

Martin Eimer · José van Velzen

Spatial tuning of tactile attention modulates visual processing within hemifields: an ERP investigation of crossmodal attention

Received: 29 July 2004 / Accepted: 30 August 2004 / Published online: 21 July 2005
© Springer-Verlag 2005

Abstract Recent event-related brain potential (ERP) studies have revealed crossmodal links in spatial attention, but have not yet investigated differences in the spatial tuning of attention between task-relevant and irrelevant modalities. We studied the spatial distribution of attention in vision under conditions where participants were instructed to attend to the left or right-hand in order to detect infrequent targets, and to entirely ignore visual stimuli presented via LEDs at two eccentricities in the left or right hemifield. Hands were located close to two of these four LEDs in different blocks. Visual N1 amplitudes were enhanced when visual stimuli in the cued hemifield were close to the attended hand, relative to visual stimuli presented at the other location on the same side. These within-hemifield attentional modulations of visual processing demonstrate that crossmodal attention is not distributed diffusely across an entire hemifield. The spatial tuning of tactile attention transfers crossmodally to affect vision, consistent with spatial selection at a multimodal level of representation.

Keywords Attention · Crossmodal · Vision · Touch · Event-related brain potentials

Introduction

Research on attention has traditionally been conducted independently for different sensory modalities. However, recent behavioural and event-related brain potential (ERP) studies have uncovered crossmodal interactions in both exogenous (involuntary) and endogenous (voluntary) spatial attention (e.g. Ward 1994; Spence and

Driver 1997; McDonald and Ward 2000; McDonald et al. 2000; Kennett et al. 2001, for exogenous attention; Hillyard et al. 1984; Eimer and Schröger 1998; Teder-Sälejärvi et al. 1999; Eimer and Driver 2000; Eimer et al. 2002, for endogenous attention).

In most ERP experiments on endogenous spatial attention, one modality is assigned the role as “primary” task-relevant modality, while another modality is “secondary” because it is task-irrelevant. A single stimulus is presented on each trial, unpredictably on the left or right side, and unpredictably in the relevant or irrelevant modality. Participants attend to the left or right side in preparation for a perceptual judgement that will be required in response to a primary modality stimulus on the attended side, while ignoring primary modality stimuli on the opposite side, and all secondary modality regardless of their location. The general finding from experiments using this general procedure is that attentional modulations of sensory-specific visual, auditory, or somatosensory ERP components are present not only for the currently task-relevant primary modalities, but also for irrelevant secondary modalities (see Eimer 2001; Eimer and Driver 2001, for reviews). This demonstrates that sensory-perceptual stages of visual, auditory, and tactile processing (i.e. stages traditionally considered to be unimodal) are affected by crossmodal links in spatial attention, consistent with the hypothesis that the selection of attended locations operates at a multimodal level of spatial representation (Farah et al. 1989).

If attended locations were selected multimodally, the spatial distribution (or “tuning”) of attention for task-relevant modalities should not differ from the spatial distribution of attention for task-irrelevant modalities. Systematic differences in the spatial distribution of attention between modalities, with attention narrowly tuned for relevant modalities, but much more diffusely spread for irrelevant modalities, would be inconsistent with such a multimodal selection view. Unfortunately, current research on crossmodal attention cannot decide between these possibilities, as the spatial tuning of attention across task-relevant and task-irrelevant

M. Eimer (✉) · J. Velzen
Department of Psychology, Birkbeck College,
University of London, Malet Street,
London, WC1E 7HX, UK
E-mail: m.eimer@bbk.ac.uk
Tel.: +44-20-76316358

modalities has not yet been investigated systematically. Most previous crossmodal studies have examined only one location in each hemifield (i.e. just one left and one right location), and could therefore not investigate the spatial distribution of attention for each modality within hemifields (but see Ferlazzo et al. 2002).

To investigate whether the within-hemifield spatial tuning of attention can transfer crossmodally from a task-relevant to a task-irrelevant modality, as implied by the hypothesis that spatial selection operates at a multimodal level of representation, we have recently investigated ERP correlates of crossmodal spatial attention in a study where visual and auditory stimuli could appear at any of four possible locations (two in the left and two in the right hemifield), with only one of these locations relevant for an auditory or visual task (Eimer et al. 2004). On each trial, a visual or auditory stimulus was presented unpredictably on the left or right side at an eccentricity of 21° (Inner location) or 52° (Outer location). When audition was task-relevant, participants had to detect infrequent target tones at one of the four locations, while ignoring tones at other locations, and all visual events regardless of their location. In another experiment, the roles of the two modalities were reversed (i.e. vision was task-relevant and audition irrelevant). Results demonstrated that the spatial tuning of attention for the task-relevant modality transfers crossmodally to the task-irrelevant modality. Sensory-specific visual N1 components triggered by irrelevant visual stimuli at the location currently relevant for the auditory task were enhanced, relative to N1 amplitudes elicited by visual stimuli in the same cued hemifield, but at the other task-irrelevant location. For auditory ERPs, an enhanced negativity starting on the descending flank of the auditory N1 component was obtained when irrelevant tones were presented at the location relevant for the visual task, as compared to the other stimulation location on the same cued side.

If crossmodal attention was merely reflected by a diffuse spread of attention across one entire hemifield for task-irrelevant secondary modalities, no such within-hemifield attentional ERP modulations should have been observed when vision and audition were task-irrelevant. Thus, the results of our previous study (Eimer et al. 2004) provide the first evidence that the spatial tuning of attention within one task-relevant modality shows crossmodal transfer to another irrelevant modality, as predicted by the hypothesis that shifts of attention are controlled at a multimodal level of representation.

The aim of the present experiment was twofold. First, we wanted to extend the existing ERP evidence for the crossmodal transfer of attentional tuning within hemifields by investigating a different combination of sensory modalities. While our previous study investigated this issue with respect to crossmodal links between vision and audition, we now focussed on tactile-visual crossmodal interactions. More specifically, we wanted to find out whether manipulating the locus of tactile-spatial

attention would result in spatially specific within-hemifield modulations of visual processing under conditions where visual stimuli could be entirely ignored. Second, we wanted to resolve an important question that was left unanswered by the results of our earlier study (Eimer et al. 2004). In that previous study, primary modality stimuli could appear at two possible locations on the cued side, of which only one was relevant for the primary modality task. In other words, participants had to discriminate between relevant and irrelevant primary modality locations in the same hemifield. It is possible that a crossmodal transfer of within-hemifield attentional selectivity to an irrelevant modality will only be observed under conditions where participants have to perform a within-hemifield attentional selection task in the primary modality. The present experiment was designed to investigate whether crossmodal transfer of attentional tuning within hemifields also takes place when there is only a single primary modality stimulus location on each side, and no within-hemifield selectivity is therefore required for the primary modality task.

The overall set up of the present experiment was similar to our earlier study (Eimer et al. 2004), except that auditory stimuli were replaced by tactile stimuli, and that touch was task-relevant throughout. On each trial, a single peripheral visual or tactile stimulus was presented. Tactile stimuli were presented to the left or right index finger, while visual stimuli were delivered by one of four LEDs (two in the left and two in the right hemifield at the same “Inner” and “Outer” positions as in our previous study). At the start of each trial, a central visual cue directed tactile attention to the left or right side. Participants were instructed to detect and respond to infrequent tactile targets when these were presented to the cued/attended hand, and to ignore tactile stimulation of the uncued hand, as well as all visual stimuli, regardless of their location. The crucial manipulation concerned hand posture. In different blocks, hands were placed either adjacent to the two Inner LEDs on the left or right side, or adjacent to the two Outer LEDs.

For somatosensory ERPs, we expected to find the typical modulatory effects of tactile-spatial attention, with enhanced sensory-specific N140 components for tactile stimuli delivered to the currently attended task-relevant hand (see Michie et al. 1987; García-Larrea et al. 1995; Eimer and Driver 2000; Eimer and Forster 2003; Hötting et al. 2003). The important crossmodal question was whether and how shifts of tactile attention would be reflected in attentional modulations of visual ERPs. To investigate between-hemifield effects of crossmodal attention, we compared ERPs triggered in response to visual stimuli adjacent to the currently cued (attended) hand with ERPs in response to visual stimuli in the opposite hemifield close to the uncued hand. Most importantly, to investigate the within-hemifield spatial tuning of crossmodal attention, we then compared ERPs to visual stimuli presented in the cued hemifield as a function of whether they were located

adjacent to the cued hand, or at the other location on the same cued side. If directing tactile attention to the left or right hand merely resulted in a diffuse hemifield-wide crossmodal attentional modulation of visual processing, these ERPs should not differ. Such a result might indicate that the crossmodal attentional modulations within hemifields will only be elicited when participants have to perform a within-hemifield attentional selection task in the primary modality (as in the Eimer et al. 2004 study). In contrast, if the spatial tuning of tactile attention transferred crossmodally to vision, enhanced visual N1 components should be observed when visual stimuli are presented close to the cued hand, relative to visual stimuli presented at the other position within the cued hemifield.

Materials and methods

Participants

Twelve paid volunteers (seven females), aged 19–40 years (mean age: 29.4 years) participated in the experiment, after giving their written informed consent. Eleven participants were right-handed, one was left-handed, and all had normal or corrected to normal vision. The experiment was performed in accordance with the ethical standards laid down in the 1964 declaration of Helsinki, and was approved by the Ethics Committee, School of Psychology, Birkbeck College.

Material and procedure

Participants sat in a dimly lit experimental chamber, with a head-mounted microphone positioned 2 cm in front of the mouth. Head position was fixed with a chin rest. A computer monitor was placed centrally in front of the participant at a viewing distance of 55 cm. Central symbolic visual cue stimuli consisted of two adjacent triangles, which covered a visual angle of $3.5 \times 2.5^\circ$, and were presented centrally at the bottom of the computer screen at an angle of about 30° below eye level. One of the triangles was red, the other blue, and they always pointed in opposite directions (“ $> <$ ” or “ $< >$ ”). These two alternative cue arrangements were presented with equal probability and randomly distributed in each block. A central fixation cross, located in the space between the two triangles, was continuously present on the computer screen throughout the experimental blocks.

Peripheral visual stimuli were 200 ms illuminations of an ensemble of green LEDs, consisting of six segments arranged in a circle plus one central segment (angular size: 1.9°). Four of these LED ensembles were placed on a table on top of four cardboard boxes (which were cut open at the front to allow index fingers to be placed inside these boxes; see below) at horizontal eccentricities of 21° (Inner position) and 52° (Outer position) to the left and right of fixation. These positions were laid out

on a virtual semicircle centred on the subject’s head at a constant viewing distance of 55 cm.

Tactile stimuli were presented using 5-V solenoids, which drove a metal rod with a blunt conical tip to the radial side of the middle phalanx of the left and right index fingers. The rod made contact with a finger whenever a current was passed through the solenoid. White noise (65 dB SPL, measured from the position of the participants’ head) was continuously present to mask any sounds made by the tactile stimulators. Tactile stimuli were vibrations (200 ms duration), generated by presenting 20 brief pulses. The stimulus onset asynchrony between successive pulses was 10 ms, corresponding to a stimulation frequency of 100 Hz. For “soft” vibrations (targets), the contact time between rod and skin was 2 ms, followed by a 8 ms interpulse interval. For “strong” vibrations (non-targets), contact time was 3 ms, followed by a 7 ms interpulse interval. These settings produced vibrations with identical frequency, but different intensity.

Twelve experimental blocks were run, each consisting of 112 trials. Hand posture was manipulated between blocks. In six successively delivered blocks, participants positioned their left and right index fingers in the boxes supporting the left and right LED ensembles at the Inner positions. In the other six successive blocks, index fingers were positioned in the boxes supporting the Outer LEDs. Order of hand posture conditions was balanced across participants.

Each trial started with the presentation of a central cue (100 ms duration), followed after an interval of 600 ms by a tactile or visual peripheral stimulus. Inter-trial interval was 1000 ms. Participants were instructed to maintain central fixation throughout each trial, to respond vocally (by saying “yes”) whenever a tactile target (a soft vibration) was presented to the hand indicated by the cue, and to completely ignore all visual stimuli, regardless of their location. The side relevant for a tactile target/non-target discrimination on any given trial was signalled by the direction of one of the triangles. For six participants, blue triangles were relevant (i.e. a cue stimulus array containing a left-pointing blue triangle instructed participants to direct their tactile attention to the left hand, while a right-pointing blue triangle indicated a rightward attention shift). For the other six participants, red triangles were relevant.

In 48 trials per block, a tactile non-target stimulus (a strong vibration) was presented with equal probability to the left or right hand. These tactile non-targets were preceded with equal probability by a left or right cue, resulting in 12 trials for each combination of cued side (left versus right) and stimulated hand (left versus right). Sixteen trials per block contained tactile target stimuli. In 12 of these trials, tactile targets were delivered to the cued hand, and thus required a vocal response. In four other trials, targets were delivered to the uncued hand. In the remaining 48 trials per block, visual stimuli were presented with equal probability one of the four locations (left and right Inner and Outer position). These

stimuli were preceded with equal probability a cue directing attention to the left or right hand, resulting in six trials per block for each combination of cued side (left side versus right side), stimulus side (left hemifield versus right hemifield), and stimulus eccentricity (Inner position versus Outer position). Prior to the onset of the first experimental block, training blocks were run until task performance and eye movement control were satisfactory. These training blocks were identical to experimental blocks, except that they contained fewer trials (76 instead of 112).

EEG recording and data analyses

The EEG was recorded with Ag–AgCl electrodes and linked-earlobe reference from F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, and P8 (according to the 10–20 system), and from OL and OR (located halfway between O1 and P7, and O2 and P8, respectively). Horizontal EOG was recorded bipolarly from the outer canthi of both eyes. The impedance for all electrodes was kept below 5 k Ω . The amplifier bandpass was 0.1–40 Hz, and no additional filters were applied to the EEG waveforms prior to analysis. The EEG and EOG were sampled with a digitization rate of 200 Hz and stored on disk. Voice onset times were measured for each vocal response.

The EEG and EOG were epoched off-line into 1400 ms periods, starting 100 ms prior to cue onset, and ending 600 ms after the onset of a peripheral stimulus. Trials where horizontal eye movements (HEOG exceeding ± 30 μ V relative to baseline) were detected throughout this period (usually indicating an eye movement towards the cued side) were excluded from analysis. Likewise, trials with eye blinks (Fpz exceeding ± 60 μ V relative to baseline), or other artifacts (a voltage exceeding ± 60 μ V at any electrode location relative to baseline) obtained in 600 ms interval following the onset of a peripheral stimulus were excluded from analysis. Averaged HEOG waveforms obtained in response to left and right cues were then scored for deviations of eye position in the cued direction. Residual HEOG deflections were below ± 2 μ V for all participants.

The ERPs in response to tactile non-target stimuli and to peripheral visual stimuli were averaged separately, relative to a 100 ms pre-stimulus baseline, for all combinations of hand position (Inner versus Outer), cue direction (left versus right), stimulus side (left versus right), and stimulus eccentricity (Inner versus Outer; for visual ERPs only). Statistical analyses were conducted separately for midline electrodes (Fz, Cz, and Pz), and for lateral electrodes (F3, F4, C3, C4, P3, and P4). For somatosensory ERPs, mean amplitudes were obtained within post-stimulus latency windows centred on the somatosensory P100, N140, and N2 components (90–120, 130–160, and 200–280 ms, respectively). Mean amplitude values were then analysed with repeated measures ANOVAs, which were conducted separately for midline electrodes and for lateral

electrodes for the factors attention (stimulation of cued/attended versus uncued/unattended hand), hand posture (Inner versus Outer position), stimulus side (left versus right hand), electrode site (frontal versus central versus parietal), and recording hemisphere (left versus right, for lateral electrodes only).

For visual ERPs, mean amplitude values were obtained within post-stimulus latency windows centred on the visual P1 and N1 components (90–130 and 150–190 ms, respectively). In addition, another set of analyses was conducted for a longer-latency time window (200–300 ms), which was identical to the measurement interval used in our previous study (Eimer et al. 2004). Across-hemifield crossmodal attention effects were analysed in repeated measures ANOVAs, which included ERPs for trials where visual stimuli were located adjacent to the left and right hand (that is, visual stimuli delivered at Near positions on blocks where participants' hands were located at these Near positions, and at Far positions when hands were located there). As for the somatosensory ERPs, statistical analyses were conducted for midline electrodes (Fz, Cz, and Pz), and for lateral electrodes (F3, F4, C3, C4, P3, and P4), and included the factors across-hemifield attention (visual stimulus close to cued hand versus visual stimulus in the opposite hemifield), stimulus eccentricity (visual stimulus at Near versus Far position), stimulus side (left versus right visual hemifield), electrode site, and recording hemisphere (for lateral electrodes only). Additional analyses were conducted separately for lateral occipital electrodes (OL and OR). Within-hemifield crossmodal attention effects were analysed on the basis of ERPs triggered on those trials where visual stimuli were delivered in the cued hemifield. In these analyses, the factor across-hemifield attention was replaced by within-hemifield attention (visual stimulus close to the cued hand versus visual stimulus at the other location on the cued side). When appropriate, Greenhouse-Geisser adjustments to the degrees of freedom were performed, and the adjusted *P*-values are reported.

Results

Behavioural data

Mean vocal reaction time to cued tactile targets was 678 ms. There were no significant effects of stimulus location or hand position on response latencies. Participants missed 7.3% of all cued tactile targets. False Alarms to uncued tactile targets, or to tactile or visual non-targets, occurred on less than 1% of those trials.

Somatosensory ERPs: effects of unimodal tactile attention

Figure 1 shows ERPs to tactile non-targets delivered to the cued versus uncued hand, collapsed across both hand postures (Inner versus Outer position). No

significant effects of attention were obtained for the P100 component. In contrast, tactile-spatial attention resulted in markedly enhanced N140 amplitudes for tactile stimuli presented to the cued hand. This was reflected in main effects of attention at lateral electrodes [$F(1,11)=7.7$; $P<0.02$] as well as at midline electrodes [$F(1,11)=5.2$; $P<0.05$]. In both analyses, significant electrode site \times attention interactions were obtained [$F(2,22)=15.4$ and 19.1 ; both $P<0.001$; $\epsilon=0.568$ and 0.693 , for lateral and midline sites, respectively]. Subsequent analyses conducted separately for single electrode sites revealed that significant effects of attention on N140 amplitudes were present at all central and parietal sites [C3/4, P3/4, Cz, and Pz, all $F(1,11)>5.9$; all $P<0.04$], but were absent at more anterior electrodes (Fz, F3/4). No interactions between attention and hand posture were present at lateral or midline electrodes (both $F<1$), demonstrating that attentional modulations of N140 amplitudes were not affected by the manipulation of hand position.

Figure 1 also shows enhanced N2 components when tactile non-targets were delivered to the currently attended hand, and this was reflected in main effects of attention on N2 mean amplitudes for lateral electrodes [$F(1,11)=8.3$; $P<0.02$] as well as at midline electrodes [$F(1,11)=7.0$; $P<0.02$]. Although electrode site \times attention interactions were observed [$F(2,22)=8.0$ and 7.0 ; $P<0.02$ and 0.03 ; $\epsilon=0.716$ and 0.597 , for lateral and midline sites, respectively], follow-up analyses showed that effects of attention on N2 amplitudes were reliably

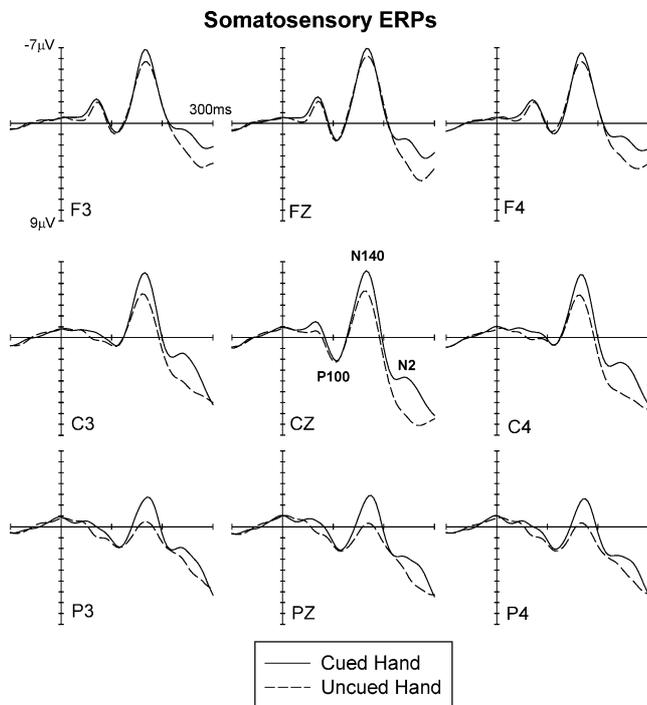


Fig. 1 Grand-averaged somatosensory ERPs (collapsed across left and right tactile stimuli) triggered in the 300 ms interval following stimulus onset by tactile non-target stimuli delivered to the cued/attended hand (solid lines) and to the uncued/unattended hand (dashed lines)

elicited at all analysed sites, except for Fz and Pz, where attentional modulations were almost significant [$F(1,11)=4.6$ and 4.7 ; both $P<0.06$]. Again, no interactions between attention and hand posture were present at lateral or midline electrodes (both $F<1$).

Visual ERPs: across-hemifield effects of crossmodal attention

Figure 2 shows ERPs triggered when visual stimuli were presented from LEDs adjacent to the left or right hand, displayed separately for visual stimuli delivered close to the cued hand (solid lines), or close to the uncued hand (dashed lines). These ERPs are collapsed across stimulus eccentricities and hand postures. While no significant effects of across-hemifield attention were observed at any electrode site for P1 amplitudes, crossmodal links in spatial attention from touch to vision were reflected in enhanced N1 components for visual stimuli presented close to the task-relevant cued hand. Significant effects of across-hemifield attention were present for N1 amplitudes at lateral and at midline electrodes [$F(1,11)=37.8$ and 35.0 , respectively; both $P<0.001$], as well as at OL/R [$F(1,11)=26.3$ $P<0.001$]. A main effect of stimulus eccentricity at lateral electrodes [$F(1,11)=5.7$; $P<0.04$] and at OL/R [$F(1,11)=15.8$; $P<0.002$] reflected the unsurprising fact that N1 amplitudes were larger in response to Near relative to Far

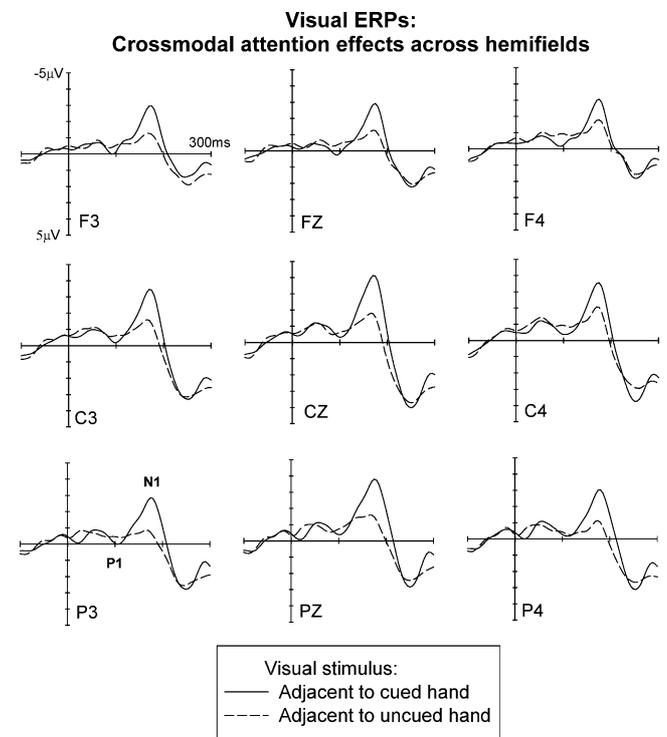


Fig. 2 Grand-averaged visual ERPs (collapsed across left and right visual stimuli) triggered in the 300 ms interval following stimulus onset by visual non-target stimuli located adjacent to the cued/attended hand (solid lines) and in the opposite visual hemifield adjacent to the uncued/unattended hand (dashed lines)

visual stimuli (not shown in Fig. 2). However, and more importantly, there was no indication of any stimulus eccentricity \times across-hemifield attention interactions for lateral and midline sites or at OL/R [all $F(1,11) < 1.6$], thus indicating that crossmodal attentional modulations of visual N1 amplitudes were not affected by whether visual stimuli were presented at the Near or Far location.¹ No significant effects of crossmodal attention were present in the subsequent longer-latency analysis window (200–300 ms post-stimulus).

Visual ERPs: within-hemifield effects of crossmodal attention

Figures 3 and 4 shows ERPs triggered by visual stimuli presented on the cued side as a function of whether they were located adjacent to the task-relevant hand (solid lines), or at the other position on the same cued side (dashed lines). Figure 3 shows ERPs in response to visual stimuli at Near positions, while Fig. 4 shows ERPs triggered by visual stimuli at Far positions. While within-hemifield crossmodal attention had no effect on P1 amplitudes, these figures clearly show that N1 amplitudes were enhanced when visual stimuli were presented adjacent to the attended hand, regardless of their eccentricity. This fact was reflected in main effects of within-hemifield attention on N1 mean amplitudes at lateral electrodes [$F(1,11) = 9.9$; $P < 0.01$] as well as at midline electrodes [$F(1,11) = 6.7$; $P < 0.03$], and at OL/R [$F(1,11) = 7.2$; $P < 0.03$]. Stimulus eccentricity had a main effect on lateral and midline N1 amplitudes (both $F(1,11) > 9.7$; both $P < 0.01$), due to the unsurprising fact that the N1 component was larger in response to visual stimuli at Inner (Fig. 3) relative to Outer positions (Fig. 4). However, and more importantly, there was no trace of any eccentricity \times within-hemifield attention interaction at lateral or midline electrodes, or at OL/R (all $F < 0.3$), thus underlining the fact illustrated in Fig. 3 and 4 that within-hemifield crossmodal attentional modulations of visual N1 components were present for visual stimuli at Inner and at Outer positions.² No reli-

¹Two other significant higher-order interactions were found for the N1 analysis window. At lateral electrodes, an across-hemifield attention \times recording hemisphere \times stimulus side interaction [$F(1,11) = 22.5$; $P < 0.001$] indicated that attentional N1 modulations were more pronounced contralateral to the side of visual stimulus presentation. However, additional analyses revealed significant across-hemifield attention effects for contralateral as well as ipsilateral electrodes (both $F(1,11) > 25.0$; both $P < 0.001$). At midline electrodes, an across-hemifield attention \times electrode site was present [$F(2,22) = 4.9$; $P < 0.04$; $\epsilon = 0.691$], but further analyses confirmed that crossmodal attention effects were significant at all three midline sites (all $F(1,11) > 22.2$; all $P < 0.001$).

²A within-hemifield attention \times recording hemisphere \times stimulus side interaction [$F(1,11) = 4.8$; $P < 0.05$] was found at lateral electrodes, reflecting the fact that attentional N1 modulations were more pronounced contralateral to the side of visual stimulus presentation. Additional analyses revealed significant crossmodal within-hemifield attentional modulations for both contralateral and ipsilateral sites [both $F(1,11) > 8.4$; both $P < 0.02$].

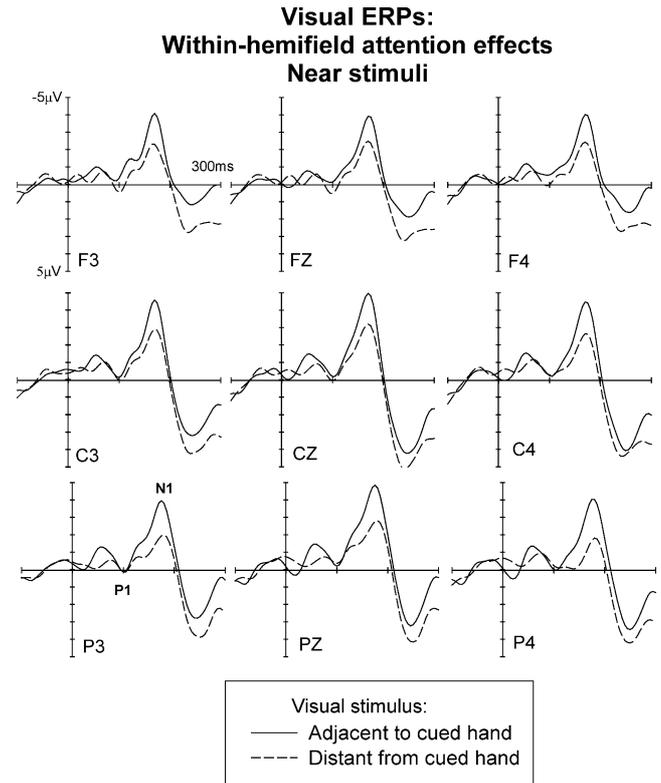


Fig. 3 Grand-averaged visual ERPs (collapsed across left and right visual stimuli) triggered in the 300 ms interval following stimulus onset by visual non-target stimuli presented at the Near location in the cued hemifield when this location was adjacent to the cued/attended hand (solid lines) and when it was distant from the cued/attended hand (dashed lines)

able effects of within-hemifield attention were present in a subsequent analysis window (200–300 ms post-stimulus).³

Discussion

The purpose of the present ERP study was to investigate whether the spatial tuning of attention would transfer crossmodally from touch to vision, thereby confirming and extending previous ERP evidence for the crossmodal transfer of attentional tuning between vision and audition (Eimer et al. 2004). We manipulated the locus of tactile-spatial attention by instructing participants to position their hands at Inner or Outer locations in different blocks, and to attend to the left or right hand in order to detect and respond to infrequent tactile targets delivered there. The to-be-attended side was indicated by visual precues at the start of each trial. Task-irrelevant visual stimuli could be delivered from LEDs positioned at Inner and Outer locations on the left and right side.

³This also applies to the amplitude differences apparent in Fig. 3 between 200 and 300 ms post-stimulus for near visual stimuli as a function of their distance from the cued hand, which failed to reach overall statistical significance [$F(1,11) = 3.5$; $P > 0.08$].

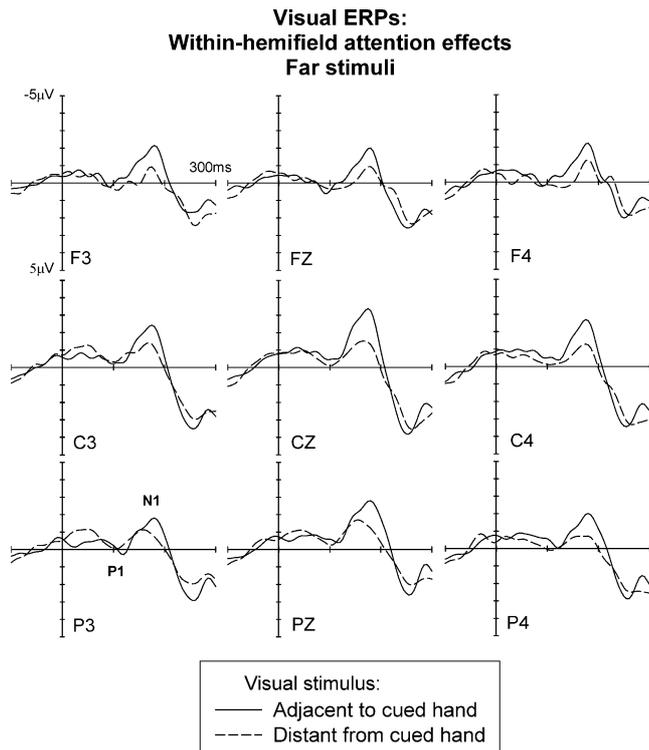


Fig. 4 Grand-averaged visual ERPs (collapsed across left and right visual stimuli) triggered in the 300 ms interval following stimulus onset by visual non-target stimuli presented at the Far location in the cued hemifield when this location was adjacent to the cued/attended hand (*solid lines*) and when it was distant from the cued/attended hand (*dashed lines*)

When ERPs to tactile stimuli presented to the cued versus uncued hand were compared, attentional modulations of the somatosensory N140 component as well as a subsequent sustained attentional negativity were observed (see Fig. 1), thereby confirming observations from previous ERP experiments on tactile-spatial attention (Michie et al. 1987; García-Larrea et al. 1995; Eimer and Driver 2000; Eimer and Forster 2003), and demonstrating that the experimental procedures adopted in the present study were successful in directing attention to the cued hand. The absence of any interaction between hand posture and attention indicated that attentional modulations of somatosensory ERPs were unaffected by hand position.

Across-hemifield effects of crossmodal attention were analysed by comparing visual ERPs elicited by task-irrelevant visual stimuli delivered from LEDs at locations adjacent to the left or right hand as a function of whether this hand was either cued (attended) or uncued. Similar to our earlier ERP investigations of crossmodal visuo-tactile links in spatial attention (Eimer and Driver 2000), enhanced N1 components were elicited when visual stimuli were presented close to the cued hand, relative to visual stimuli close to the other hand located on the opposite side (Fig. 2). This observation again confirms the presence of crossmodal attentional links from touch to vision, which result in spatially specific

modulations of visual processing as a result of directing attention to one side versus the other for a tactile task.⁴

Most importantly, the question whether effects of crossmodal attention on visual ERPs would be present within hemifields was investigated by comparing ERPs triggered by visual stimuli on the cued side as a function of whether these were presented adjacent to the currently attended hand, or on the same cued side, but distant from the attended hand (that is, at the Near location when hands were positioned at Far locations, or at the Far location when hands were placed at Near locations). Results demonstrated that the current focus of tactile attention induces spatially specific within-hemifield modulations of visual processing, even though visual stimuli could be entirely ignored. Regardless of whether visual stimuli were presented at Near (Fig. 3) or at Far locations (Fig. 4), attentional enhancements of N1 amplitudes were observed whenever these stimuli were presented adjacent to the cued hand, relative to trials where they were presented at the other location on the same side.

Figure 5 shows the impact of crossmodal attention on visual N1 amplitudes at central and parietal sites, separately for across-hemifield effects (obtained by subtracting N1 mean amplitudes in response to visual stimuli close to the uncued hand from N1 amplitudes triggered by visual stimuli close to the cued hand), and for within-hemifield effects (obtained by subtracting N1 amplitudes in response to visual stimuli presented on the cued side, but distant from the cued hand, from N1 amplitudes triggered by visual stimuli adjacent to the cued hand). Although within-hemifield effects of crossmodal attention tended to be numerically smaller than across-hemifield effects, they were clearly present at all electrode sites. Moreover, additional post hoc analyses which directly compared the size of these crossmodal across-hemifield and within-hemifield effects on N1 mean amplitudes showed that there were no significant differences in the magnitude of attentional N1 modulations caused by across-hemifield and within-hemifield crossmodal attention.

The presence of within-hemifield attentional modulations of visual ERPs elicited as a function of the current locus of tactile attention, and the fact that these modulations were not significantly smaller than the effects observed for across-hemifield attention confirms and extends previous findings that the spatial tuning of attention transfers crossmodally from vision to audition, and vice versa (Eimer et al. 2004) by demonstrating that similar principles also apply to crossmodal links from touch to vision. In this earlier study, primary

⁴It should be noted that no crossmodal attentional modulation of the visual P1 component was observed in the present study. Effects of crossmodal spatial attention on P1 amplitudes have generally been found less consistently than crossmodal effects on N1 amplitudes (see Hillyard et al. 1984; Eimer and Schröger 1998; Eimer et al. 2004, for audio-visual ERP studies which did not observe crossmodal attentional effects on the P1, but see Eimer and Driver 2000 for effects of tactile attention on visual P1 amplitudes).

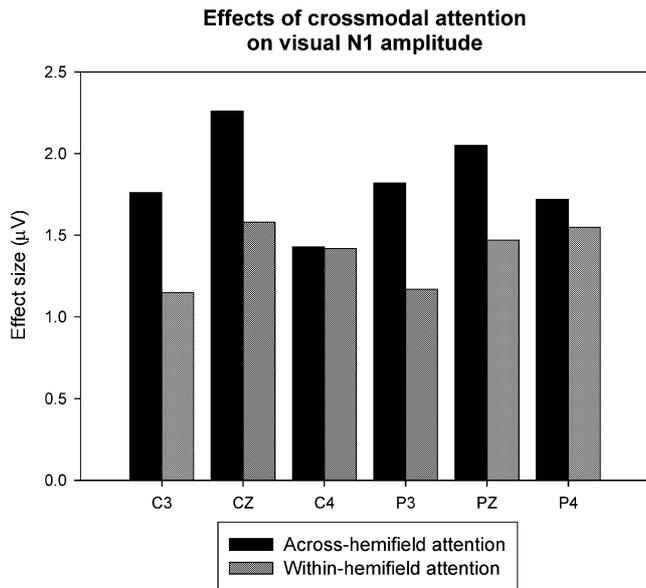


Fig. 5 Across-hemifield and within-hemifield effects of crossmodal attention on visual N1 amplitudes at selected electrode sites. Bars represent difference amplitudes obtained by subtracting mean amplitudes in the N1 time range (150–190 ms post-stimulus) for visual stimuli at tactually unattended locations from mean amplitudes in response to visual stimuli presented close to the cued hand. *Black bars* illustrate across-hemifield attention effects (visual stimuli at cued hand minus visual stimuli at uncued hand), and *grey bars* show within-hemifield effects (visual stimuli at cued hand minus visual stimuli at irrelevant location on cued side)

modality stimuli could appear at one task-relevant as well as at one task-irrelevant location in the same hemifield. In contrast, only a single tactile stimulation location on each side was used in the present experiment, where participants were therefore not required to discriminate between attended and unattended primary modality locations on the same side. In spite of this important difference, within-hemifield effects of crossmodal attention on visual processing were again obtained, and these attentional modulations of visual ERPs were similar to the effects found in our earlier audio-visual study (Eimer et al 2004). This pattern of results demonstrates that the spatial tuning of attention within hemifields shows crossmodal transfer regardless of whether or not within-hemifield spatial selection is required in the task-relevant modality.

Overall, the present results demonstrate that the spatial focus of tactile attention transfers crossmodally to affect vision, resulting in an enhancement of visual stimulus processing close to the currently attended hand. If crossmodal links in spatial attention merely resulted in a diffuse allocation of attention across one entire hemifield for a task-irrelevant modality, ERPs to visual stimuli presented in the cued hemifield should not have been affected by whether or not these stimuli were located close to the attended hand. The current findings suggest that the spatial tuning of attention does not differ systematically between currently task-relevant and task-irrelevant modalities, and thereby lend further

support to the hypothesis that crossmodal interactions in spatial attention reflect location-selection at a multi-modal level of spatial representation. However, given the fact that visual stimulus locations in the same hemifield were separated by about 30°, we cannot yet rule out the possibility that the attentional focus for an irrelevant modality may be somewhat less sharply tuned than the focus within a primary modality. To identify possible subtle differences in the spatial tuning of attention across modalities, future studies will need to compare unimodal and crossmodal attentional effects across more closely spaced stimulation locations.

Acknowledgements This research was supported by a Programme grant from the Medical Research Council (UK). M.E. holds a Royal Society-Wolfson Research Merit Award. The authors thank Kausar Turabi and Heijo van de Werf for technical assistance.

References

- Eimer M (2001) Crossmodal links in spatial attention between vision, audition, and touch: evidence from event-related brain potentials. *Neuropsychologia* 39:1292–1303
- Eimer M, Driver J (2000) An event-related brain potential study of cross-modal links in spatial attention between vision and touch. *Psychophysiology* 37:697–705
- Eimer M, Driver J (2001) Crossmodal links in endogenous and exogenous spatial attention: evidence from event-related brain potential studies. *Neurosci Biobehav Rev* 25:497–511
- Eimer M, Forster B (2003) Modulations of early somatosensory ERP components by transient and sustained spatial attention. *Exp Brain Res* 151:24–31
- Eimer M, Schröger E (1998) ERP effects of intermodal attention and cross-modal links in spatial attention. *Psychophysiology* 35:313–327
- Eimer M, Van Velzen J, Driver J (2002) Crossmodal interactions between audition, touch and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *J Cogn Neurosci* 14:254–271
- Eimer M, Van Velzen J, Driver J (2004) ERP evidence for cross-modal audio-visual effects of endogenous spatial attention within hemifields. *J Cogn Neurosci* 16:272–88
- Farah MJ, Wong AB, Monheit MA, Morrow LA (1989) Parietal lobe mechanisms of spatial attention: modality-specific or supramodal? *Neuropsychologia* 27:461–470
- Ferlazzo F, Couyoumdjian A, Padovani T, Belardinelli MO (2002) Head-centred meridian effect on auditory spatial attention orienting. *Q J Exp Psychol* 55A:937–963
- García-Larrea L, Lukaszewicz AC, Mauguière F (1995) Somatosensory responses during selective spatial attention: the N120-to-N140 transition. *Psychophysiology* 32:526–537
- Hillyard SA, Simpson GV, Woods DL, Van Voorhis S, Münte TF (1984) Event-related brain potentials and selective attention to different modalities. In: Reinoso-Suarez F, Ajmone-Marsan C (eds) *Cortical integration*. Raven Press, New York, pp 395–414
- Hötting K, Röder B, Rösler F (2003) Crossmodal and intermodal attention modulates event-related brain potentials to tactile and auditory stimuli. *Exp Brain Res* 148:26–37
- Kennett S, Eimer M, Spence C, Driver J (2001) Tactile-visual links in exogenous spatial attention under different postures: convergent evidence from psychophysics and ERPs. *J Cogn Neurosci* 13:462–478
- McDonald JJ, Ward LM (2000) Involuntary listening aids seeing: evidence from human electrophysiology. *Psychol Sci* 11:167–171
- McDonald JJ, Teder-Sälejärvi WA, Hillyard SA (2000) Involuntary orienting to sound improves visual perception. *Nature* 407:906–908

- Michie PT, Bearpark HM, Crawford JM, Glue LCT (1987) The effects of spatial selective attention on the somatosensory event-related potential. *Psychophysiology* 24:449–463
- Spence C, Driver J (1997) Audiovisual links in exogenous covert spatial attention. *Percept Psychophys* 59:1–22
- Teder-Sälejärvi WA, Münte TF, Sperlich FJ, Hillyard SA (1999) Intra-modal and cross-modal spatial attention to auditory and visual stimuli: an event-related brain potential (ERP) study. *Cogn Brain Res* 8:327–343
- Ward LM (1994) Supramodal and modality-specific mechanisms for stimulus-driven shifts of auditory and visual attention. *Can J Exp Psychol* 48:242–259