RESEARCH ARTICLE

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Cross-modal links in endogenous spatial attention are mediated by common external locations: evidence from event-related brain potentials

Abstract Recent behavioural and event-related potential (ERP) studies reported cross-modal links in spatial attention between vision, audition and touch. Such links could reflect differences in hemispheric-activation levels associated with spatial attention to one side, or more abstract spatial reference-frames mediating selectivity across modalities. To distinguish these hypotheses, ERPs were recorded to lateral tactile stimuli, plus visual (experiment 1) or auditory stimuli (experiment 2), while participants attended to the left or right hand to detect infrequent tactile targets, and ignored other modalities. In separate blocks, hands were either in a crossed or uncrossed posture. With uncrossed hands, visual stimuli on the tactually attended side elicited enhanced N1 and P2 components at occipital sites, and an enhanced negativity at midline electrodes, reflecting cross-modal links in spatial attention from touch to vision. Auditory stimuli at tactually attended locations elicited an enhanced negativity overlapping with the N1 component, reflecting cross-modal links from touch to audition. An analogous pattern of results arose for crossed hands, with tactile attention enhancing auditory or visual responses on the side where the attended hand now lay (i.e. in the opposite visual or auditory hemifield to that enhanced by attending the same hand when uncrossed). This suggests that cross-modal attentional links are not determined by hemispheric projections, but by common external locations. Unexpectedly, somatosensory ERPs were strongly affected by hand posture in both experiments, with attentional effects delayed and smaller for crossed hands. This may reflect the combined influence of anatomical and external spatial codes within the tactile modality, while cross-modal links depend only on the latter codes.

Keywords Tactile-spatial attention · Cross-modal attention · Spatial representation · Event-related brain potentials

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Introduction

Experiments investigating mechanisms of spatial attention have traditionally focused on selective processing within single stimulus modalities. Only recently has the issue of cross-modal links in spatial attention been addressed by several behavioural and electrophysiological investigations (see Driver and Spence 1998 for an overview). Some cross-modal studies have investigated links in spatial attention between vision and audition (e.g. Spence and Driver 1996, 1997; Ward 1994; Eimer and Schröger 1998; Eimer 1999). For instance, Spence and Driver (1996) found that when visual attention was directed to one side endogenously (i.e. because visual targets were known to be more likely there), not only visual discrimination but also auditory discrimination performance was better for stimuli presented at the visually attended side (even when sound targets were actually somewhat less likely there). Similarly, when auditory attention was endogenously directed to one side, visual as well as auditory discrimination was improved there. This pattern of results suggests symmetrical cross-modal links between spatial attention in audition and vision.

In an ERP study, Eimer and Schröger (1998) found electrophysiological evidence to support such links. They measured attentional modulation of visual and auditory ERPs when participants directed attention to the left or right within either audition or vision, in order to detect infrequent targets within the single relevant modality at that location. Stimuli from the other modality were task-irrelevant and so could be completely ignored. Attentional modulations of the occipital N1 component, plus an enhanced negativity at midline electrodes, were

found for visual stimuli at a visually attended location. Critically, this attentional modulation of visual components was still present, albeit attenuated, when attending to one side or the other within audition (with vision now task-irrelevant), thus demonstrating cross-modal links. Analogously, for auditory ERPs, spatial attention resulted in an enhanced negativity at midline electrodes for attended locations when audition was relevant, and these effects remained present, albeit attenuated, when only vision was task-relevant (see also Hillyard et al. 1984 for similar results).

Investigations of cross-modal links in endogenous spatial attention involving the somatosensory modality have only just begun. Some behavioural evidence for the existence of cross-modal links between touch and vision comes from a recent study by Spence et al. (2000) (exp. 3), where participants made elevation discriminations (up vs down) in response to visual targets presented on the left or right side, and to tactile targets presented on the left or right hand. In different blocks, one target modality was more likely than the other, and targets within this primary modality were highly likely to appear on one side (while the rarer targets in the secondary modality were somewhat more likely on the other side). Reaction times (RTs) were faster for stimuli presented on the side attended in the primary modality, both within that modality and also in the secondary modality, thus demonstrating cross-modal links. Such links were found regardless of whether touch or vision was primary, indicating a tendency for spatial attention to be directed to the same side in these two modalities. However, the attentional effects were always larger for whichever modality was currently primary, suggesting that the spatial distribution of attention within one modality (here, vision or touch) spreads to the other, but in an attenuated form. This behavioural evidence for links between vision and touch is consistent with both the behavioural (e.g. Spence and Driver 1996) and the ERP results (e.g. Eimer and Schröger 1998) from previous studies of audiovisual links.

Moreover, converging electrophysiological evidence was recently reported for cross-modal links in spatial attention between touch and vision. Eimer and Driver (2000) required participants to focus attention endogenously on the left or right side within one task-relevant modality (touch or vision), to detect infrequent targets in that modality on the instructed side, while ignoring events in the other, task-irrelevant modality. For visual ERPs, attentional modulations of occipital P1 and N1 components, plus enhanced negativities at midline electrodes, were found on the visually attended side. Similar, albeit somewhat attenuated, attentional modulation was found for visual ERPs when attending to tactile stimuli on one side, thus indicating that links in spatial attention from touch to vision can affect fairly early stages of visual processing. For somatosensory ERPs elicited by tactile stimuli delivered to the left or right index finger, attentional negativities were observed at midline and lateral central electrodes when attending to one side in touch,

starting around 140 ms poststimulus. Similar, albeit somewhat attenuated, modulations of somatosensory ERPs were observed when attending to one side in just vision, reflecting links in spatial attention from vision to touch.[1]

In summary, the above studies provide initial behavioural and electrophysiological evidence for cross-modal links in spatial attention between vision, audition, and touch. Given that such links exist, one can now ask what mechanisms are involved in driving covert attention to the same side for different input modalities. Integrating spatial information across modalities is a non-trivial problem, since 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 different input modalities has to be updated with each posture change. In all the above experiments, the participant's 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. In this particular fixed posture, visual and tactile stimuli on the same side will project initially to the same hemisphere. Under these conditions, cross-modal links in spatial attention between vision and touch could be explained in terms of a simple 'hemispheric-activation' account. According to Kinsbourne (1975, 1993), activation of appropriate structures in the left hemisphere tends to result in a rightward shift of spatial attention, while right-hemisphere activation results in an attentional shift to the left side. The actual direction of attention then corresponds to the relative levels of activation of the two hemispheres. If directing attention to one side was achieved by activating structures in the contralateral hemisphere, cross-modal links in spatial attention between vision and touch (like those observed to date) may simply result from a spread of activation between visual and tactile areas within the same hemisphere. As an alternative to this hemispheric-activation account, one might argue that the cross-modal links in spatial attention are based on representations of common locations in external space across the modalities, regardless of initial hemispheric projections (see Kennett et al. 2001; Spence et al. 2000).

These two hypotheses can be distinguished by studying cross-modal links in spatial attention between vision and touch when hand posture is varied. With crossed hands, the left hand is now located on the right side of visual space, but still projects initially to the contralater-

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[1] It should be noted that effects of visual-spatial attention on somatosensory ERPs were only obtained when occasional responses were required to infrequent tactile targets regardless of their location, that is, when tactile stimuli could not be entirely ignored, but were potentially task-relevant on both sides. In contrast, no attentional SEP modulations were found when tactile stimuli were completely response-irrelevant. This suggests that, unlike vision and audition (where modulations can be found even when entirely task-irrelevant), touch may be decoupled from attentional orienting within another modality unless it is potentially relevant

al (right) hemisphere. If endogenously directing tactile attention to the left hand was achieved simply by activating appropriate structures in the contralateral hemisphere, then a simple hemispheric-activation account predicts that cross-modal links in attention should continue to benefit the left side of visual space (even though the left hand now lies on the other side). Thus, on the hemispheric-activation account, attending to a particular hand should advantage the same side of visual space, regardless of where that hand is placed. By contrast, if cross-modal links depend more on common external location than on initial hemispheric projections, then the advantaged side of visual space should reverse when the hands are crossed.

Preliminary behavioural evidence for the latter possibility was reported by Spence et al. (2000) (experiments 4 and 5), who found that crossing the hands reversed the pattern of cross-modal links that was observed when considered in terms of hemispheric projections (while leaving it unchanged when considered in terms of locations in external space). In the present study, ERPs were used to address this issue for the first time, examining how cross-modal links in spatial attention between touch and vision (experiment 1), and also between touch and audition (experiment 2), operate under different postures.

Experiment 1 investigated effects of tactile-spatial attention on somatosensory ERPs, and also (cross-modally) on visual ERPs, when the hands were either uncrossed or crossed. Left or right visual stimuli, or tactile stimuli delivered to the left or right index finger, were presented equiprobably, one at a time, in a random order. Participants were instructed to direct their tactile attention to the left or right side in order to detect infrequent tactile target stimuli (two pulses with a gap, rather than one continuous pulse as for the more common non-targets). They performed this 'oddball' detection task only for the tactile stimuli delivered to the currently attended hand. Tactile stimuli on the other hand, or visual stimuli on either side, were simply to be ignored. Hand posture (crossed versus uncrossed) was varied between blocks.

Tactile-spatial attention was expected to affect somatosensory ERPs, with larger early components elicited by tactile stimuli on the attended side, and enhanced negativities for attended relative to unattended stimuli beyond 150 ms poststimulus (see Michie 1984; Michie et al. 1987; García-Larrea et al. 1995; Eimer and Driver 2000 for previous ERP studies of tactile-spatial attention). Any cross-modal links in spatial attention from touch to vision should lead *visual* ERPs also to be systematically affected by which side was attended in touch. With uncrossed hands, visual stimuli on the same side as the attended hand (and projecting to the same hemisphere) were expected to elicit enlarged occipital ERP components, as well as enhanced negativities at midline electrodes (see Eimer and Driver 2000 for recent findings of this kind). The crucial new question to be investigated in experiment 1 was how visual ERPs would be cross-modally modulated by tactile-spatial attention when hands were crossed. If cross-modal links in spatial

attention between touch and vision are based on initial hemispheric projections, then attending to one hand when crossed should continue to enhance visual ERPs on the same side as previously found when uncrossed (i.e. now the opposite side to where the crossed hand lay). In contrast, if the cross-modal links are determined by common external locations across the modalities, then attending to one hand should now enhance visual ERPs for the opposite visual hemifield to that observed with uncrossed hands (i.e. the visual hemifield where that crossed hand lay).

Experiment 1: cross-modal links between touch and vision, for different hand postures

Materials and methods

Participants

Fifteen paid volunteers participated. Two had to be excluded due to a large number of eye blinks during trials, one because of insufficient eye-fixation control (see below). Thus 12 participants (4 females), aged 19–22 years (mean age: 20.3 years), remained in the sample. Eleven were right handed, one was left handed, and all had normal or corrected vision by self-report. The experiment (as well as experiment 2) was approved by the Psychology Ethics Committee and all participants gave their informed consent.

Stimuli and apparatus

Participants sat in a dimly lit experimental chamber, with a head-mounted microphone positioned about 2 cm in front of the mouth. Tactile stimuli were presented using two 12-V solenoids, each of which drove a metal rod with a blunt conical tip through a small hole onto the outside of the index finger (see Spence et al. 1998). The rod made contact with the pad of the participant's index finger whenever a current was passed through the solenoid. The rods and fingertips were occluded, so that participants could not see any movements. White noise was presented from a central loudspeaker at 70 dB(A) throughout the experimental blocks, in order to mask any sounds made by the operation of the tactile stimulators. Visual stimuli were presented by illuminating one of two ensembles of green light-emitting diodes (LEDs), each consisting of six segments arranged in a circle plus one central segment (see Fig. 1). The angular size of each LED was 0.65°, and the diameter of the circle was 2.4°. A small black cross printed on paper and attached to the central loudspeaker at about 30° below eye level served as the fixation point. The two tactile stimulators and the two LED ensembles were each placed on a table at 25° to the left or right of the central fixation cross, with the tactile and visual stimulators on any one side in close spatial register, at a viewing distance of about 45 cm from the participant's eyes (see Fig. 1).

Tactile non-target stimuli consisted of one rod tip contacting the participant's index finger for 200 ms. The rarer tactile target stimuli (oddballs) had a gap, where this continuous contact was interrupted for 10 ms after a duration of 95 ms. Visual non-target stimuli consisted of the continuous illumination of one LED ensemble for 200 ms. For the rarer visual gap stimuli, the LED ensemble was illuminated for 95 ms, turned off for 10 ms, and illuminated again for 95 ms, analogously to tactile targets. The latter stimuli were included to prevent participants performing their purely tactile task via amodal gap detection. Vocal response onset times to the tactile oddball targets on the relevant hand were measured with a voice key.
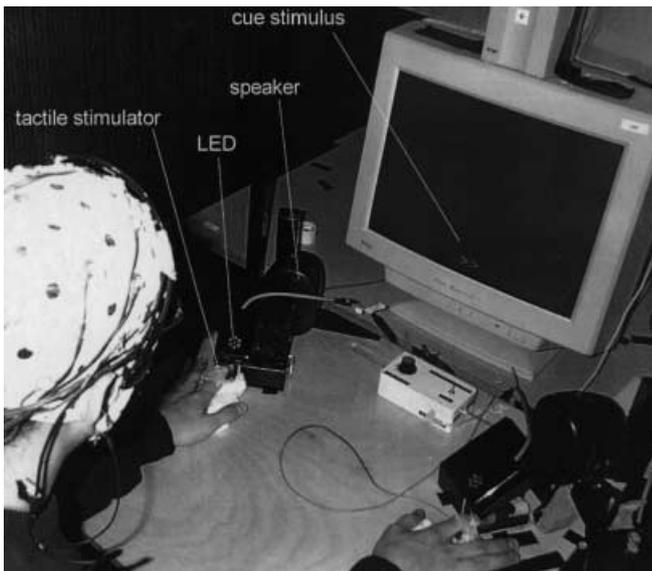
Fig. 1 Illustration of the experimental setup used in this study. EEG was recorded while single tactile stimuli (experiments 1 and 2) or visual stimuli (experiment 1) or auditory stimuli (experiment 2) were presented on the left or right side. Tactile stimuli were delivered by stimulators attached to the left and right index finger; visual stimuli were brief flashes of LEDs; and auditory stimuli were presented via loudspeakers. In experiment 2 (shown here), the relevant hand was indicated at the beginning of each trial by a symbolic precue. In experiment 1, where the relevant hand was constant for a block of trials, no computer screen was present, and a small black cross attached to the central loudspeaker delivering the masking noise served as the fixation point

Procedure

The experiment consisted of 20 experimental blocks of 88 trials each, with an intertrial interval of 1000 ms (all our previous cross-modal ERP studies had also used fixed intervals between trials, e.g. Eimer and Schröger 1998; Eimer and Driver 2000). For 60 of the 88 trials, a visual or tactile non-target was presented with equal probability and in random order on the left or right side. In the remaining randomly intermingled 28 trials, a visual or tactile stimulus with a gap was presented with equal probability on the left or right side. In separate blocks, participants were instructed to direct their attention to the left or right hand in order to detect tactile target stimuli presented on that hand only. A vocal response ("yes") was required whenever a tactile gap target was delivered at the relevant hand. All other stimuli were to be ignored (i.e. tactile stimuli on the other hand, and visual stimuli on both sides). In half of the blocks, hands were uncrossed (left index finger stimulated by tactile stimulator on the left side, and vice versa); in the other blocks, posture was crossed (left index finger stimulated by the tactile stimulator on the right side of the table, and vice versa). The combination of relevant location within touch (left vs right side) and hand posture (uncrossed vs crossed) resulted in a total of four task conditions, each delivered for five successive blocks. The order of delivery of these blocked task conditions was counterbalanced across participants.

Participants were instructed to respond as quickly and accurately as possible to tactile oddball targets on the relevant hand, and to maintain central eye-fixation throughout the blocks. Several training blocks were run prior to the beginning of the first experimental block. Eye movements were closely monitored during these training blocks. Whenever the HEOG revealed that participants did not maintain central eye fixation, they were reminded again of the necessity of continuously fixating the central cross throughout an experimental block. Additional training blocks were run until fixation control was regarded as satisfactory.

Recording and data analysis

EEG was recorded with Ag-AgCl electrodes and linked-earlobe reference from Fpz, Fz, Cz, Pz, C3, and C4 (according to the 10–20 system), and from OL and OR (located halfway between O_1 and T_5, and O_2 and T_6, respectively). HEOG was recorded bipolarly from the outer canthi of both eyes. The impedance for the EOG electrodes was kept below 10 kΩ and for all other electrodes below 5 kΩ. The amplifier bandpass was 0.1–40 Hz. EEG and EOG were sampled with a digitization rate of 200 Hz and stored on disk. Vocal response onset times were measured for each response.

EEG and EOG were epoched offline into 800-ms periods, starting 100 ms prior to and ending 700 ms after the onset of the stimulus. Only EEG epochs obtained for non-target trials were further analysed, to avoid contamination by vocal responses. Trials with eyeblinks (Fpz exceeding ±60 µV relative to 100 ms prestimulus baseline), horizontal eye movements (HEOG exceeding ±30 µV relative to baseline), other artefacts (a voltage exceeding ±60 µV at any electrode location relative to baseline), or vocal responses recorded on non-target trials were all excluded from analysis. Averaged HEOG waveforms elicited by visual or tactile stimuli presented on the left or right side were scored for systematic deviations of eye position, indicating any residual tendencies to move the eyes to the location of target stimuli. A residual HEOG deviation exceeding ±2 µV led to the disqualification of one participant.

The EEG to the non-target stimuli was averaged separately for all combinations of stimulus modality (vision vs touch), stimulus location (left vs right), hand posture (crossed vs uncrossed) and relevant location within touch (left vs right side), resulting in 16 ERP waveforms for each participant and electrode site. All ERP measures were taken relative to the mean voltage of the 100 ms pre-stimulus baseline interval, and all latencies are given relative to stimulus onset. Mean amplitude values were computed separately for visual and somatosensory ERPs. Based on predictions drawn from previous work (see Eimer and Driver 2000), attentional modulation of early, modality-specific sensory responses were analysed for the somatosensory N80 and N140 components (70–100 ms and 130–170 ms poststimulus, respectively) at lateral central sites; and for the visual P1 and N1 components (100–150 ms and 160–200 ms, respectively) at lateral occipital sites. Additional analyses were conducted for midline ERPs in the N1 and N140 measurement windows (for visual and tactile stimuli, respectively). In addition, later attentional modulations were analysed within two successive 55-ms intervals (200–255 ms and 260–315 ms poststimulus). Separate repeated measures ANOVAs were performed on ERP mean amplitude values for the within-subject factors of relevant location (attended vs unattended side within touch), stimulus side (left vs right), hand posture (crossed vs uncrossed), and electrode location (Fz vs Cz vs Pz, for midline electrodes; left vs right, for lateral central and occipital electrodes). Note that, for these analyses, the tactually relevant location was considered for visual ERPs to be the visual hemifield in which the tactually attended hand currently lay (e.g. the left visual field for an attended left hand when uncrossed, but the right visual field for the same attended left hand when in a crossed posture). That is, the visual ERP results were analysed in terms of external location relative to the attended hand, rather than initial hemispheric projections in relation to that hand.

Trivial results (e.g. laterality of sensory responses) will not be reported unless interacting with experimental factors of interest. When appropriate, Greenhouse-Geisser adjustments to the degrees of freedom were performed, and the adjusted *P* values are reported. One-tailed paired *t*-tests were performed to investigate predicted spatial attention effects at single recording sites.
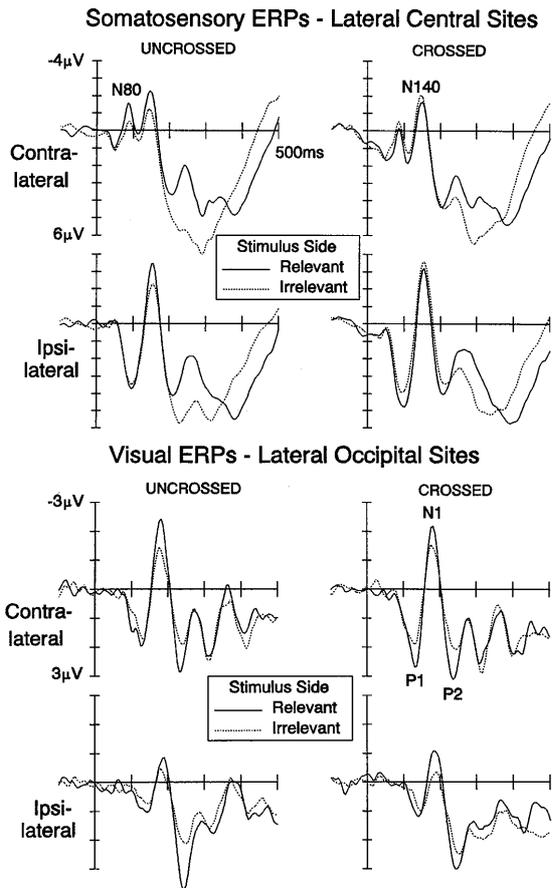
Somatosensory ERPs - Lateral Central Sites

Visual ERPs - Lateral Occipital Sites

Fig. 2 Experiment 1. *Top* Grand-averaged somatosensory ERPs elicited by tactile stimuli at attended (relevant) locations (*solid black lines*) and unattended (irrelevant) locations (*dashed grey lines*), at central sites (C3, C4) contralateral and ipsilateral to the anatomical side of the stimulated hand in the uncrossed hands condition (*left*) and the crossed hands condition (*right*). *Bottom* Grand-averaged visual ERPs elicited by visual stimuli at tactually relevant locations (*solid black lines*) and tactually irrelevant locations (*dashed grey lines*), at occipital sites (OL, OR) contralateral and ipsilateral to the side of stimulus presentation in the uncrossed hands condition (*left*) and the crossed hands condition (*right*)

Somatosensory ERPs - Midline Electrodes

Fig. 3 Experiment 1. *Left and middle* Grand-averaged somatosensory ERPs elicited at midline electrodes by tactile stimuli at attended (relevant) locations (*solid black lines*) and unattended (irrelevant) locations (*dashed grey lines*) in the uncrossed hands condition (*left*) and the crossed hands condition (*middle*). *Right* Difference waveforms obtained at midline electrodes by subtracting ERPs elicited by tactile stimuli at irrelevant locations from ERPs elicited by tactile stimuli at relevant locations in the uncrossed hands condition (*solid black lines*) and the crossed hands condition (*dashed grey lines*)

Results

Behavioural performance

Mean vocal RT to tactile targets (measured relative to the onset of the target-defining gap), in the uncrossed hands and crossed hands conditions, were 461 ms and 464 ms respectively; these values did not differ significantly. Participants missed 0.8% of all targets, and the rate of false alarms to non-target stimuli was 0.3%.

Attentional modulations of ERPs to tactile stimuli

Figure 2 (top) shows somatosensory ERPs elicited by non-target tactile stimuli at attended (relevant) versus unattended (irrelevant) hands, at lateral central electrodes con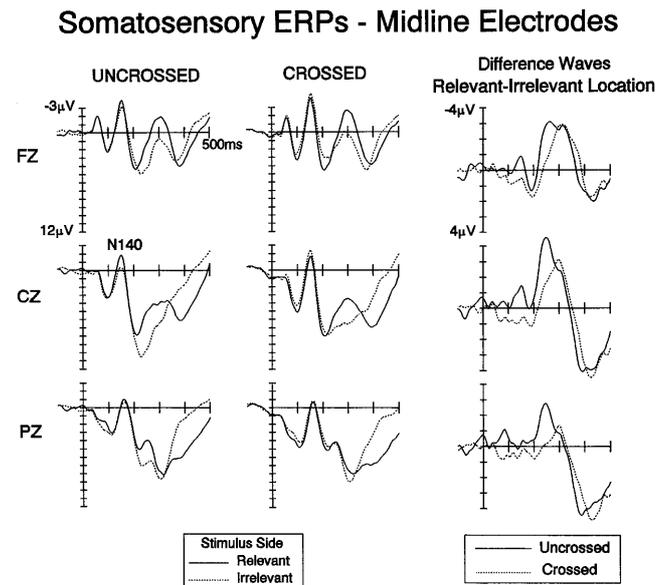tralateral and ipsilateral to the anatomical side of the stimulated hand. Figure 3 shows somatosensory ERPs elicited at midline electrodes by tactile stimuli at relevant and irrelevant locations, together with the resulting relevant-minus-irrelevant-location difference waveforms. ERPs are shown separately for the uncrossed and crossed hands blocks. Unexpectedly, hand posture had a marked effect on attentional ERP effects within touch. With uncrossed hands, attentional modulations of early somatosensory ERP components (N80, N140) were present at lateral central electrodes, most notably at contralateral sites. These early effects seem absent or even tending towards reversal when hands were crossed (Fig. 2, top). In addition, sustained attentional negativities at midline electrodes, as well as at lateral central sites, started earlier (at about 200 ms poststimulus), and were larger with uncrossed hands than with crossed hands (Fig. 3).

These observations were confirmed by statistical analyses. Highly significant relevant location × hand posture interactions were obtained for the contralateral N80 component, as well as for the N140 measured at ipsilateral and contralateral central electrodes ($F_{(1,11)}$=14.1 and 12.7; $P<0.003$ and 0.004, respectively). This interaction was also found within the N140 time interval at midline sites ($F_{(1,11)}$=12.0; $P<0.005$). Subsequent t-tests revealed enhanced N80 and N140 components for attended relative to unattended stimuli at contralateral central sites in the uncrossed hands condition ($t_{(11)}$=2.74 and 1.82; $P<0.01$ and 0.05, respectively), but no significant atten-

tional modulations of these components when hands were crossed. In contrast, attentional enhancements of the ipsilateral N140 (Fig. 2, top) and the enhanced negativity in the N140 time range at Fz and Cz (Fig. 3) in the uncrossed hands condition failed to reach statistical significance in both task conditions.

Figure 2 (top) also suggests that a positive component elicited at central electrodes ipsilateral to the stimulated hand around 100 ms poststimulus (P100) may have been affected by tactile-spatial attention, particularly in the crossed hands condition. Analyses of ERP mean amplitudes obtained at ipsilateral central sites between 80 and 120 ms poststimulus showed neither a main effect of relevant location nor a relevant location × hand posture interaction (both $F<2$), and t-tests did suggest that tactile stimuli at attended locations elicited a significantly enlarged P100 in the crossed hands condition ($t_{(11)}=2.24$; $P<0.047$, two-tailed), though not when hands were uncrossed. However, given that this P100 effect did not produce reliable terms in the ANOVA, we shall not base strong conclusions upon it.

Significant relevant location × hand posture interactions were obtained in the 200–255 ms measurement interval, both at midline and at lateral central electrodes ($F_{(1,11)}=11.0$ and 9.2; $P<0.007$ and 0.011, respectively), reflecting the fact that attentional negativities were delayed in the crossed hands condition relative to the uncrossed hands condition (Fig. 3). When the data from the two hand posture conditions were analysed separately, main effects of relevant location were obtained for the uncrossed hands condition ($F_{(1,11)}=12.2$ and 6.9; $P<0.005$ and 0.024, for lateral central and midline electrodes, respectively), but not for the crossed hands condition. In the subsequent analysis window (260–315 ms poststimulus), main effects of relevant location were observed both at lateral central sites and at midline sites ($F_{(1,11)}=23.9$ and 21.7; both $P<0.001$, respectively). No relevant location × hand posture interaction was present for this time window, indicating equivalent attentional ERP effects for both hand postures in this latency range.

Modulations of ERPs to task-irrelevant visual stimuli by tactile attention

Figure 2 (bottom) shows ERPs elicited by visual non-target stimuli, on the same side of external space as the attended (relevant) or unattended (irrelevant) hand, at occipital electrodes contralateral and ipsilateral to the side of visual stimulation. Figure 4 shows visual ERPs elicited by visual stimuli on the tactually attended (relevant) versus unattended (irrelevant) side of external space, at midline electrodes, together with the resulting relevant-minus-irrelevant-location difference waveforms. ERPs are shown separately for the uncrossed hands and crossed hands conditions (recall that the visual hemifield designated as 'relevant' when attending a particular hand actually reverses, in our analyses for visual stimuli, when the hands are crossed versus uncrossed). Attention-

al ERP modulations appear similar across the two hand postures, when analysed in terms of external location relative to the current position of the relevant hand. At occipital sites, the ERPs shown in Fig. 2 (bottom) suggest the presence of similar attentional P1, N1, and P2 enhancement in the crossed as well as the uncrossed hands posture. At midline sites, visual stimuli at the tactually relevant side elicited an enhanced negativity between 150 and 200 ms poststimulus, and these ERP modulations were again present for both hand postures (Fig. 4).

Although Fig. 2 (bottom) suggests possible enhancement of the occipital P1 for visual stimuli at tactually attended locations, the effect of relevant location on occipital P1 mean amplitudes did not reach statistical significance. However, when P1 peak amplitudes were analysed, a nearly significant effect of relevant location was obtained ($F_{(1,11)}=4.59$; $P<0.055$). Main effects of relevant location were reliably present for N1 amplitude at lateral occipital sites ($F_{(1,11)}=5.6$; $P<0.037$). Relevant location × hand posture interactions were entirely absent ($F<1$), indicating that attentional N1 effects on visual ERPs at occipital electrodes were not affected by hand posture (Fig. 2, bottom) when considered in terms of the common external location of a visual stimulus and an attended hand.[2]

A highly significant main effect of relevant location was also obtained at occipital electrodes between 200 and 255 ms poststimulus ($F_{(1,11)}=21.6$; $P<0.001$), reflecting an enlarged P2 component for visual stimuli at tactually attended locations (see Fig. 2, bottom). Again, no relevant location × hand posture interaction was present within this latency range ($F<1$). Enhanced negativities for visual stimuli at tactually relevant locations from midline electrodes in the N1 time range (160–200 ms

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[2] Note that we could have analysed the visual ERP results for crossed hands in terms of common initial hemispheric projections for particular visual stimuli with respect to the attended hand, rather than in terms of common external location. Considering the data in hemispheric terms is equivalent to reversing which visual hemifield is designated as 'relevant' for the crossed hands blocks (as right visual stimuli project to the same hemisphere as the right hand, even when that hand is crossed into a left position, and analogously for the left visual field and left hand). Rescoring the data in this way in effect means that the previously significant main effect of relevant location across postures now becomes the term in the ANOVA for an interaction between relevant location and posture (while the previous interaction term now becomes the main effect term). When the data are analysed in this way, there are no significant main effects of relevant location on occipital P1 and N1 amplitudes, but a reliable relevant location × posture interaction for the N1 component. In other words, when considered in terms of hemispheric projection, the visual ERP results change significantly when hand posture is crossed, as attending to one hand is now associated with enhanced ERPs for an (anatomically) different visual hemifield to that enhanced by attending to the same hand when uncrossed. The visual ERP results are thus unchanged across posture only when considered in terms of the external spatial locations of the attended hand, and the enhanced visual field. This point applies for all the subsequent analyses in this paper; that is, finding a main effect of relevant location, with no interaction with posture, in the analyses for external location, is equivalent to an interaction with posture for the same data when considered in terms of hemispheric projections
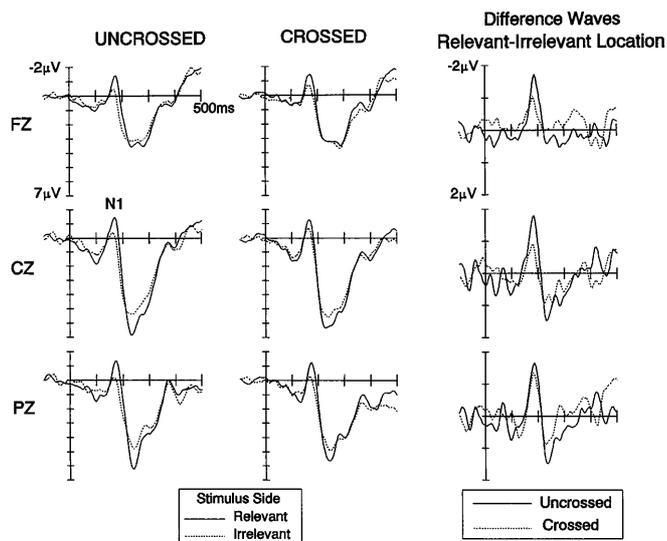
Visual ERPs - Midline Electrodes

Fig. 4 Experiment 1. *Left and middle* Grand-averaged visual ERPs elicited at midline electrodes by visual stimuli at tactually relevant locations (*solid black lines*) and tactually irrelevant locations (*dashed grey lines*) in the uncrossed hands condition (*left*) and the crossed hands condition (*middle*). *Right* Difference waveforms obtained at midline electrodes by subtracting ERPs elicited by visual stimuli at tactually irrelevant locations from ERPs elicited by visual stimuli at tactually relevant locations in the uncrossed hands condition (*solid black lines*) and the crossed hands condition (*dashed grey lines*)

poststimulus) were reflected in a main effect of relevant location ($F_{(1,11)}$=9.5; P<0.01). Again, there was no sign of any relevant location × hand posture interaction (F<1) when considered in terms of external spatial locations (see footnote 2), indicating that these ERP modulations were present for both hand postures (see Fig. 4). No significant effects of tactile-spatial attention on visual ERPs were found at midline electrodes in the 200–255 ms measurement window and at any recording site in the 260–315 ms latency range.

Discussion of experiment 1

In this study, effects of tactile-spatial attention were measured for somatosensory ERPs to tactile stimuli on the left or right hand, and also for visual ERPs elicited by task-irrelevant flashes in the left or right visual field, while the hands lay in an uncrossed or crossed posture. Participants directed tactile attention to the left or right side in order to detect infrequent (oddball) tactile targets delivered to the attended hand. Cross-modal links in spatial attention were expected to be reflected in modulations of ERPs elicited by task-irrelevant visual stimuli as a function of which hand was relevant for the tactile task. If such links operate on the basis of the common external location of the lights and touches on one side, then any effects of tactile-spatial attention on visual ERPs should be largely independent of hand posture un-

der the present analyses (which considered visual stimuli in terms of the external location relative to the current position of the attended hand; see footnote 2). By contrast, if cross-modal links reflect the initial hemispheric projections of the attended hand and visually stimulated hemifield (as on hemispheric-activation accounts for cross-modal links), then the manipulation of hand posture should strongly affect the observed attentional modulations of visual ERPs when analysed in terms of external positions.

The results obtained for visual ERPs provide clear-cut evidence for cross-modal links in spatial attention between touch and vision operating on the basis of common external locations, not initial hemispheric projections. With uncrossed hands, attending to one hand led to an enhancement of occipital N1 and P2 components, plus an enhanced negativity in the N1 time range at midline electrodes, for visual stimuli on the same side of external space as the attended hand. This pattern of results is very similar to that reported by Eimer and Driver (2000), and provides additional electrophysiological evidence for the existence of cross-modal links in spatial attention from touch to vision. The critical new point is that essentially the same visual ERP effects were found in the crossed hands condition, when considered in terms of external locations. This result is equivalent to the ERP effects completely reversing in terms of the visual hemifield that shows the larger amplitude ERP components when our results are reconsidered in terms of initial hemispheric projection rather than external location (see footnote 2).

These findings are inconsistent with the hemispheric-activation account, which predicts that the attentional effects on visual ERPs should have interacted with posture in our main analyses (in terms of external space), when hands were crossed versus uncrossed. In agreement with the behavioural findings of Spence et al. (2000), the visual ERP results obtained in experiment 1 thus suggest that cross-modal links in endogenous spatial attention between vision and touch are mediated by the proximity of visual stimuli to the current location of an attended hand, and not by fixed hemispheric projections.

In contrast to the results obtained for visual ERPs, hand posture had an unexpected impact on attentional modulations of somatosensory ERPs. With uncrossed hands, tactile-spatial attention was reflected in an enhancement of N80 and N140 components at contralateral central electrodes, plus sustained enhanced negativities at lateral central and midline electrodes, starting around 200 ms poststimulus. When hands were crossed, attentional N80 and N140 modulations were absent (or even tended to be reversed), and the onset of subsequent attentional negativities was considerably delayed. The only possible exception to this general pattern was the observation of an enhanced P100 component at ipsilateral central electrodes by tactile stimuli delivered to the attended hand in the crossed hands condition. While this effect may reflect a genuine attentional enhancement of the P100, it could also result from a sustained negativity

elicited in the crossed hands condition by tactile stimuli at unattended locations between 80 and 200 ms poststimulus, overlapping with the P100 and N140 components (see Fig. 2, top).

The overall pattern of results thus suggests that the crossed posture disrupted attentional effects within touch, yet without disrupting the cross-modal effect upon vision (when considered in terms of common external locations). We return to this apparent paradox later. First, however, since the effect of posture on attentional modulations within touch was unpredicted, it seemed necessary to replicate this. Experiment 2 was designed to do so, while also examining any cross-modal links between touch and audition, for the first time.

Experiment 2: cross-modal links between touch and audition, for different hand postures

Experiment 1 provided initial electrophysiological evidence for the hypothesis that cross-modal links between touch and vision are mediated by common locations in external space, rather than by initial hemispheric projections. In addition, the tactile ERP results suggested rather surprisingly that variations in hand posture can have systematic effects on spatially selective processing within the somatosensory modality (yet without affecting the cross-modal influence on visual ERPs). Experiment 2 was conducted to further investigate both this effect of hand posture within touch, and also possible cross-modal links between touch and *audition*. As in experiment 1, participants had to direct attention to the left or right hand, in order to detect infrequent tactile targets, while hand posture was varied between blocks. Instead of irrelevant visual stimuli, irrelevant auditory stimuli were now randomly intermingled with tactile stimuli. These stimuli were entirely task-irrelevant, just as for the visual stimuli in the previous study, which they replaced. If there are cross-modal links in spatial attention from touch to audition, these should be reflected in systematic differences between auditory ERPs elicited by stimuli at tactually attended versus unattended locations. In a previous ERP study on cross-modal links between vision and audition (Eimer and Schröger 1998), enhanced negativities were elicited by auditory stimuli at locations attended within vision, and these effects overlapped with the auditory N1 component, reflecting cross-modal links from vision to audition. If analogous links existed between touch and audition, similar auditory ERP modulations should be observed in experiment 2.

Analogously to experiment 1, one central question in our second experiment was whether the manipulation of hand posture would influence any cross-modal effects of tactile-spatial attention on auditory ERPs. If cross-modal links in spatial attention from touch to audition were based on locations in external space, similar effects should be found with uncrossed and with crossed hands when considered in terms of external locations. However, if a hemispheric-activation account applies to tactile-auditory links in spatial attention, attentional modulations of auditory ERPs should differ systematically between these two postures in terms of the external locations affected in audition by attending a particular hand.

The second objective of experiment 2 was to follow up the unexpected result of experiment 1, that hand posture had a profound effect on the attentional modulations of somatosensory ERPs. To confirm and extend this surprising finding, a different procedure was used in experiment 2 to manipulate tactile-spatial attention. While participants had maintained attention on a specific hand throughout an entire experimental block in experiment 1 (sustained attention), the relevant hand could now change within a block, being indicated anew by central symbolic precues at the beginning of each trial in experiment 2. That is, spatial attention had to be frequently shifted, between successive trials, from the left to the right hand, and vice versa (thus producing a situation of 'transient' spatial attention; note that in unimodal visual-spatial attention, there are systematic differences in the pattern of attentional ERP effects elicited for transient versus sustained attention situations; see Eimer 1996). Experiment 2 thus investigated whether the effects of hand posture on attentional modulations of somatosensory ERPs, as observed in the first experiment, are specific to sustained tactile-spatial attention, or can be replicated when tactile attention is manipulated in a transient manner on a trial-by-trial basis.

Materials and methods

Participants

Sixteen new paid volunteers participated in the experiment. One of them had to be excluded because of insufficient eye-fixation control in the cue-target interval (see below); the data from one other participant had to be discarded because of technical problems with triggering signals. Thus 14 participants (10 females), aged 18–49 years (mean age: 26.4 years), remained in the sample. Thirteen participants were right handed, one was left handed, and all had normal or corrected vision by self report.

Stimuli and apparatus

The experimental setup as shown in Fig. 1 was similar to experiment 1, except that auditory stimuli were delivered instead of visual stimuli, and the relevant hand was now specified on a trial-by-trial basis, by left-pointing or right-pointing double arrow cues ('<<' and '>>'), covering a visual angle of about 1.5°×0.6°. These cues were presented at the centre of a computer screen at an angle of about 30° below eye level and at a viewing distance of about 50 cm. Two horizontally aligned dots ':', located in the space between the two segments of the double-arrow cues, were continuously present on the computer screen throughout the experimental blocks, to serve as the fixation stimulus (see Fig. 1). Tactile stimuli were identical to experiment 1. Auditory stimuli were bursts of white noise (200 ms duration, including 5 ms rise and 5 ms fall times; amplitude 80 dB(A) SPL), presented from a loudspeaker located on the left or right side, in close spatial register with the tactile stimulator on that side. Most auditory stimuli consisted of a continuous white noise burst. For auditory gap stimuli, the noise was interrupted after 90 ms by a 20-ms silent interval, after which the noise was turned on again for 90 ms. As in experiment 1, low-amplitude white noise was presented continuously from a central location to mask the slight sounds made by the tactile stimulators.

Procedure

The experiment consisted of 20 experimental blocks of 80 trials each, with an intertrial interval of 1000 ms. Each trial started with a 100-ms presentation of a left-pointing or right-pointing arrow cue, which was followed after a cue-target interval of 700 ms by the presentation of a tactile or auditory stimulus on the left or right side. In 64 of the 80 trials in each block, a tactile or auditory stimulus was presented that did not have gaps. Eight trials were delivered in random order for each combination of cue direction (left vs right), stimulus location (left vs right), and stimulus modality (tactile vs auditory). In the remaining randomly intermingled 16 trials, tactile or auditory stimuli with gaps were presented. In eight trials per block, a tactile gap target was delivered at the location indicated by the cue. Only these target stimuli required a vocal response. In four trials, tactile gap stimuli were presented at the uncued location (currently task-irrelevant) and in the remaining four trials, auditory gap stimuli were delivered (all sounds were task-irrelevant). Participants were instructed to maintain central eye fixation and to direct their tactile attention to the side indicated by the pre-cue in order to detect any tactile targets (i.e. with gaps) presented on the hand on that side. All other stimuli were to be ignored. Note therefore that while we used central arrow cues, these were not used to manipulate whether a trial was validly or invalidly cued; instead, all cues indicated the relevant hand to be attended.

In half of the blocks, hands were uncrossed; in the other half, hands were crossed. Five successive blocks were delivered for each hand posture, after which hand posture was changed. The order of delivery of these hand posture conditions was counterbalanced across participants.

Recording and data analysis

EEG recording was identical to experiment 1. EEG and EOG were epoched offline into 1600-ms periods, starting 100 ms prior to the onset of the cue and ending 700 ms after the onset of the imperative stimulus. As in experiment 1, trials with horizontal eye movements, blinks, other artefacts, and overt response errors were excluded from analysis. After artefact removal, the computer-averaged HEOG for each participant was scored for systematic deviations of eye position during the cue-target interval, in response to left-pointing versus right-pointing arrow cues. A residual HEOG deviation exceeding ± 2 μV (indicating a tendency to move the eyes in the cues' direction) led to the disqualification of one participant. EEG analysis was similar to experiment 1, except that audition replaced vision as the secondary modality. Analysis windows for somatosensory ERPs were identical to experiment 1. Auditory ERPs elicited at midline electrodes were analysed within the N1 time range (120–180 ms poststimulus), and within two subsequent 60-ms intervals between 200 ms and 315 ms poststimulus. This follows previous studies (e.g. Hansen and Hillyard 1983) which have shown that auditory ERP components such as the N1 are typically largest at midline sites, even for lateral stimuli.

Results

Behavioural performance

Mean vocal RT to tactile targets (measured relative to the onset of the target-defining gap) was 503 ms and 508 ms, in the uncrossed hands and crossed hands conditions respectively; these scores were not significantly different. Participants missed 4.8% of all targets, and the rate of false alarms to non-target stimuli was 0.3%.
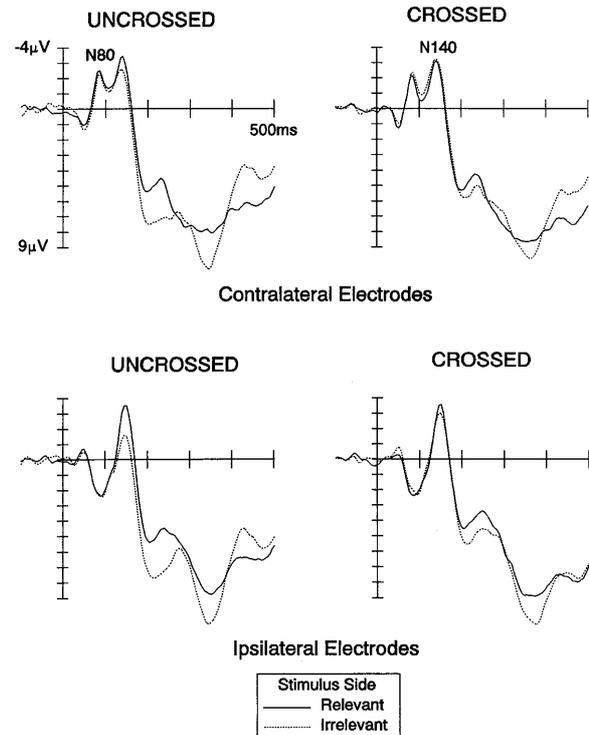
Somatosensory ERPs - Lateral Central Sites

Fig. 5 Experiment 2. Grand-averaged somatosensory ERPs elicited by tactile stimuli at attended (relevant) locations (*solid black lines*) and unattended (irrelevant) locations (*dashed grey lines*), at central sites (C3, C4) contralateral (*top*) and ipsilateral (*bottom*) to the anatomical side of the stimulated hand in the uncrossed hands condition (*left*) and the crossed hands condition (*right*)

Attentional modulations of ERPs to tactile stimuli

Figure 5 shows somatosensory ERPs elicited by non-target stimuli on attended (relevant) versus unattended (irrelevant) hands, at lateral central electrodes contralateral and ipsilateral to the anatomical side of the stimulated hand. Figure 6 shows somatosensory ERPs elicited at midline electrodes by tactile stimuli at attended (relevant) and unattended (irrelevant) locations, and the resulting relevant-minus-irrelevant-location difference waveforms. ERPs are shown separately for the uncrossed hands and crossed hands conditions. Similarly to the surprising tactile results of experiment 1, hand posture again had a marked effect on attentional effects for somatosensory ERPs. With uncrossed hands, attentional modulations of the somatosensory N140 component are visible at lateral central electrodes as well as at midline sites, and these effects seem absent when hands were crossed. In addition, attentional negativities beyond 200 ms poststimulus started earlier and were larger in the uncrossed hands condition than in the crossed hands condition (see Figs. 5, 6).

These observations were confirmed by statistical analyses. In contrast to experiment 1, no attentional modulations of the contralateral N80 component were found,

Somatosensory ERPs - Midline Electrodes
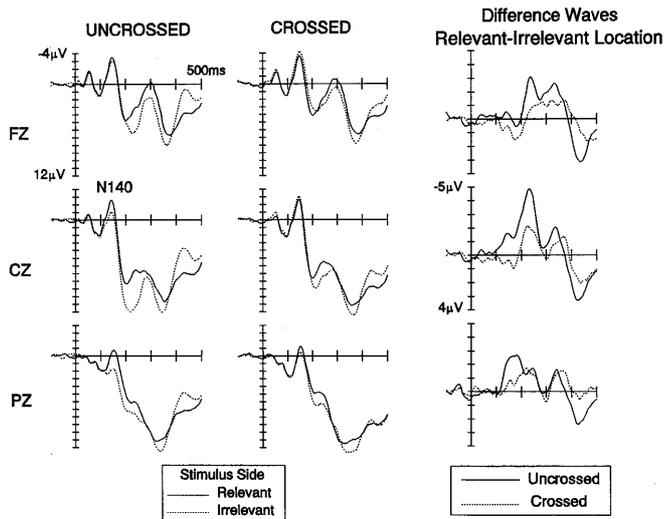

Auditory ERPs - Midline Electrodes

Fig. 6 Experiment 2. *Left and middle* Grand-averaged somatosensory ERPs elicited at midline electrodes by tactile stimuli at attended (relevant) locations (*solid black lines*) and unattended (irrelevant) locations (*dashed grey lines*) in the uncrossed hands condition (*left*) and the crossed hands condition (*middle*). *Right* Difference waveforms obtained at midline electrodes by subtracting ERPs elicited by tactile stimuli at irrelevant locations from ERPs elicited by tactile stimuli at relevant locations in the uncrossed hands condition (*solid black lines*) and the crossed hands condition (*dashed grey lines*)
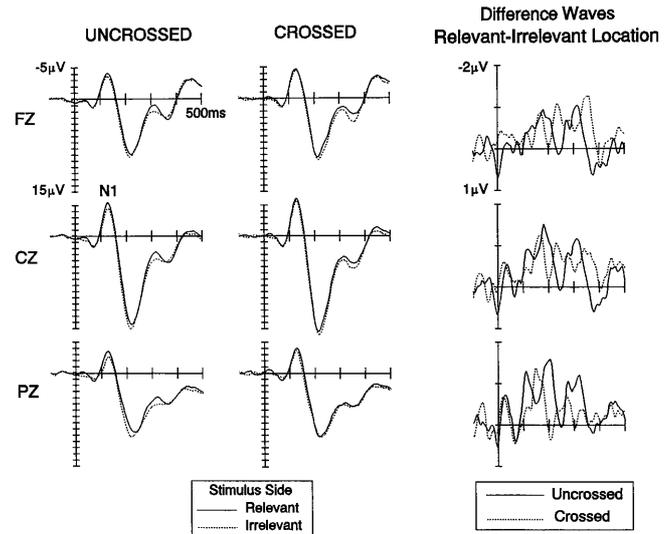
Fig. 7 Experiment 2. *Left and middle* Grand-averaged auditory ERPs elicited at midline electrodes by auditory stimuli at tactually relevant locations (*solid black lines*) and tactually irrelevant locations (*dashed grey lines*) in the uncrossed hands condition (*left*) and the crossed hands condition (*middle*). *Right* Difference waveforms obtained by subtracting ERPs elicited by auditory stimuli at tactually irrelevant locations from ERPs elicited by auditory stimuli at tactually relevant locations in the uncrossed hands condition (*solid black lines*) and the crossed hands condition (*dashed grey lines*). Note the change in scale from previous figures

and the P100 component was also unaffected by tactile-spatial attention. For the N140 measured at ipsilateral and contralateral central electrodes, relevant location × hand posture interactions were present ($F_{(1,13)}$=5.5 and 9.1; $P<0.036$ and 0.01, respectively). This interaction was also found within the N140 time interval at midline sites ($F_{(1,13)}$=8.0; $P<0.014$). Subsequent *t*-tests revealed an enhanced N140 component for tactile stimuli on the relevant versus irrelevant hand, at contralateral as well as at ipsilateral central sites in the uncrossed hands condition ($t_{(13)}$=2.24 and 4.73; $P<0.019$ and 0.005, respectively); but no such effects were reliable when hands were crossed. At midline sites, enhanced negativities for stimuli at attended locations were present in the N140 time window at Cz and Pz when hands were uncrossed ($t_{(13)}$=3.5 and 4.24; $P<0.002$ and 0.001, respectively), but not in the crossed hands condition (Fig. 6).[3]

In the 200–255 ms measurement interval, main effects of relevant location on somatosensory ERPs were obtained both at midline and at lateral central electrodes ($F_{(1,13)}$=18.3 and 17.0; both $P<0.001$, respectively). At midline sites, this effect was accompanied by a relevant location × electrode location interaction ($F_{(2,26)}$=11.0; $P<0.002$; ε=0.694), and a marginally significant relevant location × hand posture interaction ($F_{(1,13)}$=4.2;

$P<0.060$). Attentional negativities were larger at Cz and Fz than at Pz, and tended to be larger in the uncrossed hands condition (Fig. 6). In follow-up analyses conducted separately for each midline electrode, main effects of relevant location were present at all three midline sites (all $F_{(1,13)}>8,0$; all $P<0.014$), and relevant location × hand posture interactions were found at Fz and Cz (both $F_{(1,13)>}6.1$; both $P<0.028$). Additional *t*-tests found significant attentional negativities in the crossed hands condition at Cz and Pz (both $t_{(13)}>2.6$; both $P<0.024$), but not at Fz. In contrast to experiment 1, no effects of relevant location were obtained between 260 and 315 ms poststimulus.

Modulations of ERPs to task-irrelevant auditory stimuli by tactile attention

Figure 7 shows ERPs elicited by auditory non-target stimuli on the same side of external space as the relevant versus irrelevant hand, at midline electrodes, together with the resulting relevant-minus-irrelevant-location difference waveforms. ERPs are shown separately for the uncrossed and crossed hands conditions. Tactile-spatial attention resulted in enhanced negativities for auditory stimuli presented on the same side as the relevant hand, overlapping the auditory N1 component as well as additional negativities beyond 200 ms poststimulus. As can be seen in the difference waveforms (Fig. 7, right), these

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[3] In fact, a significantly enhanced negativity for tactile stimuli on the *irrelevant* hand was obtained at Fz in the N140 latency range in the crossed hands condition ($t_{(13)}$=2.2; $P<0.047$, two-tailed; see also Fig. 6)

auditory ERP modulations were generally small, but appear to be present for both hand postures, when considered in terms of external location relative to the current position of the attended hand. (Note that an analogous argument applies, for the present auditory ERPs, to that made for visual ERPs in footnote 2 as to whether the effects change across posture when considered in terms of hemispheric projections rather than external location.)

A main effect of relevant location was obtained within the 120–180 ms measurement-window overlapping the auditory N1 ($F_{(1,13)}$=9.8; P<0.008), reflecting larger negativities for auditory stimuli on the same side of external space as the attended hand. No indication of any relevant location × hand posture interaction was obtained (F<1), suggesting that these effects (when considered in terms of external location) were not significantly affected by the variation of hand posture. Follow-up t-tests revealed enhanced negativities for auditory stimuli on the side of the attended versus unattended hand, at all three midline sites in the uncrossed hands condition (all $t_{(13)}$>2.15; all P<0.026). In the crossed hands condition, effects of tactile-spatial attention on auditory ERPs in the N1 time range were absent at Fz, and numerically small at Cz and Pz (amounting to mean amplitude differences of 0.9 μV and 1.0 μV, respectively). Nevertheless, these differences were statistically reliable ($t_{(13)}$=1.92 and 2.17; P<0.039 and 0.025, for Cz and Pz, respectively). Because the auditory N1 component is relatively stable in timing and amplitude, it not unusual to find reliable effects even when relatively small (see, e.g. Alho et al. 1986).

No effect of relevant location was observed between 200 and 255 ms poststimulus. In the 260–315 ms latency range, a main effect of relevant location was found ($F_{(1,13)}$=4.8; P<0.048), reflecting enhanced negativities for auditory stimuli at tactually relevant locations (see Fig. 7, right). No relevant location × hand posture interaction was present within this time interval (F<1), when considered in terms of external location.

Discussion of experiment 2

In experiment 2, effects of tactile-spatial attention were examined for somatosensory ERPs to tactile stimuli delivered on the left or right hand, and also for auditory ERPs elicited by task-irrelevant auditory stimuli on the left or right side, while hands were either uncrossed or crossed. Tactile-spatial attention was now manipulated by central symbolic precues, indicating which hand was relevant on each trial, with participants having to detect tactile targets (oddballs) delivered to the cued hand. One novel aim of this experiment was to investigate for the first time whether there are cross-modal links in endogenous spatial attention from touch to audition; a further aim was to determine whether any such links are based on common positions in external space across the modalities, or instead on initial hemispheric projections. When hands were uncrossed, enhanced negativities were elicited by auditory stimuli at tactually attended locations.

These overlapped with the auditory N1 component, but were also present at latencies beyond 200 ms poststimulus (Fig. 7). These effects are similar to the effects of visual-spatial attention on auditory ERPs observed by Eimer and Schröger (1998), both in terms of their latencies and overall magnitudes. They demonstrate for the first time the existence of cross-modal links in endogenous spatial attention between touch and audition, as indexed by ERPs. A very similar pattern of results (when considered in terms of external locations) was obtained in the crossed hands condition. As in experiment 1, the absence of any relevant location × hand posture interaction for auditory ERPs within these analyses indicates that spatially similar effects of tactile-spatial attention upon ERPs for the secondary modality were found for both hand postures. This strongly suggests that cross-modal links in spatial attention between touch and audition are not primarily based on differential activations of cerebral hemispheres, but instead on representations of location in external space (see also footnote 2).

It should be noted that while experiment 2 provides initial electrophysiological evidence for cross-modal links in spatial attention between touch and audition, we did not fully investigate possible behavioural consequences of such links, since our study was designed to assess ERPs rather than the speed or accuracy of performance (we collected RTs only for occasional oddball targets, with accuracy close to ceiling). Lloyd et al. (2001) have recently conducted the first full behavioural test for any tactile-auditory links in endogenous spatial attention, though in their study the sounds appears at some distance away from the tactile events, unlike our situation (see Fig. 1).

The other main objective of experiment 2 was to investigate further the unexpected effects of hand posture on attentional ERP modulations within the somatosensory modality that had been found in experiment 1. In contrast to experiment 1, where tactile attention had to be sustained at the same hand throughout entire blocks, tactile-spatial attention was now manipulated transiently via trial-by-trial cueing. As can be seen from Figs. 5 and 6, the main somatosensory findings from experiment 1 were replicated. Again, hand posture had a profound effect on attentional modulations of somatosensory ERPs, which were considerably delayed when hands were crossed. While the somatosensory N140 component was enhanced at lateral central and at midline electrodes for tactile stimuli at attended locations in the uncrossed hands condition, no such effects were present in the crossed hands condition. In fact, and similar to experiment 1, attentional ERP modulations even showed some tendency to reverse in this latter posture (and this 'reversed' attention effect actually reached statistical significance at Fz; see footnote 3). As in the first experiment, attentional negativities elicited beyond 200 ms poststimulus were reduced in amplitude for crossed hands relative to uncrossed hands.

One notable difference between the two experiments is that tactile-spatial attention did not affect the somato-

sensory N80 component at contralateral central electrodes in the uncrossed hands condition of experiment 2. It is possible that this change for the N80 component is due to some difference between transient (trial-by-trial cuing) and sustained (constant throughout a block) tactile-spatial attention. Tactile attention may be focused more efficiently when it can be maintained at one location for an extended period of time (see Eimer 1996 for related results in vision). This difference between sustained and transient tactile-spatial attention may also account for the fact that attentional negativities elicited beyond 200 ms poststimulus were more short lived in experiment 2 than in experiment 1, as well as for the fact that the cross-modal effects on auditory ERPs in experiment 2 were generally smaller than the cross-modal effects on visual ERPs found in experiment 1.

In summary, experiment 2 confirmed and extended the results obtained in the first experiment, by demonstrating with ERPs that there are cross-modal links in spatial attention from touch to audition also; that these links are primarily based on common external locations (as demonstrated by the results for the two postures); and that attentional modulations of somatosensory ERPs (but not the cross-modal effects) are strongly affected by variations in hand posture. With respect to this latter finding, experiment 2 both replicated the unexpected pattern of results found in the first experiment, and showed that these effects of posture are not restricted to sustained attention, but can also be found under transient attention conditions.

General discussion

The main aim of these experiments was to use event-related brain potentials to investigate the spatial coordinates of cross-modal links in spatial attention, involving touch. Such links could in principle simply reflect increased activation of the contralateral hemisphere when attention is directed to the left or right within one modality (Kinsbourne 1975, 1993), with this activation then spreading to affect representations of other modalities within the same activated hemisphere. Alternatively, cross-modal links may be based on a more abstract spatial reference-frame, specifying the relative location of stimuli from different modalities within external space. To decide between these hypotheses, effects of tactile-spatial attention on visual ERPs elicited by irrelevant light flashes (experiment 1), or on auditory ERPs elicited by irrelevant bursts of white noise (experiment 2), were measured for stimuli on the left or right side, while participants directed tactile attention to the left or right hand, with their hands either crossed or uncrossed. The tactile task was to detect infrequent somatosensory targets delivered to the attended hand, and this hand was either constant for an entire block (sustained attention, experiment 1), or was indicated by a precue at the beginning of each trial (transient attention, experiment 2).

With such a design, cross-modal links in spatial attention should be reflected in attentional modulations of ERPs elicited by the task-irrelevant visual or auditory stimuli. If such spatial links were based on an external reference frame, effects of tactile-spatial attention on visual and auditory stimuli should lead to larger ERP amplitudes for these stimuli when on the same side of external space as the attended hand, regardless of posture. In contrast, if the hemispheric-activation account was correct, variations in hand posture should lead to larger amplitudes for a stimulus on the same side as the attended hand when uncrossed, but on the opposite side to the attended hand when crossed (as this particular side remains contralateral to the hemisphere which the attended hand initially projects to, regardless of posture).

The results obtained for visual and auditory ERPs provide strong support for the idea that cross-modal links in endogenous spatial attention are not based upon initial hemispheric projections, but rather on external spatial frames of reference. With uncrossed hands, systematic attentional modulations of visual and auditory ERPs were observed. These effects were similar to the effects obtained in previous ERP experiments studying tactile-visual links (Eimer and Driver 2000) or visual-auditory links (Eimer and Schröger 1998), and they provide further electrophysiological evidence for the existence of cross-modal links in spatial attention from touch to vision, plus new ERP evidence that cross-modal links from touch to audition also exist. Most importantly, stimuli on the same side of external space as the attended hand showed the same ERP enhancements when the hands were crossed. This is inconsistent with the hemispheric-activation hypothesis, which predicts substantial relevant location × hand posture interactions for ERPs elicited by secondary modality stimuli, reflecting a reversal of the effects of tactile-spatial attention on the secondary modality when hands are crossed (see above). No such interactions were obtained, indicating that cross-modal links in spatial attention are not based just on the differential activation of cerebral hemispheres, but depend on common external locations. This pattern was found for both visual and auditory ERPs across experiments 1 and 2, thus suggesting that cross-modal links are mediated by a spatial reference frame that represents locations in external space for vision, audition, and touch. Changes in hand posture are evidently compensated for by suitable remapping of the spatial codes responsible for integration of spatial selectivity between touch, vision, and audition, so that a different auditory or visual hemifield is enhanced by attention to a particular hand, when that hand is crossed versus uncrossed. Hence such enhancement applies to whichever auditory or visual stimuli are at the same place as the currently attended hand, regardless of whether this hand is crossed or uncrossed.

At the single cell level, tactile-visual-postural interactions may be mediated by multimodal neurons responding to both visual and tactile events. Such neurons have been observed in cortical regions such as parietal (e.g. area 7b; Graziano and Gross 1994) and premotor areas (i.e. area 6; Graziano et al. 1994). The receptive fields of

these neurons are typically organized in close spatial register across the modalities, so that a similar region of space is responded to in both vision and touch by a given cell. Many multimodal neurons show a degree of remapping across changes in posture. For example, a neuron with a tactile receptive field on one hand will typically respond to visual events near that hand, in such a manner that its visual field actually shifts across the retina if the hand posture is changed. Gross and Graziano (1995) describe neurons in premotor cortex whose visual receptive fields will even follow a crossed hand into a different visual hemifield, consistent with neurons of this kind being involved in the cross-modal interactions observed in our study.

It should be noted that evidence for cross-modal links in spatial attention was found both under sustained attention conditions (experiment 1) and for transient spatial attention (experiment 2). This is in line with previous behavioural and electrophysiological studies, which found effects of cross-modal links both for transient attention (Spence and Driver 1996, 1997; Eimer and Schröger 1998) and for sustained attention (Spence and Driver 1996; Spence et al. 2000; Hillyard et al. 1984; Eimer and Driver 2000). However, as noted above, the present ERP evidence for cross-modal links was somewhat stronger with sustained (experiment 1) than transient (experiment 2) in the primary modality, perhaps as attention becomes more focussed on a single location in the former case (see Eimer 1996).

In contrast to the ERP results obtained for the secondary modalities, hand posture had a strong and unexpected impact on effects of tactile-spatial attention within the primary modality (i.e. on somatosensory ERPs), within both our experiments. With uncrossed hands, tactile-spatial attention was reflected in an enhancement of early somatosensory components at lateral central electrodes, as well as in sustained enhanced negativities at lateral central and at midline sites. When hands were crossed, the somatosensory ERP effects were reduced or eliminated, or even showed some tendency to reverse (i.e. with numerically larger early components elicited by stimuli at the nominally unattended hand when crossed). In addition, sustained attentional negativities were delayed and reduced in amplitude for somatosensory ERPs in the crossed hands conditions. This effect of hand posture on attentional modulations of somatosensory ERPs was obtained for sustained tactile-spatial attention (experiment 1), and was also found in experiment 2, where tactile attention was manipulated transiently in a trial-by-trial cueing paradigm. Given the stability of these findings across experiments, this pattern of results suggests that spatial selectivity within the somatosensory modality is strongly affected by postural changes. Tactile-spatial attention seems to operate less efficiently when hands are crossed than when hands are located in their usual position.

To explain these effects of hand posture on attentional modulations of ERPs elicited by tactile stimuli, one can assume that crossing the hands results in a conflict within somatosensory information-processing, between a spatial code referring to the position in external space where the hand is currently located, and a spatial code representing the anatomical side of the responding hand. This type of conflict is commonly assumed to be responsible for the well-known fact that variations in hand posture can affect the speed of manual performance. Choice RTs are substantially delayed when hands are crossed relative to an uncrossed-hands posture (Nicoletti et al. 1982, 1984; Riggio et al. 1986). Under normal conditions, both spatial codes may be involved in directing tactile-spatial attention to the left or right hand. That is, when hands are located in their standard uncrossed position, there is a natural link between the attentional selection of a left or right location and the selection of the anatomically corresponding hand. When hands are crossed, however, a conflict between incongruent anatomical and external spatial codes could interfere with the selection of appropriate hand. The fact that this conflict was not reflected in significantly delayed vocal response times in the crossed hands conditions of experiments 1 and 2 is most likely due to the insufficient sensitivity of our RT measures; vocal responses were only required to a small subset of all stimuli, and fast responding was not specifically encouraged.

While crossing the hands apparently disrupted the selection of the appropriate somatosensory location, it had no such influence on the cross-modal influence that attending to one or other hand exerted upon vision (experiment 1) or audition (experiment 2). This leads to an apparent paradox, whereby selection within touch can be disrupted by hand-crossing (so that somatosensory ERP effects are attenuated or even reversed), yet selection of one hand can still continue to have an equivalent cross-modal effect regardless of hand-crossing (so that visual or auditory ERPs are enhanced for stimuli on the same side of external space as the attended hand, regardless of whether the hands are crossed or uncrossed). One possible resolution to this paradox is to suppose that there may be both unimodal and multimodal levels of spatial representation, consistent with recent evidence from neurophysiology (e.g. Andersen et al. 1997) and functional imaging (e.g. Macaluso et al. 2000). For instance, in the case of touch, there may be unimodal representations of tactile location (e.g. distinguishing left versus right hands anatomically, as in S1; see Macaluso et al. 2000), plus multimodal levels of representation for tactile location (i.e. where current hand posture, as signalled proprioceptively and/or visually, can be taken into account when coding the location of an attended hand, as in some parietal regions; see Driver and Spence 1998). The disruption caused by hand-crossing for attentional effects on somatosensory ERPs may reflect a conflict between these two codes, as suggested above, with both codes conjointly affecting the observed electrophysiological response to somatosensory stimuli. However, within such a multilevel system, the cross-modal effects observed for vision and audition might be determined solely by the 'higher' level of multimodal spatial representation; in-

deed, this by definition would be the only level where the modalities could communicate with each other directly. Selection of one hand at this multimodal level of representation (where posture is taken into account) could then produce cross-modal ERP effects that are undisrupted by hand-crossing, as we observed for visual and auditory stimuli, even while strictly unimodal anatomical codes for tactile location (uncorrected for current posture) disrupt the selection of one hand versus another within touch itself.

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