Tactile–Visual Links in Exogenous Spatial Attention Under Different Postures: Convergent Evidence from Psychophysics and ERPs

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Abstract

■ Tactile–visual links in spatial attention were examined by presenting spatially nonpredictive tactile cues to the left or right hand, shortly prior to visual targets in the left or right hemifield. To examine the spatial coordinates of any cross-modal links, different postures were examined. The hands were either uncrossed, or crossed so that the left hand lay in the right visual field and vice versa. Visual judgments were better on the side where the stimulated hand lay, though this effect was somewhat smaller with longer intervals between cue and target, and with crossed hands. Event-related brain potentials (ERPs) showed a similar pattern. Larger amplitude occipital N1 components were obtained for visual events on the same side as the preceding tactile cue, at ipsilateral electrode sites. Negativities in the Nd2 interval at midline and lateral central sites, and in the Nd1 interval at electrode Pz, were also enhanced for the cued side. As in the psychophysical results, ERP cuing effects during the crossed posture were determined by the side of space in which the stimulated hand lay, not by the anatomical side of the initial hemispheric projection for the tactile cue. These results demonstrate that crossmodal links in spatial attention can influence sensory brain responses as early as the N1, and that these links operate in a spatial frame-of-reference, which can remap between the modalities across changes in posture. ■

INTRODUCTION

Mechanisms of spatial attention prioritize sensory information at attended locations relative to other locations. These mechanisms have been intensively studied with a variety of methods including psychophysics, event-related brain potentials, functional imaging, and single-cell recording (e.g., see Parasuraman, 1998, for reviews of findings from all of these methods). This work has led to a host of replicable findings, and to some important distinctions. Covert shifts of spatial attention have been demonstrated in the absence of overt receptors shifts (e.g., Mangun, Hillyard, & Luck, 1993; Posner, 1978). Moreover, stimulus-driven exogenous mechanisms have been distinguished from expectancy-driven endogenous mechanisms (e.g., Hopfinger & Mangun, 1998; Jonides, 1981; Posner, 1978). The former are typically studied by using spatially nonpredictive peripheral cues, the latter by central cues or instructions indicating the likely target location. Both forms of cuing can lead to performance advantages at the cued location, but exogenous and endogenous mechanisms are thought to differ in several ways, including the time course of their effects (e.g., exogenous effects are usually more short-lived following the cue; see Müller & Rabbitt, 1989), the degree of

control a participant has over them (e.g., exogenous orienting is often considered to be reflexive; see Jonides, 1981), and the neural structures thought to be involved (Robinson, Bowman, & Kertzman, 1995; Robinson & Kertzman, 1995; Rafal, Henik, & Smith, 1991; Butter, 1987).

Until recently, the majority of research on attention within the cuing tradition only considered attention for a single modality at a time, usually for vision. But in daily life, all of our senses are typically stimulated, and information about particular objects may be available to several modalities at the same time (as when we both touch and see an object). It may be useful for spatial attention to be coordinated across the modalities, as when an abrupt touch (or sound) warns of an object that will soon come into view. Several recent psychophysical studies have confirmed the existence of various crossmodal links in spatial attention (e.g., Spence & Driver, 1996; Spence, Nicholls, Gillespie, & Driver, 1998), and neuroscience has begun to uncover crossmodal interactions in many of the structures implicated in the control of spatial attention (e.g., Andersen, Snyder, Bradley, & Xing, 1997; Groh & Sparks, 1996b; Graziano & Gross, 1994; Stein & Meredith, 1993). Here we focus specifically on possible links between vision and touch in exogenous/reflexive aspects of spatial attention: Can a salient tactile event draw visual atten-

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tion to its location; and if so how, and in which spatial coordinates?

There have been relatively few studies of tactile–visual interactions within attentional paradigms. Groh and Sparks (1996a) showed that people and monkeys can rapidly saccade to tactile targets in darkness, suggesting a link between touch and "overt" visual orienting. Some tactile–visual links in "covert" attention have also been studied, to examine whether touch can affect internal processing of a visual target. Butter, Buchtel, and Santucci (1989) reported that visual detection was faster following a tactile cue at the location of the visual target. However, their tactile cues were "predictive" of likely target location, so endogenous/voluntary attention may have been involved rather than just the exogenous/reflexive attention considered here. Tassinari and Campara (1996) found no facilitation of visual detection immediately after a spatially "nonpredictive" tactile event on the same side, but their tactile and visual events appeared from very different locations even when ipsilateral tactile stimulation was applied to the shoulder (visual targets appeared on a screen in front of the participant). Some effects of nonpredictive tactile stimulation on visual judgments have been reported using a "line-motion illusion" (Hikosaka, Miyauchi, Takeichi, & Shimojo, 1996). Tactile events induced the illusion that a static line shot away from the touched position when presented shortly after. However, several researchers have since challenged any attentional interpretation of such line-motion illusions (e.g., Downing & Treisman, 1997; Steinman & Steinman, 1997).

Spence et al. (1998) recently provided positive evidence for tactile–visual links in exogenous covert spatial attention, with a different method. Spatially nonpredictive tactile stimulation on one hand facilitated discrimination latencies for visual targets nearby, compared with tactile stimulation of the other hand on the opposite side of space. In addition to this emerging psychophysical evidence for tactile–visual links in exogenous covert spatial attention in humans, single-cell recording in several species has begun to uncover tactile–visual spatial interactions within several brain structures, including the superior colliculus plus parietal and premotor cortex (e.g., Graziano & Gross, 1994; Graziano, Hu, & Gross, 1997; Groh & Sparks, 1996b; Wallace, Meredith, & Stein, 1993).

In the studies of tactile–visual links in human attention just described, participants typically adopted a single default posture, with the left hand lying at a fixed location in the left visual field and the right hand at a homologous location in the right visual field. By contrast, in daily life posture changes continuously, so that a particular hand can appear arbitrarily at any retinal location. The fixed posture of past human studies means that the observed tactile–visual links in attention could operate in any of several spatial frames-of-reference. For instance, since both the left hand and the left visual field initially project to the same (right) cortical hemisphere (and analogously the right hand and right visual field both project to the left hemisphere), all the observed advantages for same-side crossmodal pairings in exogenous cuing studies to date might be explained in terms of activation of one hemisphere versus another (e.g., as in Kinsbourne's, 1975, 1987 hemispheric-competition model of spatial attention). Alternatively, the same-side advantage might be due to a particular hand and visual target occupying the same location in external space, regardless of initial hemispheric projections.

One way to assess this is to compare the usual uncrossed posture to a "crossed" posture, where the left hand is now placed in the right visual field, and vice versa (see Spence, Pavani, & Driver, in press; Aglioti, Smania, & Peru, 1999; Groh & Sparks, 1996a; Hikosaka et al., 1996; Wallace, 1971, 1972, for previous studies of such crossed postures). If initial hemispheric projections entirely determine tactile–visual links in exogenous covert attention, then stimulation of the left hand should still advantage the left visual field even when the left hand is placed in the "right" visual field. Conversely, if location in external space is the sole critical factor, then stimulation of the left hand should have the reverse effect in the crossed posture, now advantaging the right visual field. Note that the latter outcome would imply some degree of spatial remapping for crossmodal links between the modalities. Of course, the initial hemispheric projection and also the position in external space may "both" matter; or remapping across postures may be only partial. If so, some intermediate result would be expected with crossed hands.

Several previous studies have compared crossed and uncrossed hand postures in a variety of tasks. Most were concerned with stimulus–response compatibility (Bradshaw, Howard, Pierson, Phillips, & Bradshaw, 1992; Riggio, Gawryszewski, & Umilta, 1986; Umilta, Rizzolatti, Anzola, Luppino, & Porro, 1985; Wallace, 1971, 1972) or with neurological phenomena (e.g., Aglioti et al., 1999), rather than with crossmodal links in normal spatial attention (though see Hikosaka et al., 1996). Recently, Spence et al. (in press) demonstrated that crossmodal links in "endogenous" covert attention between vision and touch get fully remapped when the hands are crossed, versus uncrossed. They found that the advantage of directing tactile and visual attention to the same versus opposite sides was unaffected by the change in posture, when considered in terms of external spatial location rather than hemispheric projections. However, the reflexive mechanisms of "exogenous" covert attention may be more primitive than endogenous mechanisms, and different neural structures are thought to be involved (e.g., Robinson & Kertzman, 1995; Robinson et al., 1995; Rafal et al., 1991; Butter, 1987). Visual attention might even be drawn initially toward the "wrong" side when one hand is touched in a crossed posture (i.e., drawn to the anatomically associated side). Indeed, in

their study of overt gaze shifts, Groh and Sparks (1996a) presented preliminary results in which some saccades to tactile targets were initially directed toward the wrong side when the hands were crossed (although note that this was reported only for a very brief pilot study). Here we study related issues, but for covert exogenous attention rather than overt orienting, and with tactile events serving only as spatially nonpredictive cues, prior to visual targets. Thus, unlike Groh and Sparks' overt orienting study, the tactile events were not the imperative targets for any response in our study, but served merely as task-irrelevant cues prior to visual targets.

In the psychophysical part of our study, we adapted the ''orthogonal cuing'' method used in recent crossmodal studies by Spence and Driver (1996, 1997). A tactile stimulator was located on each index finger at a fixed position on one side. Two lights were positioned close to each stimulator, one above and one below (see Figure 1A). On each trial, one tactile stimulator was activated, followed by any one of the four possible lights. The task was an up/down ''visual'' judgment; that is, a speeded discrimination of whether each visual event came from an upper or lower position, ''regardless of its side''. The tactile event was to be ignored, serving only as a spatially nonpredictive cue to one side or other. The methodological advantage of the up/down visual task is that the vertical judgment is orthogonal to the lateral direction of tactile cuing (i.e., left vs. right), so the lateral cue cannot produce any response bias for the judgment (see Spence & Driver, 1994, 1997). The posture of the hands was either uncrossed or crossed (see Figure 1A). In addition, the stimulus onset asynchrony (SOA) between tactile cue and visual target was varied, with two levels, to examine whether any crossmodal attentional interactions depend on close temporal contiguity for the events in the two modalities (recall that exogenous cuing effects are usually short-lived; e.g., see Müller & Rabbitt, 1989). These SOAs were randomly intermingled, as were the possible cue and target locations. The tactile cue was nonpredictive spatially, neither indicating a likely side nor elevation for the visual target, which was always equally likely to appear from any one of the four possible visual locations. Central fixation was required and monitored.

In addition to implementing psychophysical tests of where visual attention might get drawn toward by tactile events, we also measured event-related brain potentials (ERPs) at the scalp. The ERP method can provide a temporally fine-grained measure of neural activity in different attentional conditions, so it could potentially determine how early in the sensory response any tactile–visual crossmodal interactions might arise. Since the only existing studies of visual–tactile links in exogenous covert spatial attention to date have used purely behavioral measures, it is entirely unknown at what level such crossmodal links arise. It remains possible that they affect only relatively ''late'' stages of processing (e.g., response decisions). Alternatively, they could in principle affect quite early stages of sensory processing, as previously shown for several ''unimodal'' attentional effects (e.g., Mangun et al., 1993; Mangun, 1995). For example, it has recently been suggested that crossmodal interactions could arise as a result of back-projections from multimodal cells to unimodal brain areas (Driver &

Figure 1. Schematic view of the apparatus and participant's position for both hand postures (A) in the psychophysical study and (B) in the ERP study.
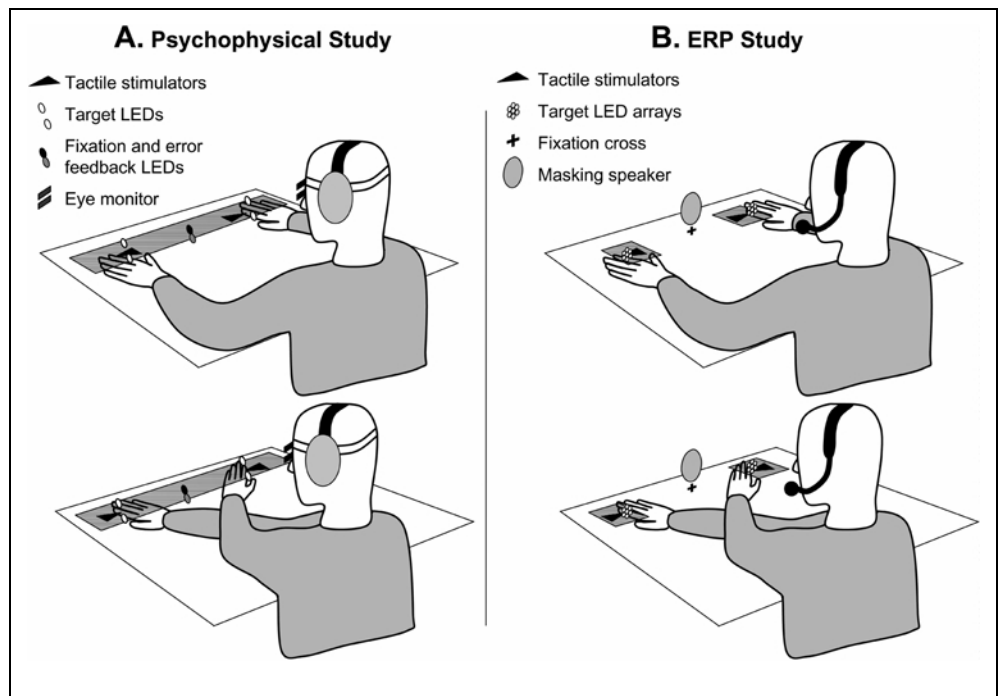
Spence, 1998). Such a mechanism could be revealed in the present study if early visually evoked responses are found to be modulated by the task-irrelevant tactile events. ERPs might also reveal how early in the neural response the current posture can affect any crossmodal links (e.g., when comparing crossed vs. uncrossed hand postures).

There have been many previous ERP studies of "endogenous" covert spatial attention (e.g., Heinze et al., 1994; Eimer, 1993; Mangun & Hillyard, 1991; for reviews, see Hillyard & Anllo-Vento, 1998; Mangun et al., 1993; Mangun, 1995), including a few crossmodal studies (e.g., Eimer & Schröger, 1998; Hillyard, Simpson, Woods, Van Voorhis, & Münte, 1984). However, there have been considerably fewer ERP studies of "exogenous" spatial attention, in part due to methodological challenges that we discuss later. Eimer (1994) conducted a unimodal ERP study of visual exogenous attention, in which a spatially nonpredictive peripheral cue was followed, at an SOA of 900 msec, by a visual target at the same (cued) location or in the opposite visual hemifield (uncued). Posterior P1 components were larger for uncued trials, suggesting an initial inhibition for targets presented at the same location as the cue (possibly related to the attentional phenomenon known as inhibition of return; Posner & Cohen, 1984). In contrast, enhanced negativities were recorded for cued trials at midline electrodes between 120 and 300 msec posttarget onset, with a first peak (Nd1) at the parietal electrodes, and a second peak (Nd2) more broadly distributed across midline sites. It was suggested that these Nd effects might reflect an enhanced processing of targets at cued locations as a result of exogenous covert orienting triggered by the peripheral cue. In a more recent unimodal ERP study of exogenous covert attention, also within vision, Hopfinger and Mangun (1998) reported enhanced occipital P1 components for stimuli at cued locations when cue–target intervals were short (34–234 msec), suggesting that exogenous spatial attention may affect the same early stages of visual processing as endogenous attention. With cue–target intervals comparable to the Eimer study, Hopfinger and Mangun observed larger P1 amplitudes for stimuli at "uncued" locations instead, just as Eimer had found at such intervals.

In the ERP part of the present study, ERPs were measured in response to visual stimuli preceded by spatially nonpredictive tactile cues, from stimulators identical to those in the psychophysical part of our study. Participants in the ERP sessions again had to ignore the nonpredictive tactile cue that preceded the visual event, and the general methodology was kept similar to the psychophysical procedure. However, some changes in detail were essential given the differing requirements of psychophysical and ERP measures. Instead of responding to every visual stimulus to provide a psychophysical measure of visual performance, partic-

ipants now responded only to infrequently presented visual "oddballs" (lights that flickered rather than "standard" lights, which did not). In order to prevent overlap of sensory ERPs (and their potential attentional modulation) with components related to responding, only ERPs to the more common visual nontargets (receiving no overt motor response) were analyzed at cued and uncued locations. Any effects of tactile spatial cuing on visually evoked ERP components were analyzed at lateral occipital electrodes, and attentional Nd1 and Nd2 effects were measured at midline and lateral central sites. If crossmodal links in exogenous spatial attention between touch and vision can affect visual components, then ERP effects for visual targets may be obtained in the present study similar to those reported in the unimodal studies of Hopfinger and Mangun (1998) and Eimer (1994), even though the cues were now tactile instead of visual.

As in the psychophysical experiment, the hands were either crossed or uncrossed (see Figure 1B), and there were two cue–target SOAs. The SOA manipulation again tested whether any crossmodal attentional effects varied with temporal contiguity between events in the different modalities, as for many of the crossmodal interactions found at the single-cell level (e.g., Stein & Meredith, 1993), and as for the short-lived cuing effects in behavioral studies of exogenous attention (e.g., Müller & Rabbitt, 1989). SOA also served another purpose, in the interpretation of ERP findings. Using two different SOAs may allow us to distinguish between ERP modulations due to genuinely attentional crossmodal interactions, versus ERP changes due merely to the summing at the scalp of a visual response to a particular light, together with an entirely separate tactile response to a closely preceding stimulus on the same versus opposite side. Unlike studies of endogenous attention, it is unavoidably the case in studies of "exogenous" attention that the attentional manipulation of cued side is confounded to some extent with variations in stimulation (i.e., with the side of the cue), because exogenous attention is stimulus-driven by definition. However, note that ERP effects of crossmodal exogenous attention upon visual processing should be time-locked to the onset of "visual" stimuli, while ERP effects related merely to the side of the cues per se should vary with the relative onset time of these "tactile" cues. If the latencies of any ERP spatial cuing effects were to remain constant relative to the onset of visual stimuli, despite variations in cue–target SOA, this would provide strong evidence that these effects reflect true influences of exogenous spatial attention, rather than merely the nonattentional summing of a visual response with an entirely separate tactile response. Note also that the crossed-hands manipulation should shed further light on this issue. Tactile stimulation of (say) the left hand could produce very different attentional effects on (say) right field visual stimuli when that hand is placed in the

right versus left visual field (these correspond to cued crossed and uncued uncrossed trials respectively, as discussed earlier). In contrast, no such differences between cued and uncued trials should be present in purely somatosensory ERPs for either hand posture, since tactile cues were uninformative and always preceded the visual stimuli.

For both the ERP and psychophysical sessions, the tactile cue was always equally likely to be on the left or right hand for each trial, and its side did not predict where the subsequent visual stimulus would appear, which remained equally likely to be in the left or right visual field. The comparison of crossed versus uncrossed hand postures should reveal whether any crossmodal effects of tactile spatial cuing (as measured by ERPs or psychophysical performance) reflect merely the initial hemispheric projections of the sensory stimulation. They might instead reflect some higher-level reference frame, such that the relative location of tactile and visual events in external space is more important, with the results changing for crossed versus uncrossed postures.

RESULTS

Psychophysical Study

Participant median reaction times (RTs) for each condition were calculated. The interparticipant means of these are shown in Table 1, where "cued" versus "uncued" visual targets refer to those on the same side of "external space" as the tactile cue (thus a right visual field light after stimulation of the right hand would be a cued target with the hands uncrossed, but would become an uncued target with the hands crossed).

It can be seen in Table 1 that RTs were typically faster for cued than uncued targets, usually with supporting trends in the accuracy data. However, for the case of crossed hands at the longer SOA only, a potential speed/accuracy trade-off arises, since the cued targets showed an apparent RT advantage but accuracy disadvantage. Accordingly, to take any possible speed/accuracy trade-offs into account, we computed an efficiency measure,

which is a standard way to combine RT and accuracy measures of performance (Townsend & Ashby, 1978, 1983). Following previous authors (Murphy & Klein, 1998; Christie & Klein, 1995; Akhtar & Enns, 1989), we calculated inverse efficiency (whereby a higher value indicates worse performance, just as for RT and error measures) as the median RT divided by the proportion of trials correctly responded to in a given condition. This provides a measure of processing efficiency that discounts possible criterion shifts or speed/accuracy trade-offs. Figure 2 plots the cuing effects (i.e., difference between uncued vs. cued side of space) in this efficiency measure, for the four different conditions produced by combining the SOAs with the hand postures. The 95% confidence intervals on each cuing effect are indicated. As Figure 2 shows, cuing was strongest at the shorter SOA, and with uncrossed hands, being significant for all combinations except the crossed hands at the long SOA. Note that a confidence interval that does not include zero in Figure 2 is equivalent to a significant difference between cued and uncued trials by t test, at $p < .05$.

These observations were confirmed by a three-way within-participant analysis of variance (ANOVA) on the inverse efficiency data. The factors were spatial cuing (visual target on the same vs. opposite side of external space as the tactile cue; i.e., cued vs. uncued side); SOA (short vs. long); and hand posture (uncrossed vs. crossed). This analysis revealed a main effect of spatial cuing [$F(1, 23) = 13.9, p = .001$] as visual judgments were more efficient for cued targets (mean efficiency score of 433 msec) than uncued targets (444 msec) overall. The interaction between spatial cuing and SOA was significant [$F(1, 23) = 6.4, p = .02$], with smaller cuing effects at the longer SOA (see Figure 2). The interaction between spatial cuing and hand posture was also significant [$F(1, 23) = 14.7, p = .001$], because cuing effects were larger with uncrossed hands than with crossed hands. Two-tailed paired t tests on uncued-minus-cued differences in efficiency confirmed that a reliable spatial cuing effect was found at both SOAs with the hands uncrossed [both $t(23) > 2.5, p < .02$], and also at the short SOA with crossed hands [$t(23) = 2.2$,

Table 1. Means of Median Reaction Times, Percentage Errors, and Inverse Efficiency Measures by Experimental Condition for the Psychophysical Experiment

	Uncrossed Posture				Crossed Posture			
	Short SOA		Long SOA		Short SOA		Long SOA	
Measure	Cued	Uncued	Cued	Uncued	Cued	Uncued	Cued	Uncued
RT (msec)	413	427	389	402	410	418	395	399
Errors (%)	3.3	6.0	8.4	9.4	4.6	5.2	12.0	8.5
Inverse efficiency (msec)[a]	427	455	425	444	429	441	449	437

[a]Inverse efficiency, calculated separately for each subject in each condition, is defined as median RT divided by the proportion of trials correct.
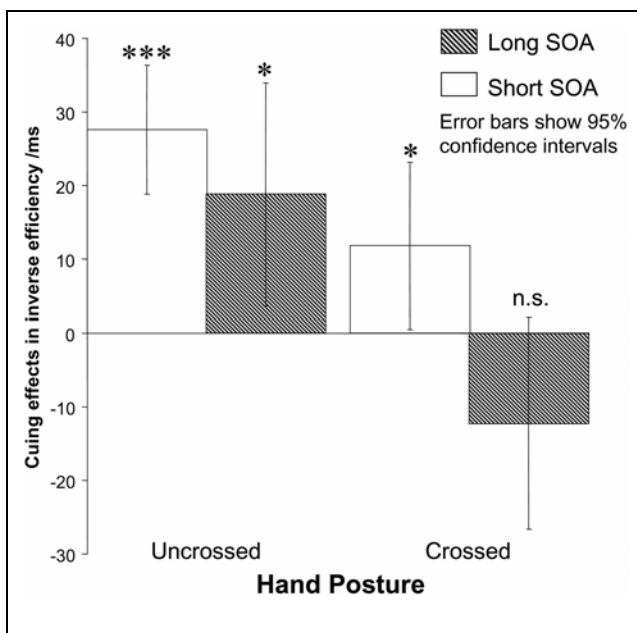
Figure 2. Mean spatial cuing effects on inverse efficiency scores for the four conditions (2 SOAs×2 Hand Postures) in the psychophysical study. Error bars denote the 95% confidence interval for the uncued-minus-cued differences. A positive cuing effect denotes more efficient performance for tactually cued lights than uncued lights, as coded with respect to common position of cue and target in "external" space. Asterisks denote the outcome of two-tailed t tests on the uncued-minus-cued differences (***$p < .001$; *$p < .05$).

$p = .04$; see also the confidence intervals in Figure 2]. Crucially, the short SOA effect with crossed hands shows that tactile stimulation of one hand drew visual attention toward its current location in external space when crossed.

Only the long-SOA/crossed-hands condition failed to show a reliable spatial cuing effect [$t(23) = 1.8, p = .09$]. Given the failure of the three-way interaction between cuing, SOA, and hand posture to reach significance [$F(1, 23) = 1.8, p = .2$], this pattern presumably reflects the additive combination of reduced cuing with crossed hands, together with reduced cuing at the longer SOA, leading to the loss of reliable cuing only when hands were crossed and there was also a long SOA. For completeness, we also ran analyses treating RT and accuracy as separate measures, rather than combining them into an efficiency measure. These analyses led to the same conclusions. In particular, two-tailed paired t tests on RTs found reliable cuing effects at both SOAs with uncrossed hands, and at the short SOA with crossed hands [all $t(23) > 2.3, p < .03$], all with supporting error trends (see Table 1). Only the long-SOA crossed-hands condition failed to show a reliable RT advantage for visual targets on the same side of external space as the tactile cue [$t(23) = 1.0, p = .3$], just as in the efficiency analysis.

In sum, these results confirm a spatial influence of nonpredictive tactile events on visual discriminations for closely following visual targets, with better visual performance on the side of the tactile cue. This crossmodal cuing effect is independently modulated by both the SOA between cue and target (larger cuing effects at the shorter SOA), and by hand posture (larger effects with uncrossed hands). Critically, however, at the short SOA with crossed hands, the tactile cue benefits visual targets at the same side of "external space" as the tactile cue. Thus, at this SOA, a touch on the right hand benefits the right visual field when the hands are uncrossed, but the left visual field when they are crossed, thus demonstrating some remapping of attentional links between the modalities to keep them in spatial register when posture is changed. Although this is a purely behavioral result, note that it does have some implications for possible neural accounts. In particular, the short SOA result with crossed hands disconfirms any simple account in terms of hemispheric activation (e.g., Kinsbourne, 1975, 1987) due to the initial hemispheric projections of the stimuli. However, the behavioral results alone cannot reveal whether the crossmodal links between touch and vision directly affected sensory processes (i.e., visual responses in the brain). The ERP data can shed light on this.

ERP Study

Participants missed only 6.5% of all flickering visual targets, and responded correctly with an average latency of 532 msec. The false-alarm rate on trials with a visual nontarget (i.e., a continuous light) was only 1%.

All ERPs were measured relative to the mean voltage of the 100 msec pretrial baseline interval; all numerical latencies are given relative to the onset of "visual" stimuli (although Figures 3, 4, and 5 place the y-axis at onset of the tactile cue). As in the Eimer (1994) unimodal study of exogenous visual attention (which had used visual rather than tactile cues), mean amplitude values were computed for the following electrodes and latency windows: P1 (100–140 msec) and N1 (160–200 msec) for lateral occipital sites; early Nd (Nd1: 110–180 msec) and late Nd (Nd2: 220–300 msec) for lateral central and midline sites.

Separate within-participant ANOVAs were performed with the factors of spatial cuing, hand posture, cue–target SOA, stimulus side, and electrode location (Fz vs. Cz vs. Pz for midline electrodes; left vs. right for lateral electrodes). When appropriate, Greenhouse–Geisser adjustments to the degrees of freedom were performed. For brevity, trivial main effects due to stimulus side producing stronger ERPs at left or right sites, or due to different electrodes showing different time courses, will not be reported; only the possible interactions of these factors with the others will be noted. Additional paired t tests were performed to test the reliability of the critical spatial cuing effects at specific electrode sites.

Figure 3. (A) Grand-averaged ERPs collapsed across right and left occipital electrodes and visual stimulus positions for cued (solid curves) and uncued (dotted curves) trials for the four conditions (2 SOAs×2 Hand Postures). (B) Grand-averaged ERPs at the short SOA for occipital electrodes ipsilateral (top) and contralateral (bottom) to the visual stimulus, collapsed across hand position. (C) Difference waveforms obtained by subtracting ERPs for uncued trials from ERPs for cued trials, summed across lateral central sites for uncrossed (solid curves) and crossed (dotted curves) hand posture, and plotted separately for long versus short SOAs. All waveforms are plotted with *y*-axes at the onset of the tactile cue and dashed vertical lines marking the onset of visual stimulus.
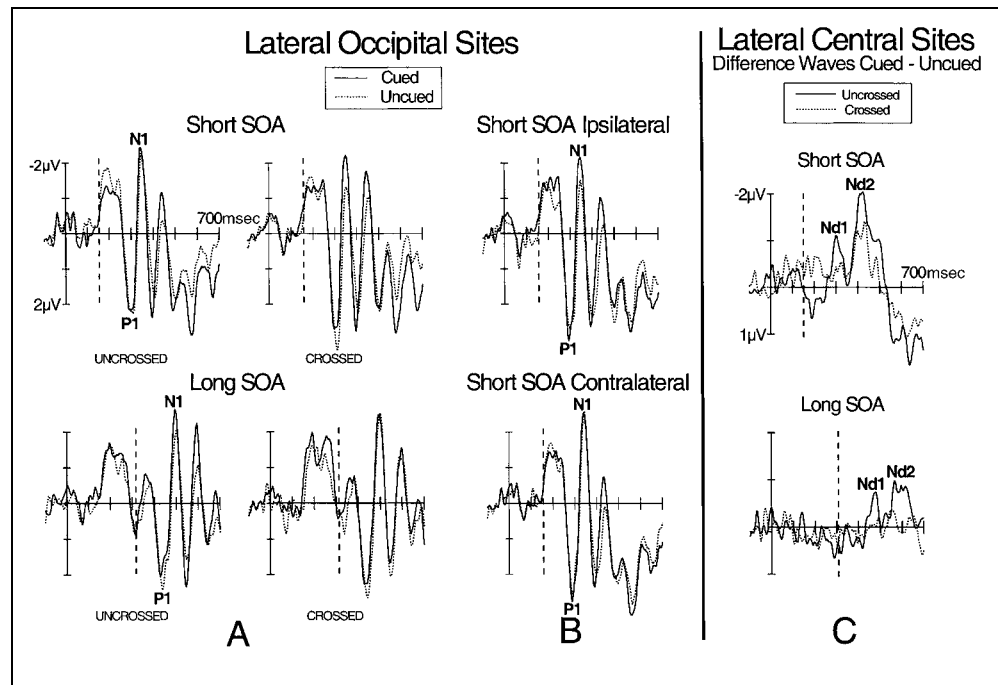

Figure 3A shows grand-averaged ERPs at the lateral occipital electrodes, pooled across electrode side and visual stimulus position, for visual stimuli from cued and uncued locations, displaying these separately for the four conditions generated by crossing the two hand positions with the two cue–target SOAs. No effects of spatial cuing or any other main effects were obtained for P1 amplitude. For the occipital N1, a highly significant main effect of spatial cuing was obtained [$F(1, 11) = 11.1, p = .007$], reflecting enlarged N1 components for visual stimuli at tactually cued versus uncued locations, and thus demonstrating a crossmodal cuing effect on ERPs. Although small in amplitude, this N1 modulation was consistently observed across participants; 11 out of 12 showed larger occipital N1 amplitudes in response to visual stimuli at cued locations.

A highly significant three-way interaction [Spatial Cuing × Side of Visual Stimulation × Electrode Side: $F(1, 11) = 10.1, p = .009$] was also obtained, suggesting that attentional N1 modulations were different at occipital sites ipsilateral and contralateral to the visual field of stimulus presentation. Follow-up ANOVAs (with the factors of spatial cuing, hand posture, and SOA), conducted separately for ipsilateral and contralateral occipital electrodes, found a highly significant main effect of attention at ipsilateral sites [$F(1, 11) = 15.8, p = .002$]. In contrast, no significant N1 effect was present at contralateral occipital sites [$F(1, 11) = 1.2, p = .3$]. This difference between ipsilateral and contralateral occipital electrodes accounts for the three-way interaction of Spatial Cuing × Side of Stimulation × Electrode Side in the N1 component. Figure 3B illustrates this pattern

of results at the short SOA when pooled across posture, displaying occipital ERPs elicited by cued and uncued stimuli, separately for ipsilateral and contralateral occipital electrodes. While an attentional N1 modulation is clearly visible ipsilaterally, this is absent at contralateral sites. This finding of larger attentional N1 modulation at ipsilateral sites accords with previous "unimodal" ERP studies of covert visual attention (e.g., Eimer, 1996; Mangun & Hillyard, 1991). Here we observe this pattern for the first time in a crossmodal situation; the implications are discussed later.

In order to verify that spatial cuing effects for the ipsilateral N1 were present in both hand postures, further ANOVAs (with the factors of spatial cuing and SOA) were conducted separately for blocks with uncrossed hands versus crossed hands, on the data from ipsilateral occipital electrodes. Simple effects of spatial cuing were observed for both hand postures [both $F(1, 11) > 10.8, p < .008$]. As in the psychophysical study, significant spatial cuing effects were thus observed in terms of the relative location of the tactile and visual stimulus in external space, both when the hands were uncrossed and also when crossed. Hence, which visual hemifield was advantaged by cuing a particular hand "reversed" when the hands were crossed versus uncrossed; this was found for the N1 effect at ipsilateral occipital electrodes, as for the psychophysical findings.

As mentioned earlier, Nd1 and Nd2 effects were also predicted in the difference waves for tactually cued-minus-tactually uncued visual stimuli, at lateral central and midline electrodes. These difference waves are shown in Figure 3C for lateral central electrodes. Figure

4 shows ERPs at midline electrodes for cued and uncued visual stimuli at the short SOA, separately for the uncrossed-hands and crossed-hands conditions, together with the resulting cued-minus-uncued difference waveforms. Figure 5 shows the equivalent for the long SOA. Spatial cuing resulted in a biphasic negative modulation of ERP waveforms, with the earlier effect (Nd1) largest at Pz, and the later effect (Nd2) more broadly distributed. These effects appear to be larger when the hands were uncrossed, and for short cue–target SOAs (see Figures 3c, 4, and 5), being virtually absent in the crossed-hands/long-SOA condition (see Figure 5). This reveals a similar pattern to the psychophysical cuing effects. In the Nd1 interval, the main effect of spatial cuing failed to reach significance at midline electrodes overall [$F(1, 11) = 3.3, p = .1$], but a Spatial Cuing × Electrode Location interaction [$F(2, 22) = 11.64, p < .001, e = .95$] indicated that cuing affected ERP waveforms differently at different midline electrodes. A significant Nd1 spatial cuing effect was obtained at Pz [$F(1, 11) = 7.33, p = .02$], accompanied by an almost significant Cuing × Hand Posture interaction [$F(1, 11) = 4.57, p < .06$], reflecting larger Nd1 effects with uncrossed hands. Additional t tests conducted separately for all four task conditions revealed reliable parietal Nd1 effects with uncrossed hands for short and long SOAs [both $t(11) > 2.35$, both $p < .02$], but not for the crossed-hands conditions [both $t(11) < 1.2$]. At Cz, a Cuing × SOA interaction was found [$F(1, 11) = 4.71$,

$p = .05$], and subsequent t tests revealed a significant Nd1 spatial cuing effect for the uncrossed-hands/short-SOA condition [$t(11) = 2.21, p < .03$]. No reliable spatial cuing effects were obtained within the Nd1 interval at lateral central electrodes.

In the Nd2 interval, a main effect of spatial cuing [$F(1, 11) = 14.5, p = .003$] at midline electrodes was accompanied by a Spatial Cuing × SOA interaction [$F(1, 11) = 6.1, p = .03$] and a Marginal Cuing × Hand Posture interaction [$F(1, 11) = 4.0, p = .07$]. As can be seen from Figures 3c, 4, and 5, Nd2 effects were largest in the uncrossed-hands/short-SOA condition, and were virtually absent in the crossed-hands/long-SOA condition, thus showing once again the same general pattern apparent for the psychophysical measures. The Nd2 spatial cuing effects were further tested with paired t tests. At Cz and Pz, significant effects were obtained for all task conditions [all $t(11) > 2$, all $p < .04$], except for the crossed-hands/long-SOA condition [$t(11) < 1$]. At Fz, significant effects were only present for the uncrossed-hands/short-SOA condition [$t(11) = 2.7, p = .02$]. Turning to lateral central electrodes, a main effect of spatial cuing [$F(1, 11) = 15.0, p = .003$] in the Nd2 interval was accompanied by a Cuing × SOA interaction [$F(1, 11) = 9.1, p = .01$]. Paired t tests revealed significant Nd2 cuing effects for both hand postures with short SOA [both $t(11) > 3.0$, both $p < .01$]. This effect failed to reach significance for the uncrossed-hands/long-SOA condition [$t(11) = 1.7, p$

Figure 4. Grand-averaged ERPs, collapsed across visual stimulus side, obtained at Fz, Cz and Pz in "short"-SOA blocks for cued (solid curve) and uncued (dotted curve) trials, displayed separately for uncrossed hands (left) and crossed hands (middle). Right: Difference waveforms obtained at midline electrodes by subtracting ERPs for uncued trials from ERPs for cued trials for uncrossed-hand blocks (solid lines) and crossed-hand blocks (dotted lines). All waveforms are plotted with y-axes at the onset of the tactile cue and dashed vertical lines marking the onset of visual stimulus.
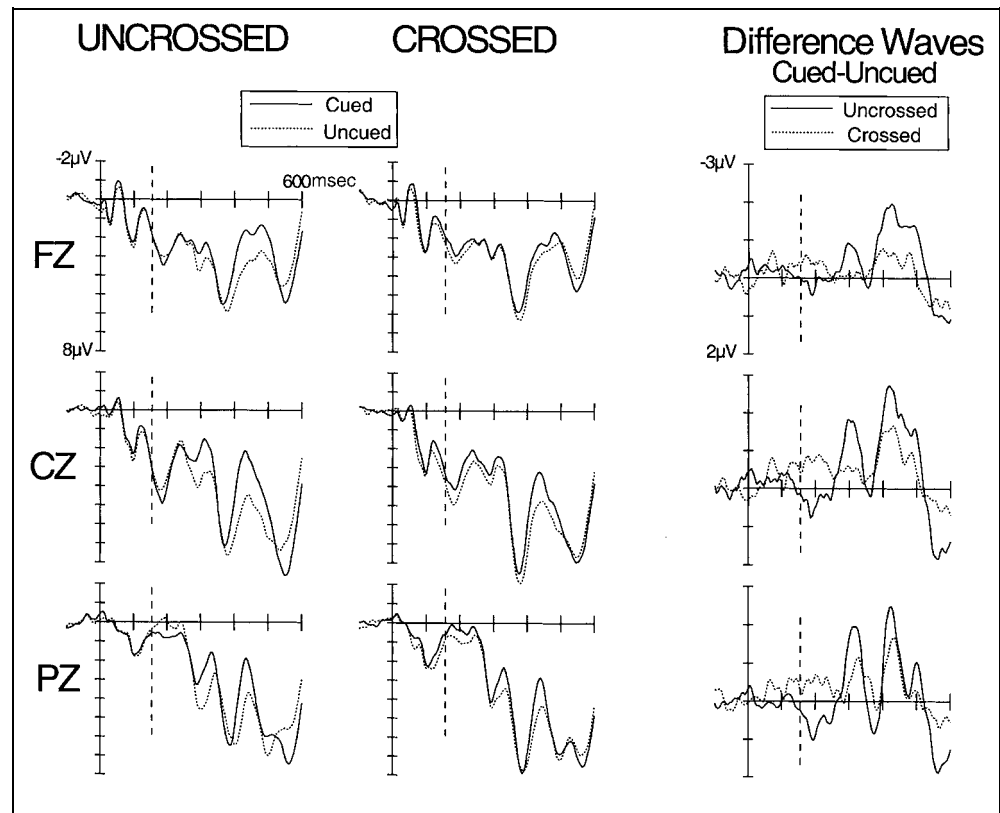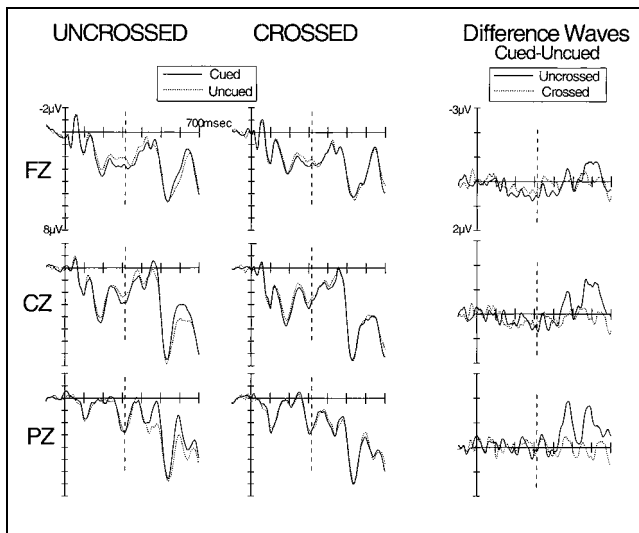
Figure 5. Grand-averaged ERPs, collapsed across visual stimulus side, obtained at Fz, Cz and Pz in ''long''-SOA blocks for cued (solid curve) and uncued (dotted curve) trials, displayed separately for uncrossed hands (left) and crossed hands (middle). Right: Difference waveforms obtained at midline electrodes by subtracting ERPs for uncued trials from ERPs for cued trials for uncrossed-hand blocks (solid lines) and crossed-hand blocks (dotted lines). All waveforms are plotted with y-axes at the onset of the tactile cue and dashed vertical lines marking the onset of visual stimulus.

< .07], and was entirely absent with crossed hands and long SOA [$t(11) < 1$].

DISCUSSION

These studies tested for crossmodal links between touch and vision in exogenous covert attention, using both psychophysical and ERP measures. Spatially nonpredictive tactile stimulation of one hand was followed (at a short or long SOA) by visual stimulation on the same or opposite side, while the hands were held in a crossed or uncrossed posture. The psychophysical measures showed that visual discriminations were more efficient on the same side of external space as the preceding touch, even when the hands were crossed over. This confirms and extends the tactile–visual link in exogenous covert attention reported by Spence et al. (1998), in which only the uncrossed-hands posture was investigated in a behavioral study. The present psychophysical findings revealed that this tactile–visual cuing effect is larger at the shorter SOA, and larger with uncrossed hands, being absent only in the long-SOA/crossed-hands condition. The finding of smaller cuing effects at the longer SOA is consistent with previous unimodal research showing that exogenous cuing effects tend to be short-lived (e.g., Müller & Rabbitt, 1989). Crucially, the cuing effect at the short SOA with crossed hands was found to favor the side of external visual space on which the stimulated hand currently lay, suggesting some remapping between the modalities, in terms of which

tactile stimulation drew attention to a particular visual field. Thus, with uncrossed hands a touch on the right hand advantaged the right visual field, but the same touch advantaged instead the left visual field with crossed hands (and vice versa for a touch on the left hand). This new result argues against any neural account of crossmodal links in exogenous covert spatial attention that appeals solely to ''hemispheric activation'' (Kinsbourne, 1975, 1987) due to the initial cortical projection of the various stimuli. It also shows that postural signals, presumably involving proprioception, are integrated with the tactile event before visual covert orienting is complete.

The ERP data likewise revealed crossmodal cuing effects, with larger amplitude ERPs for visual events at the same external location as a preceding tactile cue, even when the hands were placed in the crossed posture. This was found for occipital N1 components, and for later Nd1 and Nd2 components at lateral central and midline sites. Attentional modulation of occipital N1 components has been found in many previous ''unimodal'' studies of covert visual attention, and has commonly been interpreted as an influence on sensory visual processes at quite early stages of processing (e.g., Mangun & Hillyard, 1991; Mangun, 1995; Heinze et al., 1994). In this context, it is important to note that in the present crossmodal study, the N1 attention effect was primarily elicited at occipital electrodes ipsilateral to the field of visual stimulation (see Figure 3B). This pattern of ipsilaterally maximal attentional modulation of the N1 component has been found consistently in previous unimodal trial-by-trial cuing studies of visual attention, both for endogenous attention (Eimer, 1996; Mangun & Hillyard, 1991) and for exogenous attention (Eimer, 1994). Although the causes for the usual ipsilaterality of the N1 attention effects are not yet known, our experiment replicated this pattern, but now using ''tactile'' cues prior to visual stimuli. This suggests that the spatially selective processes observed in the present ''crossmodal'' study, for the N1 component, are similar to those processes elicited in ''unimodal'' studies of visual–spatial attention. Moreover, the timing of this N1 modulation is also consistent with a crossmodal effect upon sensory visual processes. The peak of the N1 component showing the cuing effect was at approximately 190 msec, thus demonstrating a relatively early crossmodal influence on visual ERPs. Although the N1 may reflect several underlying generators, at this latency, the more ventral occipito-temporal generator is thought to be predominant (Johannes, Münte, Heinze, & Mangun, 1995).

The influence of tactile cuing on visual ERPs also revealed enhanced negativity in the Nd1 time range at Pz, and in the Nd2 time range at midline and at lateral central electrodes, again for visual events at the same external spatial location as the preceding tactile cue. In contrast to the N1 component, attentional negativities in the Nd1 and Nd2 time windows are less modality-

specific. Attentional Nd1 effects are not only elicited by visual stimuli at attended locations, but also by attended "auditory" stimuli, showing highly similar latencies and scalp distributions across these two modalities (Eimer, 1998). Nd1 effects can be reliably observed for transient attention conditions (i.e., with trial-by-trial cuing), but not for sustained attention instructions, where attention has to be kept at a specified location for an extended period (e.g., throughout a block; Eimer, 1996). Such observations suggest that Nd effects reflect spatially selective processes triggered in response to attentional cues, which are to some extent independent of input modality.

Importantly, the crossmodal modulation of the ERP effects observed in the present electrophysiological study showed a similar pattern to the psychophysical crossmodal cuing effects. The crossmodal influences were typically larger at the shorter SOA, and with uncrossed hands, usually being absent only for the crossed-hands/long-SOA condition.

Crucially, any crossmodal ERP effects with crossed hands at the short SOA always showed larger amplitudes for visual targets at the "same external location" as the preceding touch, thus implying some remapping between the modalities across the change in posture, just as for the psychophysical results.

The ERP data suggest, for the first time, that spatially selective modulations of "visual" components can be obtained by exogenous spatial cuing with "tactile" events[1]showing that crossmodal links can influence sensory responses as early as the N1 component. Although we observed effects of tactile cuing at several electrode sites, and in several components (i.e., N1, Nd1, and Nd2), the N1 modulation at ipsilateral occipital electrodes is perhaps the most critical ERP finding, in several respects. Since it was the first to arise, it might in principle play a causal role in the modulations apparent in the later components. More importantly, the N1 result specifically suggests that tactile cuing may modulate sensory visual processes. In suggesting that such unimodal (visual) processes can be modulated crossmodally (by a tactile cue), these results provide the first evidence that crossmodal links in exogenous covert spatial attention might operate via a feedback mechanism from multimodal structures to unimodal areas (as proposed by Driver & Spence, 1998, on purely theoretical grounds).

Before our ERP results can be interpreted unequivocally in such terms, a potential methodological objection has to be considered. As mentioned earlier, the difference between ERPs in response to visual stimuli at cued and uncued locations might, in principle, be due to a partial overlap at the scalp of entirely independent tactile and visual ERP waveforms. Since the tactile cue had to be presented to a different hand on cued versus uncued trials (within a given posture), an apparent change in visual ERPs might conceivably be an artifact

of a constant visual waveform overlapping with different tactile waveforms elicited by cue onsets and/or offsets. To minimize this overlap, we had deliberately used very short (10 msec) tactile cues for the ERP study (see Methods), having first confirmed in a pilot study that behavioral spatial cuing effects could still be observed with such brief cue events. More importantly, several aspects of our empirical ERP data argue strongly against an account of our N1, Nd1 and Nd2 findings in terms of mere overlapping of visual and tactile components. First, crossing the hands at the short SOA actually "reversed" which visual field showed enhanced ERP components following stimulation of a particular hand. This would not be expected if the cuing effects merely reflected summation of the visual response with an independent, purely tactile response that partially overlapped in time.[2]Second, by examining those components that showed modulation by cuing for the two different SOAs, one can determine whether the latency of these components is time-locked to the onset of the "visual" stimulus (as would be expected if the effects reflect attentional influences on visual processing as we suggest), or instead shows modulation that depends on the relative onset of the "tactile" cue (as would be expected if the apparent crossmodal cuing were due to summation of entirely separate components). Overlay with different tactile components should lead to a shift in peak latencies for the visual components between the two SOAs, when time-locked to the visual stimuli. Inspection of the ERP waveforms showed that this did not apply for the critical components; instead, time-locking to the visual onsets clearly applied, consistent with modulation of visual processing.

For example, Figure 6A shows cued-minus-uncued difference waves obtained at Pz, for short and long cue–target SOAs in the uncrossed-hands condition (where crossmodal cuing effects were found at both SOAs), time-locked to the onset of the "tactile" cue (left) or instead to the subsequent "visual" stimulus (right), respectively. Note that the peak latencies of the attentional Nd1 and Nd2 modulations are virtually identical for the two SOAs when time-locked to the "visual" stimulus (Figure 6A, right). This strongly suggests that these effects reflect differences in the processing of visual stimuli at cued versus uncued locations, due to an attentional shift triggered by the tactile cue, rather than merely the overlap of visual ERPs with different tactile cues on cued versus uncued trials. The latter possibility should have shifted the peak latency of the attentional modulations when time-locked to the visual stimulus, which was not found. Note that unlike other, more analytic methods (e.g., Woldorff, 1993) for separating potentially overlapping ERP components, which require many more SOAs than were available in our dataset, the present argument does not depend on any assumptions of linear summation for overlapping components.
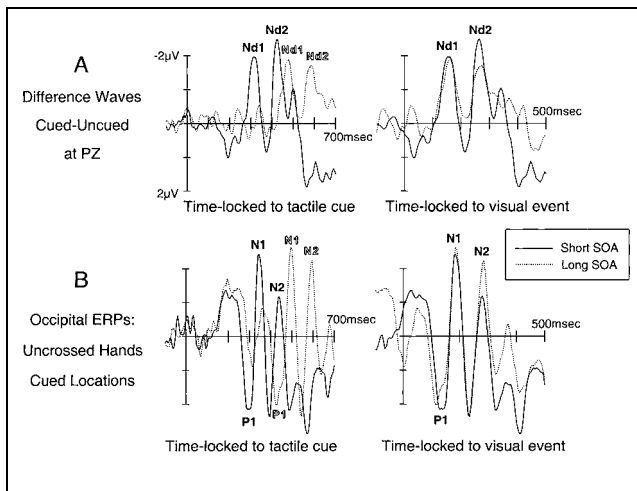
Figure 6. (A) Difference waveforms (cued − uncued trials) at Pz with uncrossed hands for short and long cue–target SOA, collapsed across visual stimulus side. Waveforms are plotted time-locked to tactile cue onset (left) and visual stimulus onset (right). Note that Nd1 and Nd2 components from short-SOA trials align with the same components from long-SOA trials when time-locked to visual stimulus onset. (B) Grand-averaged occipital ERPs, summed across left and right occipital electrodes and visual stimulus positions, obtained for cued trials and uncrossed hands with short and long cue–target SOA. Waveforms are plotted time-locked to tactile cue onset (left) and visual stimulus onset (right). Note that the N1 and N2 components from short-SOA trials align with the same components from long-SOA trials when time-locked to visual stimulus onset (right graph).

Figure 6B shows occipital ERPs obtained in cued trials with uncrossed hands for short and long SOAs, again time-locked either to tactile cue onset (left) or visual stimulus onset (right). Some ERP activity related to tactile stimulus onset is clearly present at occipital sites prior to the onset of the visual P1 component (Figure 6B, left), consistent with the possibility of summation of tactile and visual responses. Such summation could be responsible for the P1 latency shift, relative to the visual onset, for the short versus long cue–target SOAs, apparent in Figure 6B (right). However, the occipital N1 (and N2) components for these two SOAs overlap almost perfectly when time-locked to visual stimulus onset (Figure 6B, right). Thus, all the components for which we found reliable attentional modulation (i.e., N1, Nd1, and Nd2) appear to be unaffected by temporally overlapping somatosensory ERP components. The critical N1 effect thus appears to be a true influence of crossmodal covert attention, rather than being merely due to the summation of overlapping but otherwise independent visual and tactile components. However, the overlapping problem may have applied to the occipital P1 component. Thus, crossmodal spatial cuing effects might have been observed even for this earlier component, were it not for the possibility of overlapping responses to visual and tactile events.

The psychophysical and ERP effects of crossmodal cuing that we did observe were still present with crossed hands at the short SOA, thus demonstrating some spatial remapping between the modalities across the change in posture. However, these effects were typically somewhat reduced with crossed hands (and often absent at the longer SOA in this posture). In this respect, the present results differ from the behavioral findings of Spence et al. (in press) for tactile–visual links in "endogenous" rather than "exogenous" covert attention, demonstrating a new difference between these two forms of attention, in addition to those previously identified by unimodal studies (e.g., Rafal et al., 1991; Jonides, 1981). The reduced cuing effects with crossed hands in the present exogenous study might be due to opposing influences at different levels of the system. A remapped attentional modulation might favor the common location in external space of a visual stimulus and a crossed hand, while a more primitive "fixed-mapping" influence (perhaps due to hemispheric-competition mechanisms in some neural structures) could favor the anatomically linked side of space (i.e., the other visual field for a crossed hand) at a different level of the system. These two influences would sum together in the uncrossed posture, but be opposed in the crossed posture, which could explain the reduced psychophysical cuing effect we found with crossed hands. Although the ERP results did not find any evidence for some level of the system actually shifting toward the "wrong" (i.e., anatomically linked) side under the crossed posture, any such influence might in principle have arisen subcortically in structures (e.g., the superior colliculus; Groh & Sparks, 1996b) which have little influence on scalp recordings. This possibility could be addressed with functional imaging of the whole brain in a similar experimental paradigm.

The positive evidence we found for remapping of stimulus-driven crossmodal links in spatial attention (i.e., at the short SOA with crossed hands) is consistent with recent neuropsychological findings on crossmodal interactions in brain-damaged patients suffering from suspected deficits in spatial attention. Ladavas, di Pellegrino, Farne, and Zeloni (1998) and di Pellegrino, Ladavas, and Farne(1997) studied right-hemisphere patients with left-sided extinction. These patients can detect tactile stimulation on the impaired (contralesional) left hand in isolation, but are typically unaware of the same left-hand stimulation (which is thus "extinguished" from awareness) if the right hand is touched simultaneously. Such extinction can also arise crossmodally, as when a right visual event extinguishes left-hand sensation (Mattingley, Driver, Beschin, & Robertson, 1997). Di Pellegrino et al. and Ladavas et al. recently showed that such crossmodal interactions in the patients depend on the current proximity of visual information and tactile events in external space, with postural changes thus influencing the results (see also Aglioti et al., 1999).

Recent neuroscience findings have uncovered tactile–visual–postural interactions at the single-cell level, in

several species including monkeys. Multimodal neurons responding to both visual and tactile events have been observed in various brain areas, including subcortical structures such as the superior colliculus (Groh & Sparks, 1996b; Stein & Meredith, 1993; Wallace et al., 1993) and the putamen (Graziano & Gross, 1993), and also cortical regions such as parietal (e.g., area 7b; Graziano & Gross, 1994; Hyvärinen, 1981) and premotor areas (i.e., area 6; Graziano, Yap, & Gross, 1994; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981a, Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981b). Importantly, the receptive fields of such 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 (e.g., Rizzolatti et al., 1981b). Moreover, many of these 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. Neurons of this kind might be involved in the crossmodal interactions documented here. For instance, Gross and Graziano (1995, their Figure 5) describe neurons in the premotor cortex whose visual receptive fields will even follow a crossed hand into a different visual hemifield to some extent. Intriguingly, although substantial remapping is observed in such cells, the visual receptive field tends to fall somewhat behind the hand when this is moved into a different hemifield, which could explain the somewhat reduced cuing effects found here with crossed hands.

Although convergence of information in such multimodal neurons provides one possible mechanism for generating crossmodal cuing effects, modulations arising in neural populations of this kind could also feedback to influence earlier, purely unimodal levels of the system. A tactile event might initially interface with visual coding by means of multimodal neurons that pool information across modalities; but the outcome of this interaction, rendering one particular region of space as most "salient," may then affect earlier levels via back-projections (Hahnloser, Douglas, Mahowald, & Hepp, 1999; Driver & Spence, 1998). If so, then crossmodal influences would not be restricted to multimodal structures, but might affect unimodal structures also. The latter structures would remain "unimodal" in the sense of receiving afferent input from only one modality; but would nevertheless be influenced by the spatial congruence of events in that afferent modality with immediately preceding stimulation in a "different" modality, due to attentional back-projections from multimodal areas. The present ERP data provide initial evidence consistent with such a possibility. We found that a tactile stimulus can exert an influence on subsequent visual responses as early as the N1 component, maximally at ipsilateral occipital sites. While posterior N1 is likely to consist of

functionally distinct occipital–temporal and occipital–parietal subcomponents (see Johannes et al., 1995), it has generally been assumed that all such components reflect modality-specific visual processing in the extrastriate cortex (see Mangun, 1995), yet here we find a tactile influence upon such processing.

Thus, the present N1 effects suggest that "crossmodal" links in exogenous spatial attention can actually influence "unimodal" stages of sensory processing, presumably via feedback projections from multimodal areas. Further evidence on the neural substrate of these crossmodal cuing effects could be provided by applying functional imaging measures (PET or fMRI) to the tasks introduced here, to obtain spatially fine-grained anatomical information to complement the temporally fine-grained ERP findings we have reported.

METHOD

Psychophysical Study

Participants

Twenty-four healthy volunteers (13 female, 11 male) aged 19–40 years (mean age: 25 years) participated in this study. They were paid £5 for their time, and were naïve as to the purpose of the experiment. Twenty-one participants were right-handed and three left-handed. All had normal or corrected-to-normal vision and touch (by self-report).

Stimuli and Apparatus

The experimental layout is shown in Figure 1A. Each participant sat at a table with head movements restricted by an adjustable chin rest. The room was dimly lit with sufficient light to see the experimental array and the participant's own arms.

Tactile stimulation was provided by a 2-mm-thick metal rod propelled by a 12-V solenoid. One rod was positioned next to each hand so it could firmly strike the medial surface (with hand placed prone) of the middle segment of each index finger. The hands were positioned such that the point of tactile stimulation was 530 mm from the participant's eyes and 25° to the left or right of central fixation. Visual targets were green 5 mm light-emitting diodes (LEDs) that were arranged in two vertical pairs, a pair on each side with one LED above the tactile stimulator, and the other LED below (see Figure 1A). The lights in each pair had a vertical separation of approximately 7°. Each LED pair was placed at the same visual angle as one of the tactile stimulators and 50 mm closer to the participant's eyes. The fixation stimulus was a centrally located red 2 mm LED positioned 25°–35° (according to the height of the chin rest) below eye level. The position of the right eye was monitored using a Skalar Iris 6500 infrared eye-tracker, which interfaced with the controlling computer using a

12-bit analogue–digital converter to provide online feedback. Participants were instructed to look straight ahead at the fixation light throughout the experiment. Recalibration of this device was performed prior to each block to ensure an accurate signal. Error feedback was provided by a yellow 5 mm LED placed immediately below fixation.

Each participant continuously depressed two foot pedals, placed underneath their right foot (one beneath the toes, one beneath the heel). Responses were made by a speeded release of one or other of the pedals (the toe pedal following a visual target from a higher LED; the heel pedal following a lower LED). Throughout the experiment, white noise was presented through whole-ear headphones (80 dB(A) to each ear) to mask any sounds made by the tactile stimuli or foot pedals.

A tactile cue consisted of three 50-msec strikes separated by 20 msec to one or the other index finger (total duration: 190 msec). Visual targets were the illumination of one of the four green LEDs for 100 msec. Response error feedback was provided by the illumination of the central yellow LED for 350 msec at the end of any trial in which response was either incorrect, before target onset or too slow (2,000 msec after target onset). Excessive deviation of eye position (i.e., greater than ± 3°) and blinks were signaled at trial end, and after any response error feedback, by the flashing of the same yellow LED four times (50 msec each, separated by 50 msec).

Procedure

Each participant performed six blocks of 96 trials, with 2-min rests between each block (one participant performed only four blocks). Each trial started with the illumination of the fixation light. After a variable delay (380–580 msec), a tactile cue was presented (lasting 190 msec) with equal likelihood to either the left or right index finger. Following an interstimulus interval (equi-probably 10 or 160 msec), a single visual target was presented (to give two cue–target SOAs of 200 and 350 msec). This target could unpredictably be in any of the four possible locations, thus on half the trials it was ipsilateral to the tactile cue and on the remainder it was contralateral to it. Participants were instructed to provide a speeded judgment of the target's elevation (upper vs. lower) by lifting the toes of the right foot for an upper light or the heel for a lower light. Note that the response given concerned a dimension (up vs. down) entirely orthogonal to the dimension cued (left vs. right). Note also that no relationship existed between the cued location and the likely target location or response type. Participants were informed of this and instructed simply to ignore the tactile cues. As soon as a pedal response was recorded, or if no response was made within 2,000 msec of target onset, the fixation light was extinguished and any feedback was given. There was

an intertrial interval of 400 msec before the illumination of the fixation light started the next trial.

Hand position was changed after each block. In half of the blocks participants placed their left hand on the tactile stimulator behind the left pair of target lights and their right hand on the stimulator behind the right pair of target lights (hands uncrossed). In the other half, participants crossed their arms and now placed their "right" hand behind the left targets and vice versa (hands crossed; see Figure 1A, bottom). The posture adopted for the first block was counterbalanced across participants. Prior to the start of the experimental blocks, each participant performed 50 trials as practice, adopting the posture of their first experimental block.

Following data collection, trials were removed from the analysis if they fell outside the acceptable RT range of 100–2,000 msec after target onset (less than 1% of all trials). Trials with blinks or eye movements were also excluded (a further 3% of all trials). Response errors in the up/down judgments were recorded as a percentage of remaining trials for each condition and discarded from the RT analysis.

ERP Study

Participants

Thirteen healthy volunteers, naïve as to the purpose of the experiment, were paid £12 each for their time. One was excluded because of poor eye fixation control (see below). Thus, 12 participants (seven female, five male), aged 18–41 years (mean age: 23 years) remained in the sample. Ten participants were right-handed, two were left-handed, and all had normal or corrected-to-normal vision and touch (by self-report). None had taken part in the psychophysical study.

Stimuli and Apparatus

The experimental layout is shown in Figure 1B. Each participant sat in a dimly lit experimental chamber, with head movements precluded by an adjustable chin rest. Tactile stimulators were as in the psychophysical study and again one was attached to each index finger. The hands were positioned such that the point of tactile stimulation was at a distance of 550 mm from the participant's eyes and 18° to the left or right of central fixation. Visual stimuli were presented by illuminating an ensemble of green LEDs (consisting of six 5 mm LEDs arranged in a circle, plus one central LED, see Figure 1B) placed near to a tactile stimulator on either side. This larger ensemble was used in preference to single LEDs to ensure a substantial visual ERP. Each LED ensemble was placed at the same visual angle as one of the tactile stimulators and 50 mm closer to the participant's eyes. A small black printed cross was placed centrally, level with the visual stimuli, at an angle of about 32° below

horizontal eye level, to serve as central fixation. A head-worn microphone was positioned about 2 cm in front of the mouth to record vocal responses to the rare "oddball" visual targets. White noise was presented from a central loudspeaker (at 73 dB(A), as measured from the participant's head position) throughout the experimental blocks, in order to mask any sounds made by the tactile stimulators.

Tactile cues consisted of a 10-msec strike to one or the other index finger. This short duration cue was chosen to minimize possible overlap of tactile-cue-related brain responses with visual-target-related responses (see earlier discussion of possible summation of separate brain responses, and Figure 6). We conducted an initial psychophysical pilot study using these very brief tactile cues, to confirm that they could still produce the usual spatial cuing effect on judgments for subsequent visual targets.[3] In the ERP study, visual nontarget stimuli consisted of the continuous illumination of one LED ensemble for 200 msec. For the rare visual "oddball" targets, one LED ensemble was illuminated for 90 msec, turned off for 20 msec, and illuminated again for 90 msec (total duration: 200 msec).

Procedure

The ERP experiment consisted in total of 24 experimental blocks, with a longer break period included after 12 blocks were completed. In each trial, a tactile stimulus (cue) was presented for 10 msec and was followed at an SOA of 160 or 310 msec by a visual stimulus. There was then an interval of 1,000 msec prior to the start of the next trial. Each block consisted of 72 trials. In 60 trials, a single visual nontarget (continuous LED illumination) was presented, in the remaining and randomly intermingled 12 trials, a single visual "oddball" target (interrupted LED illumination) was presented. The participant's task was to ignore the tactile cue and to provide a speeded vocal response (by saying "yes") whenever they detected an oddball visual target. Tactile cue stimuli were applied randomly and with equal probability to the left or right index finger. Visual stimuli were presented randomly and with equal probability on the left or right side. Thus, visual stimuli were equally likely at tactually cued and uncued locations. For nontarget trials, a total of 15 trials was presented in each block for each combination of side of visual stimulation (left vs. right) and spatial cuing (cued vs. uncued location). For target trials, a total of three trials were presented in each block for each of these combinations. Only ERPs for nontarget trials were analyzed to exclude any response components.

The factors of cue–target SOA (short vs. long) and hand position (uncrossed vs. crossed) were varied between blocks. The SOA condition was blocked, unlike the psychophysical session, to prevent differential ERP expectancy effects between the two SOAs in the cue–target interval (Eimer, 1993). Each participant switched between the crossed and the uncrossed position after the completion of 6 out of 12 blocks within each experimental half (i.e., between Blocks 6 and 7 and again between Blocks 18 and 19). The order in which these two postures were delivered in each experimental half was counterbalanced across participants. Within each run of six blocks where hand position was kept constant, three blocks with short SOAs and three blocks with long SOAs were delivered, resulting in a total of six blocks for each combination of hand position and cue–target SOA. The order in which short SOA and long SOA blocks were delivered within these runs of six blocks was randomized for each participant individually.

Participants were instructed to respond as quickly and accurately as possible to visual oddballs and to maintain central eye fixation throughout the blocks (monitored with EOG). To familiarize them with the specific task requirements, one or two training blocks were run prior to the beginning of the first uncrossed and crossed experimental blocks.

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). Horizontal EOG was recorded bipolarly from the outer canthus of each eye. The impedance for the EOG electrodes was kept below 10 kΩ and for all other electrodes below 5 kΩ. The amplifier bandpass was 0.1 to 40 Hz. EEG and EOG were sampled with a digitization rate of 200 Hz and stored on disk.

EEG and EOG were epoched off-line into 800-msec periods starting 100 msec prior to and ending 700 msec after the onset of the tactile stimulus. Only EEG epochs obtained for nontarget trials were further analyzed. Trials with blinks (VEOG exceeding ± 60 mV relative to 100 msec prestimulus baseline), horizontal eye movements (HEOG exceeding ± 30 mV relative to baseline; approximately equal to ± 2.5°; Mangun & Hillyard, 1991), other artifacts (a voltage exceeding ± 60 mV at any electrode location relative to baseline), or vocal responses recorded on nontarget trials, were excluded from analysis. This resulted in the exclusion of 20.2% of all trials. The EEG to nontarget stimuli was averaged separately for all combinations of hand position (crossed vs. uncrossed), cue–target SOA (short vs. long), spatial cuing (cued vs. uncued location), and side of visual stimulus (left vs. right), resulting in 16 ERP waveforms for each participant and electrode site. After averaging, HEOG waveforms were scored for systematic deviations of eye position, indicating residual tendencies to move the eyes to the location of cue or target stimuli. One participant was excluded because the maximal residual HEOG deviation exceeded ± 2 mV.

Acknowledgments

Notes

1. Miyauchi, Hikosaka, Shimojo, and Okamura (1993) made a similar proposal based on preliminary ERP data cited only in abstract form; to our knowledge their study has never been published in full.
2. It should be noted that early somatosensory components (N80, N140) were larger with uncrossed hands than when the hands were crossed. This can be seen in Figures 4 and 5 at Fz and Cz, and was also present at the lateral central electrodes. However, since this difference between hand postures was present in cued as well as uncued trials, it cannot account for the reversal of attentional cuing effects on visual ERPs (in terms of which hand advantages which visual field) resulting from crossing the hands.
3. We ran a pilot psychophysical study, to confirm that the brief 10-msec tactile cues used in the ERP study were able to produce crossmodal cuing effects, similar to those obtained in the psychophysical study described in full in the main text. This pilot study used a speeded up/down visual discrimination task (as in the main psychophysical experiment), with spatially nonpredictive 10-msec tactile cues (exactly as used in the ERP experiment) being presented unpredictably to the left or right index finger of five new subjects, with hands in an uncrossed posture. Subsequent target lights could appear at any of four positions (two elevations on each side of central fixation, close to the possible stimulated positions on the left and right hands) after a cue–target SOA varying randomly between 160 and 310 msec. Compliance with instructions to maintain central fixation was verified using an infrared eye tracker. Visual up/down judgments were faster and more accurate on the same versus opposite side of central fixation as the preceding tactile cue (mean inverse efficiency measures were 395 msec for the cued side, 416 msec for the uncued side) leading to a significant effect of cuing [$t(4) = 2.3, p = .04$, (one-tailed)].

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