide behavioural and electrophysiological evidence for crossmodal links in exogenous spatial attention from touch and audition to vision. The fact that crossmodal links from touch to vision influenced modality-specific brain responses as early as the occipital N1 indicates that similar to endogenous spatial attention, exogenous shifts of spatial attention triggered by salient events within one modality may crossmodally affect sensory-perceptual processing stages within other modalities. The observation that these effects were also observed when hands were crossed (for short cue-target SOAs) indicates that crossmodal exogenous attention may also be similar to endogenous attention in the spatial coordinate systems involved. Crossmodal links in exogenous attention operate in a spatial frame-of-reference, where the relative position of stimuli in external space is relevant, and posture changes are taken into account. These links are evidently not based primarily on initial hemispheric projections (see also Section 4).

6. Concluding remarks

The research reviewed in this article has used ERP measures to investigate whether there are crossmodal links in endogenous spatial attention between vision, audition, and touch; which stages in the processing of visual, auditory, and tactile information are affected by such links; the spatial coordinates in which they operate; how such crossmodal links are mediated by covert attentional control mechanisms; and whether similar links also exist in exogenous attention.

With respect to the effects of crossmodal endogenous spatial attention on the processing of information within currently irrelevant modalities, the results were clear-cut. Crossmodal links in spatial attention affected early modality-specific ERP components in the first 200 ms after stimulus onset, but had less impact on later ERP components elicited beyond 200 ms. This suggests that crossmodal links in spatial attention primarily affect sensory-perceptual processes within modality-specific cortical regions, rather than 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 at the sensory-perceptual level.

In conventional stage models of information processing, sensory-perceptual processes are viewed as 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 affected by crossmodal interactions, and any crossmodal effects should be confined to subsequent central modality-unspecific stages. The current results cast serious doubt on this conception. They demonstrate that modality-specific perceptual processes are not completely modular, because they can be affected by spatially selective processes applying to other sensory modalities.

The study of anticipatory ERP modulations sensitive to the direction of an attentional shift elicited by symbolic cues directing attention to the left or right side has also revealed findings relevant to the understanding of attentional control processes. Strikingly similar ERP patterns were observed during shifts of auditory, tactile, and visual attention, suggesting that such attentional shifts may be mediated by a supramodal frontoparietal attentional control system. The observation that ERP effects of spatial attention are somewhat attenuated for currently irrelevant modalities may initially seem inconsistent with such a supramodal account. However, this apparent inconsistency might be resolved by distinguishing between the selection of relevant locations, which is controlled by a supramodal attentional system, and the tonic state of activation within modality-specific areas, which depends on the task-relevance of a specific modality (see also Ref. [47]). Finally, ERP results strongly suggest that crossmodal links in endogenous as well as exogenous spatial attention operate in an allocentric frame of reference (based on coordinates of external space), and are not merely based on differential hemispheric activation levels.

Acknowledgements

This research has been supported by a Programme Grant from the Medical Research Council (MRC), UK, to ME and JD. The authors thank two anonymous reviewers for valuable comments, and Jose van Velzen, Steffan Kennett, Friederike Schlaghecken, Heijo van de Werf, Dan Cockburn, Ben Smedley, and Kate Parmenter, for their contributions to this experimental programme.

References

[1] Alho K. Selective attention in auditory processing as revealed by event-related brain potentials. Psychophysiol 1992;29:247–63.
[2] Andersen RA, Snyder LH, Bradley DC, Xing J. Multimodal representations of space in the posterior parietal cortex and its use in planning movements. Ann Rev Neurosc 1997;20:303–30.
[3] 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.
[4] Corbetta M, Miezin FM, Shulman GL, Petersen SE. A PET study of visuospatial attention. J Neurosc 1993;13:1202–26.
[5] 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. Biol Psychol 1998;49:269–94.
[6] 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. p. 349–411.
[7] Driver J, Spence C. Attention and the crossmodal construction of space. Trends Cogn Sci 1998;2:254–62.
[8] Eason RG. Visual evoked potential correlates of early neural filtering during selective attention. Bull Psychon Soc 1981;18:203–6.
[9] Eimer M. 'Sensory gating' as a mechanism for visual-spatial orienting: Electrophysiological evidence from trial-by-trial cueing experiments. Percept Psychophys 1994;55:667–75.
[10] Eimer M. Can attention be directed to opposite locations in different modalities? An ERP study. Clin Neurophysiol 1999;110:1252–9.

[11] Eimer M, Cockburn D, Smedley B, Driver J. Cross-modal links in endogenous spatial attention are mediated by common external locations: evidence from event-related brain potentials. Exp Brain Res 2001;13:398–411.
[12] Eimer M, Driver J. An event-related brain potential study of cross-modal links in spatial attention between vision and touch. Psychophysiol 2000;37:697–705.
[13] Eimer M, Schröger E. ERP effects of intermodal attention and cross-modal links in spatial attention. Psychophysiol 1998;35:313–27.
[14] 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. J Cogn Neurosc 2001 (in press).
[15] Farah MJ, Wong AB, Monheit MA, Morrow LA. Parietal lobe mechanisms of spatial attention: modality-specific or supramodal? Neuropsychologia 1989;27:461–70.
[16] Frot M, Rambaud L, Guénot M, Maugière F. Intracortical recordings of early pain-related CO_2-laser evoked potentials in human second somatosensory (SII) area. Clin Neurophysiol 1999;110:133–45.
[17] García-Larrea L, Lukaszewicz AC, Mauguière F. Somatosensory responses during selective spatial attention: the N120-to-N140 transition. Psychophysiol. 1995;32:526–37.
[18] Harter MR, Miller SL, Price NJ, LaLonde ME, Keyes AL. Neural processes involved in directing attention. J Cogn Neurosci 1989;1:223–37.
[19] 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. p. 395–414.
[20] Hopfinger JB, Buonocore MH, Mangun GR. The neural mechanisms of top-down attentional control. Nature Neurosc 2000;3:284–91.
[21] Hopfinger JB, Jha A, Hopf JM, Girelli M, Mangun GR. Electrophysiological and neuroimaging studies of voluntary and reflexive attention. In: Monsell S, Driver J, editors. Attention and performance XVII. Cambridge, MA: MIT Press, 2000. p. 125–53.
[22] Jonides J. Voluntary vs. automatic control over the mind's eye's movement. In: Long JB, Baddeley AB, editors. Attention and performance IX. Hillsdale, NJ: Erlbaum, 1981. p. 187–203.
[23] Kastner S, Pinsk MA, De Weerd P, Desimone R, Ungerleider LG. Increased activity in human visual cortex during directed attention in the absence of visual stimulation. Neuron 1999;22:751–61.
[24] Kennett S, Eimer M, Spence C, Driver J. Tactile-visual links in exogenous spatial attention under different postures: convergent evidence from Psychophysics and ERPs. J Cogn Neurosc 2001;13:462–78.
[25] Kinsbourne M. The mechanisms of hemispheric control of the lateral gradient of attention. In: Rabbitt PMA, Dornic S, editors. Attention and performance V. London: Academic Press, 1975. p. 81–93.
[26] Kinsbourne M. Orientational model of unilateral neglect: evidence from attentional gradients within hemispace. In: Robertson IH, Marshall JV, editors. Unilateral neglect: clinical and experimental studies. Hillsdale, NJ: Erlbaum, 1993. p. 63–86.
[27] LaBerge D. Attentional processing. Cambridge, MA: Harvard University Press, 1995.
[28] Lloyd DM, Spence C, Merat N, McGlone F. Crossmodal links in covert endogenous spatial attention between audition and touch. Percept Psychophys (submitted).
[29] Mangun GR. Orienting attention in the visual fields: an electrophysiological analysis. In: Heinze HJ, Münte TF, Mangun GR, editors. Cognitive electrophysiology Boston: Birkhäuser, 1994. p. 81–101.
[30] Mangun GR. The neural mechanisms of visual selective attention. Psychophysiol 1995;32:4–18.
[31] Mangun GR, Hillyard SA. Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. J Exp Psychol Hum Perc Perf 1991;17:1057–74.
[32] Mangun GR, Hillyard SA, Luck SJ. Electrocortical substrates of visual selective attention. In: Meyer DE, Kornblum S, editors. Attention and performance XIV. Cambridge, MA: MIT Press, 1993. p. 219–43.
[33] McDonald JJ, Teder-Sälejärvi WA, Hillyard SA. Involuntary orienting to sound improves visual perception. Nature 2000; 407:906–8.
[34] McDonald JJ, Ward LM. Spatial relevance determines facilitatory and inhibitory effects of auditory covert spatial orienting. J Exp Psychol Hum Perc Perf 1999;25:1234–52.
[35] McDonald JJ, Ward LM. Involuntary listening aids seeing: evidence from human electrophysiology. Psychol Sci 2000;11:167–71.
[36] Michie PT, Bearpark HM, Crawford JM, Glue LCT. The effects of spatial selective attention on the somatosensory event-related potential. Psychophysiol 1987;24:449–63.
[37] Näätänen R. Processing negativity: an evoked-potential reflection of selective attention. Psychol Bull 1982;92:605–40.
[38] Nobre AC, Sebestyen GN, Miniussi C. The dynamics of shifting visuospatial attention revealed by event-related brain potentials. Neuropsychologia 2000;38:964–74.
[39] Posner MI, Petersen SE. The attention system of the human brain. Ann Rev Neurosc 1990;13:25–42.
[40] Rosen AC, Rao SM, Caffara P, Scaglioni A, Bobholz J, Woodley SC, Hammerke TA, Cunningham JM, Prieto TE, Binder JR. Neural basis of endogenous and exogenous spatial orienting: a functional MRI study. J Cogn Neurosc 1999;11:135–52.
[41] Spence C, Driver J. Covert spatial orienting in audition: exogenous and endogenous mechanisms facilitate sound localization. J Exp Psychol Hum Perc Perf 1994;20:555–74.
[42] Spence C, Driver J. Audiovisual links in endogenous covert spatial attention. J Exp Psychol Hum Perc Perf 1996;22:1005–30.
[43] Spence C, Driver J. Audiovisual links in exogenous covert spatial orienting. Percept Psychophys 1997;59:1–22.
[44] Spence C, Pavani F, Driver J. Crossmodal links between vision and touch in covert endogenous spatial attention. J Exp Psychol Hum Perc Perf 2000;26:1298–319.
[45] Teder-Sälejärvi WA, Münte TF, Sperlich FJ, Hillyard SA. Intra-modal and cross-modal spatial attention to auditory and visual stimuli: an event-related brain potential (ERP) study. Cogn Brain Res 1999;8:327–43.
[46] Ward LM. Supramodal and modality-specific mechanisms for stimulus-driven shifts of auditory and visual attention. Can J Exp Psychol 1994;48:242–59.
[47] Ward LM, McDonald JJ, Golestani N. Cross-modal control of attention shifts. In: Wright RD, editor. Visual attention. New York: Oxford University Press, 1998. p. 232–68.
[48] Ward LM, McDonald JJ, Lin D. On asymmetries in cross-modal spatial attention orienting. Percept Psychophys 2000;62:1258–64.
[49] 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.
[50] Woods DL, Alh K, Algazi A. Intermodal selective attention. I. Effects on event-related potentials to lateralized auditory and visual stimuli. Electroenc Clin Neurophysiol 1992;82:341–55.
[51] Yamaguchi S, Tsuchiya H, Kobayashi S. Electroencephalographic activity associated with shifts of visuospatial attention. Brain 1994;117:553–62.
[52] Yamaguchi S, Tsuchiya H, Kobayashi S. Electrophysiologic correlates of age effects on visuospatial attention shift. Cogn Brain Res 1995;3:41–49.