Research report

Influence of gaze direction on crossmodal modulation of visual ERPS by endogenous tactile spatial attention

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Abstract

Recent evidence indicates that the spatial direction of endogenous covert spatial attention in one sensory modality can crossmodally influence early processing of stimuli in a different modality. However, spatial locations are initially coded according to different frames of reference for different modalities (e.g., body-centered for touch versus retinocentric vision) and postural changes (e.g., gaze shifts) will realign these. Here, we used event-related potentials (ERPs) to investigate how the direction of endogenous tactile attention affects sensory-specific visual ERP components. Critically, by manipulating direction of gaze, we were able to test whether any crossmodal effects depend on visual and tactile projections to a common hemisphere, on common locations in external space, or on some combination of the two. We found that both P1 and N1 visual components were modulated according to the direction of endogenous tactile attention. While the P1 crossmodal effect followed purely hemispheric constraints, the attentional modulation of N1 appeared to combine both anatomical and external spatial constraints.
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1. Introduction

Our sensory systems are continuously stimulated by multiple events in the external world, with the brain having to select just the currently relevant information among this input to guide behavior and achieve current goals. The neural substrates underlying selection of spatial locations have been studied extensively both in animals (e.g., [5,25,41]) and in humans (e.g., [20,21,28]). The majority of human studies have focussed on visual modality, demonstrating modulation of brain activity in occipital visual areas that represent the currently attended location (e.g., [28]). These modulatory effects have been observed using both electrophysiological methods such as event-related potentials (ERPs) and hemodynamic methods such as functional magnetic resonance imaging (fMRI). These methodologies have produced converging results, indicating that selective spatial attention can modulate visual processing at relatively early stages. Electrophysiological studies demonstrated attentional modulation of visual potentials as early as 100 ms post-stimulus onset (e.g., [20]), while neuroimaging studies have reported modulation of brain activity even in the primary visual cortex [3,28,37].

More recently, research on spatial attention has considered the selection of spatial locations across different sensory modalities [9,10]. Behavioral studies first demonstrated crossmodal links in endogenous spatial attention (e.g., [38,39]). For example, Spence and Driver [38] showed that directing attention to one side while expecting targets in one

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modality resulted in better judgement for targets at the attended side, not only for the expected modality, but also for other modalities. Electrophysiological and neuroimaging studies have revealed increased brain activity for stimuli presented at the attended location, even when these are in a task-irrelevant modality (e.g., [16,26]). These crossmodal effects have been found to affect not only relatively late processing stages (presumably corresponding to activation of multimodal areas in the brain), but also to affect relatively early stages that are thought to reflect processing in sensory-specific areas [16,26,29].

The observations that crossmodal spatial interactions can affect sensory-specific processes open new important questions. Spatial representations in different sensory modalities initially utilize different coordinate systems. Neurons in the visual cortex code spatial locations in relation to retinal positions (e.g., [40]), while in the somatosensory cortex locations are coded in body-centered coordinates (e.g., [32]). This raises the question of how information concerning the direction of spatial attention in one modality can get mapped onto brain regions that use a different coordinate system. Moreover, it should be noted that the different receptor systems (e.g., the eyes for vision and the hands for touch) can move independently, as happens frequently in daily life, leading to continuous realignments between them in space.

At least two different possible mechanisms might underlie some of the spatially-specific crossmodal attention effects that have been observed to date. One simple possibility concerns hemispheric mapping, whereby spatial information concerning one modality may be directly relayed to brain areas within the same hemisphere that process input of different modalities. Such an account based on anatomical hemispheres could fit with some traditional models of spatial attention based on hemispheric competition (e.g., [23]). Accordingly, crossmodal spatial interactions in attention may arise because of common anatomical projections for different sensory modalities to the same hemisphere. A different possibility is that postural information (e.g., gaze direction, arm position, etc...) may also be taken into account, so that crossmodal effects of spatial attention are determined primarily by the relative position of stimuli from different modalities in external space (e.g., see [1,15,27]). Note that these two hypothetical mechanisms are not mutually exclusive, and some combination of them could also be implemented neuronally. Here we addressed these issues by studying how gaze-posture might influence cross-modal effects of endogenous tactile attention upon visual ERPs.

We measured ERPs to tactile and visual stimuli, when subjects directed covert tactile attention either to the left or to the right hand. The use of task-irrelevant visual stimuli allowed us to investigate how the direction of tactile attention (attend left hand versus attend right hand) might crossmodally affect processing of visual input. Critically, in separate blocks, the task was performed with gaze directed toward different positions: center, leftward, or rightward (see Fig. 1). During the central gaze conditions, task-irrelevant visual stimuli were delivered either in close spatial proximity to the left hand or in proximity to the right hand (see Fig. 1B, positions 2 and 3). Comparing ERPs to visual stimuli presented near to the attended versus unattended hand should reveal any spatial crossmodal effect of endogenous tactile attention on visual processing. For central gaze (as used in all previous ERP studies of any crossmodal effects from endogenous tactile spatial attention upon visual ERPs, see [10] for review), hemispheric and external space mappings are aligned, with retinally left visual stimuli presented near to the left hand in external space (and also projecting to a common contralateral right hemisphere), and retinally right visual stimuli presented near to the right hand (and both projecting to the left hemisphere). In contrast, when gaze was diverted leftward or rightward, the two mapping systems considered are no longer aligned. By shifting the 'external' position of possible visual stimuli along with changes of gaze direction (and thus keeping the retinal locations of these visual stimuli equivalent; see Fig. 1), retinally left visual stimuli could now be presented near to the right hand (i.e., stimuli at position 3 during rightward gaze, see Fig. 1C), and retinally right visual stimuli could be presented near the left hand (i.e., stimuli at position 2 during leftward gaze, see Fig. 1A).

If crossmodal effects from endogenous tactile spatial attention upon visual ERPs follow a purely hemispheric mapping, "attend left hand" conditions should always boost ERP responses to retinally left visual stimuli (position 3 during rightward gaze; Fig. 1C) and "attend right hand" conditions should always boost responses to retinally right visual stimuli (position 2 during leftward gaze; Fig. 1A). In contrast, if crossmodal effects follow an external space mapping, "attend left hand" conditions should boost ERP responses to retinally right visual stimuli during leftward gaze (visual stimuli position 2; Fig. 1A), given that these are at the same external location as the left hand. Analogously, "attend right hand" conditions should boost responses to retinally left visual stimuli during rightward gaze (visual stimuli position 3; Fig. 1C), given that these are at the same external location as the right hand. Our manipulation of gaze direction can thus be used to determine whether crossmodal spatial effects of endogenous tactile attention on visual ERPs follow a strictly hemispheric mapping (common hemispheric projections) or an external space mapping (common position in external space), or some combination thereof.

2. Methods

2.1. Participants

Twelve volunteers participated. All were right-handed (7 females and 5 males), with a mean age of 24 years (range 19–32). After receiving an explanation of the procedures,
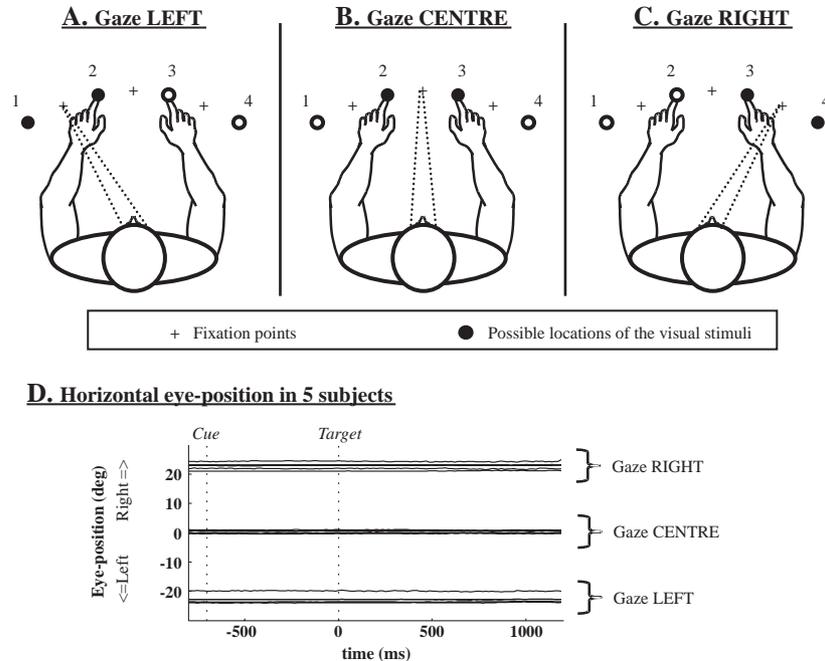
Fig. 1. Schematic depiction of possible stimulus positions and gaze directions relative to the subject's head/body. Fixation was maintained either to the left (panel A of the figure), to the center (panel B), or to the right (panel C) of the head/body midline. While the position of the arms (and thus of the tactile stimuli) was maintained constant irrespective of direction of gaze, the position of possible visual stimulation was shifted along with the current direction of gaze so that the same two retinal locations could be stimulated visually. During leftward fixation, visual stimuli could be presented at either position 1 or position 2 (see filled circles in panel A); during central fixation at either position 2 or position 3 (see panel B); and during rightward fixation at either position 3 or position 4 (see panel C). This allowed us to present visual stimuli at equivalent retinal locations across different gaze directions, while critically presenting these same retinal visual stimuli in spatial correspondence with either the left or the right hand. For example, left retinal stimulations were in close spatial proximity with the left hand during central gaze (position 2 in B), but were in spatial proximity to the right hand during rightward gaze (position 3 in C). Panel D shows the horizontal eye position with respect of the head/body mid-line for 5 subjects, for whom reliable infrared eye position data were available throughout the ERP sessions. The plot indicates that all subjects adhered to the instructions, maintaining fixation either to the right (five traces at the top of the plot), to the center (five traces at the center), or to the left (five traces at the bottom of the plot) of the head/body mid-line.

subjects gave written informed consent. The study was approved by the Ethics Committee of the School of Psychology, Birkbeck College.

2.2. Paradigm

We used a 2 × 2 × 2 × 3 factorial design to investigate how the current direction of gaze may affect modulations by endogenous tactile spatial attention of early somatosensory potentials, and critically also any crossmodal effects of tactile attention on visual ERPs. Thus, one factor was the direction of gaze (center, left, or right from the body/head midline, see Fig. 1A–C). The second factor was the direction of endogenous tactile spatial attention (attend left hand or attend right hand). The third factor was the modality of the single peripheral stimulation (visual or tactile) on any trial. The fourth factor was the side of this stimulation (left or right hand for touch; and left or right retinal hemifield for vision, with the external positions of the visual stimuli being shifted along with the current direction of gaze to maintain the same possible retinal stimulations, see Fig. 1A–C).

On each trial, subjects covertly attended to the left or the right hand to perform a tactile discrimination (short versus long tactile pulse) for stimulation on that hand only, if this

occurred, while ignoring any of the other possible forms of stimulation (i.e., touch on the other hand, or visual stimulation of either retinal hemifield). Vocal responses (quickly saying "yes") had to be made only to short pulses at the attended hand. All other type of stimulations (i.e., long tactile pulses, short pulses at the unattended hand, and all visual stimuli) did not require any response. Only ERPs to long tactile pulses or to task-irrelevant visual stimulations were analyzed (see below) to avoid contamination of ERPs by response execution.

The modality of the stimulation, the side of the stimulation, and the direction of tactile attention were randomized and unpredictable on a trial-by-trial basis. The direction of tactile attention was cued symbolically on each trial using pure tones presented over headphones. Direction of gaze changed only between acquisition blocks, being maintained centrally, leftward or rightward throughout a given block. Before the start of each block, subjects were instructed verbally about the gaze direction that they had to maintain. This was monitored on-line with a video camera equipped with infrared illumination. Quantitative infrared data about eye position were available for 5 subjects. For these subjects, average horizontal eye positions as a function of task instruction are shown in Fig. 1D. The plot

demonstrates that these subjects complied with the instructions, maintaining fixation either to the right, to the center, or to the left of the head/body mid-line.

2.3. Stimuli and task

Subjects sat in a dimly lit room, with the forearm and hands resting on wooden supports on each side (left and right of the head/body midline). Because of the dim illumination in the room, the subjects could see their hands and forearms. To ensure that subjects shifted gaze rather than rotating the head or the body, the subject's head was restrained in a straight-ahead posture using a chin rest with additional clamps tightened at the level of the cheekbones. Three LEDs marked the possible fixation positions. One was located centrally with respect to the head/body midline. The other two LEDs were 22° to the left or right of the head/body midline (marked as "+" in Fig. 1A–C). These LEDs were always visible in the dim background illumination throughout the experiment, and they were never on or off transiently. Peripheral visual stimulation in one or other retinal hemifield was delivered by one or another of 4 LED clusters (2 LEDs per cluster), placed at four equidistant locations (position 1 to 4 in Fig. 1). Thus, for each of the possible three gaze directions, there were two LED clusters (11° to the left or to the right of the current fixation point) that could be used to deliver task-irrelevant visual stimulation for that particular gaze direction. Fig. 1 shows that LED clusters in position 1 and 2 were used during leftward gaze (Fig. 1A), clusters in position 2 and 3 were used during central fixation (Fig. 1B), and clusters 3 and 4 during rightward gaze (Fig. 1C). Note that the LED clusters in positions 2 and 3 were in close proximity in external space to the left and right index fingers, respectively.

Below each index finger there was a piezoelectric component (T220-H3BS-304, Piezo Systems Inc., Cambridge, USA) to deliver tactile stimulation. A sharp plastic tip was attached to each piezoelectric bender. When the bender was activated, it produced a vibration with a maximum amplitude of 1 mm, with the plastic tip conveying the vibration to the finger. This resulted in tactile stimulations well above threshold. The tactile stimuli consisted of long (100 ms) or short (40 ms) unseen vibrations to the index finger (vibration frequency = 130 Hz). Short pulses at the currently attended hand served as imperative targets, requiring vocal responses. All visual stimuli consisted of 100 ms flashes of one of the LED clusters. Note that visual stimuli were delivered only from two possible positions during each acquisition block (left and right of the current gaze direction, see filled circles in Fig. 1A–C).

Each trial began with the presentation of a 250 ms auditory cue (pure tone 500 or 1500 Hz) that instructed the subject to attend either the left or right hand. The association between tone frequency and direction of tactile attention was counterbalanced across subjects. After 550 ms, either a tactile or a visual stimulus was presented. Irrespective of gaze direction, the subject's task was to judge tactile stimuli at the attended hand and to respond if a short pulse was delivered to that hand only. All other stimuli (long tactile pulses at the attended hand, a pulse of any duration on the currently irrelevant hand, or any visual stimulation) did not require any response. The inter-trial interval was 2.1 s.

Each subject underwent 18 acquisition blocks (6 for each gaze direction, counterbalanced within and across subjects), lasting approx. 3 min each. During each block, a total of 92 trials were presented, with conditions randomly intermingled. For 52 trials, the stimulus was a tactile pulse. For 40 of these trials, the tactile pulse was long (10 attended left, 10 attended right, 10 unattended left and 10 unattended right), while for the remaining 12 trials, the tactile pulse was short. Of these 12 short pulses, 8 were delivered to the attended hand (4 left and 4 right), thus requiring vocal responses. The remaining 4 short pulses (2 left and 2 right) were delivered to the unattended hand. These did not require any vocal response but they allowed us to check that subjects did indeed interpret the auditory cues to direct tactile attention to the left or to the right hand.

During the remaining 40 trials of the same acquisition block, a task-irrelevant visual stimulus was presented instead of a tactile stimulus. This visual stimulus was presented 11° to the left (20 trials) or the right (20 trials) of the current fixation. For each visual hemifield stimulated, 10 trials followed "attend left hand" cues and 10 followed "attend right hand" cues. Note that depending on the current direction of gaze, left retinal stimulation could be presented in spatial correspondence with either the left hand (position 2, central gaze; see Fig. 1B) or with the right hand instead (position 3, rightward gaze; see Fig. 1C). Analogously, right retinal stimulation could be presented at the same external location as the right hand (position 3, central gaze; see Fig. 1B) or as the left hand (position 2, leftward gaze; see Fig. 1A).

2.4. EEG recording and data analysis

EEG was recorded with Ag–AgCl electrodes and linked earlobe reference from 23 scalp electrodes. Horizontal EOG was recorded bipolarly from the outer canthi of both eyes (though note that eye position was also monitored with an infrared tracker; see above and Fig. 1D). Electrode impedance was kept below 5 kΩ, amplifier band-pass was 0.1–40 Hz, and digitization rate was 200 Hz. The filtering parameters were chosen according to previous work on the modulation of early ERPs by crossmodal attention [12,13,16]. No additional filters were applied to the EEG data, and all ERP analyses were based on these unfiltered data.

EEG and EOG were epoched off-line into 1500 ms periods, starting 100 ms prior to cue onset, and ending 600 ms after the onset of a peripheral stimulus. Trials where horizontal eye movements (HEOG exceeding ±30 μV relative to baseline, corresponding to approx. 3° of visual angle) were detected throughout this period were excluded from analysis. Likewise, trials with eyeblinks (Fpz exceed-

ing ± 60 μV relative to baseline), or other artifacts (a voltage exceeding ± 60 μV at any electrode location relative to baseline) obtained in 600 ms interval following the onset of a peripheral tactile or visual stimulus were excluded from analysis. The minimum number of trials accepted for ERP averaging was 15. Across all subjects and trial types, the mean number of trials used for averaging was 44.7, and the mode was 52 trials, on a possible maximum of 60 trials (i.e., when no trial was excluded).

ERPs to long tactile pulses (requiring no overt response) and to all visual stimuli (also requiring no overt response) were separately averaged relative to a 100 ms pre-stimulus baseline for all conditions (24 trial sub-types obtained by crossing the 4 factors: modality [with 2 levels] × side [2 levels] × attended hand [2 levels] × gaze [3 levels]). For each participant, ERP mean amplitudes were computed for somatosensory components (P100: 100–125 ms; N140: 155–185 ms) and early visual components (P1: 125–150 ms; N1: 165–185 ms), as identified in the grand averages. The selection of these early components was motivated by previous data showing crossmodal influences of endogenous tactile spatial attention on these early, sensory-specific components (e.g., [12]). Because we considered only these pre-selected time intervals and did not perform any running ANOVA on the ERP traces, statistical *P* values did not require correction for multiple comparisons.

Statistical analyses tested three specific experimental questions for particular components at specific electrode sites, where crossmodal attention effects were predicted (see also Fig. 5 for summary data for all electrode sites).

2.4.1. Any effect of gaze direction on the modulation of early somatosensory components by tactile spatial attention

For this we examined ERPs to long tactile stimuli, at central sites (C3 and C4), where somatosensory evoked potentials (SEPs) are more pronounced. SEPs were computed separately for electrodes contralateral and ipsilateral to the side of tactile stimulation. Repeated-measures ANOVAs assessed the effect of tactile spatial attention, direction of gaze, and possible interactions between these. These were carried out separately for contralateral and ipsilateral electrodes, and for the two temporal windows of interest (P100: 100–125 ms; N140: 155–185 ms). Greenhouse–Geisser correction for non-sphericity was applied when necessary.

2.4.2. Crossmodal modulation of early visual components by tactile spatial attention with central gaze

Here we examined ERPs to task-irrelevant visual stimuli during central gaze. Note that only during central gaze were the external locations of the hands and the visual stimuli perfectly aligned. Contralateral and ipsilateral responses were computed at occipital sites (OL and OR) and parietal sites (P3 and P4). Paired *t* tests were used to determine whether the direction of tactile spatial attention modulated visual responses in two windows of interest (P1: 125–150 ms; N1:

165–185 ms). Significance levels (*P* values) were assigned according to the hypothesis that stimuli at the attended location should elicit larger responses than stimuli at the unattended location (1-tailed *t* tests), as predicted on the basis of previous research (see [12]).

2.4.3. Effect of the direction of tactile attention on processing of visual stimuli with deviated gaze

To examine the spatial nature of crossmodal influences of endogenous tactile spatial attention on visual responses, we directly compared two hypotheses: hemispheric projections versus external space. This was done by comparing responses to visual stimuli at position 2 during leftward gaze, following "attend left hand" versus "attend right hand" cues (and similarly responses to visual stimuli in position 3, during rightward gaze). If crossmodal effects follow an external space mapping, it is predicted that responses to right retinal stimulations during leftward gaze (position 2) should be larger for attend left than attend right cues. This prediction arises because this right retinal visual stimulus is then at the same external location as the left hand (see Fig. 1A). Alternatively, if crossmodal effects are determined by the initial hemispheric projections, the responses to visual stimuli at position 2 during leftward gaze should be larger for attend right conditions than attend left conditions, given that position 2 is now a right retinal stimulation. Analogous predictions hold for visual stimuli presented at position 3 during rightward gaze. Again, contralateral and ipsilateral responses were computed at occipital (OL and OR) and parietal (P3 and P4) sites. Paired *t* tests were used to directly compare the two critical hypotheses (hemispheric-projection versus external space) in two windows of interest (P1: 125–150 ms; N1: 165–185 ms). Significant levels (*P* values) were assigned using 2-tailed *t* tests, given that opposing predictions could be motivated on this particular issue.

3. Results

3.1. Behavioral performance

Subjects correctly detected 82% of the short tactile pulses (targets) presented to the cued hand that should currently be attended, with no significant difference between central gaze (83%) and deviated gaze (81%). Critically, subjects correctly rejected 98% of the short tactile pulses presented at the unattended hand, indicating that the symbolic auditory cues were indeed used to direct spatial tactile attention. In addition, subjects incorrectly responded to long tactile stimulation ("false alarms") on only 1% of the trials. For technical reasons, accurate vocal reaction times were not available, but note that since the task required vocal responses to be made only for short tactile stimuli on the currently cued hand, accuracy (and in particular any false alarms to short tactile stimuli on the wrong hand) is the relevant index for assessing whether participants followed

instructions and directed endogenous tactile attention to the instructed hand.

3.2. Somatosensory evoked potentials (SEPs)

Fig. 2 shows somatosensory evoked potentials at central sites in response to long tactile stimuli that received no overt response. Separate SEPs are presented according to whether the stimulus was delivered to the currently attended hand (solid lines) or to the currently unattended hand (dashed lines) and also according to the current direction of gaze. The SEPs are further divided into contralateral (panels A, C and E in Fig. 2) and ipsilateral responses (panels B, D, and F in Fig. 2). At contralateral sites, the waveforms were characterized by four deflections (labeled as P45, P80, P100, N140, e.g., see Fig. 2C), while at ipsilateral sites only the latter two deflections were clearly distinguishable (compare top and bottom panels in Fig. 2). The direction of tactile attention appeared to affect the amplitude of both P100 and N140 components (as previously found by [14]). This was assessed formally with separate ANOVAs for the two SEP components and the two electrode placements (contralateral and ipsilateral to the stimulus position). This revealed significant

main effects of attention at both contralateral ($F(1,11) =$ 5.890, $P < 0.034$) and ipsilateral ($F(1,11) = 5.964$, $P < 0.033$) electrodes for the P100. For the N140, large attentional effects were found at ipsilateral electrodes ($F(1,11) =$ 21.303, $P < 0.001$), while contralateral electrodes showed only a moderate trend ($F(1,11) = 3.393$, $P < 0.093$). These attentional effects on SEPs did not interact with current gaze direction, neither at contralateral nor at ipsilateral sites, and neither for P100 nor N140 components (minimum P value = 0.566, for contralateral P100). This indicates that the current direction of gaze did not affect the modulation of early somatosensory components by endogenous tactile spatial attention.

3.3. Crossmodal effects of tactile attention on early visual evoked potentials: central gaze

Next we assessed whether the direction of endogenous tactile attention affected processing of visual input during central gaze (as previously found in [13]). Note that for this gaze direction, visual stimuli in left or right retinal hemifields were delivered in close spatial correspondence with the left or right hand, respectively, with anatomical and
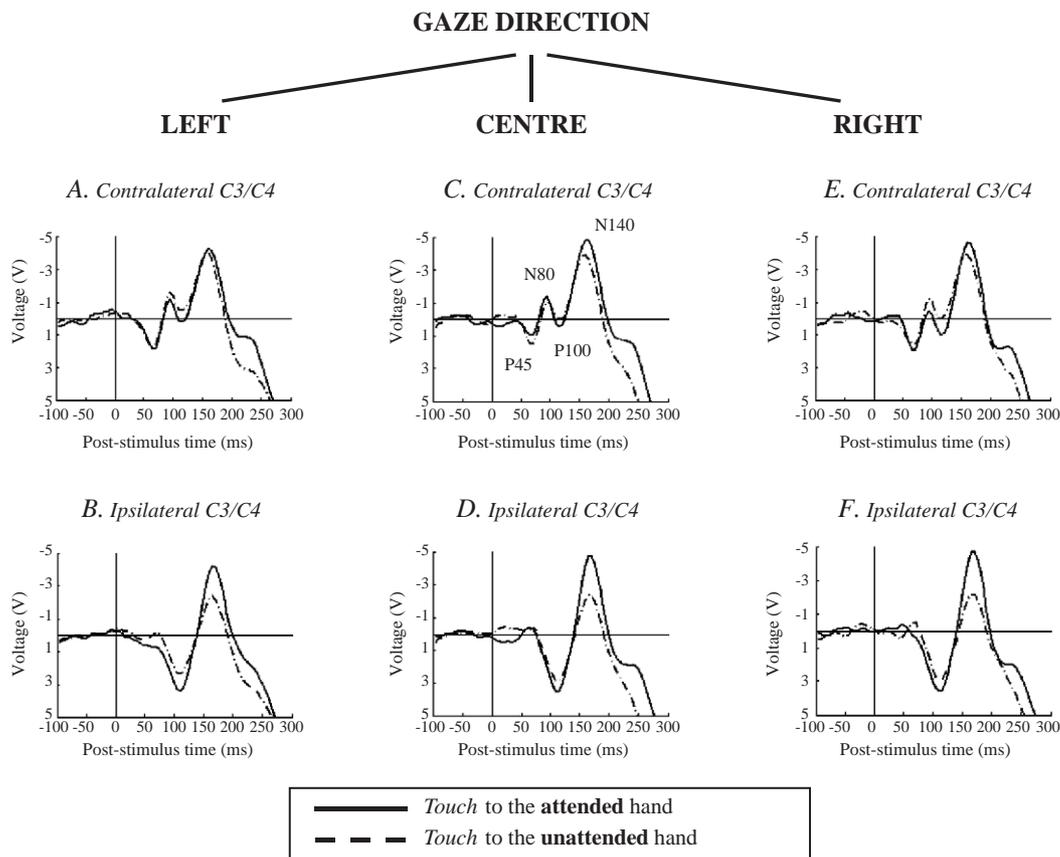
Fig. 2. Somatosensory evoked potentials: unimodal effects of endogenous tactile spatial attention. Somatosensory evoked potentials at central sites, contralateral (A, C, and E) and ipsilateral (B, D and F) to the stimulated hand. SEPs are divided according to whether the stimulus was delivered to the currently attended hand (solid lines) or the unattended hand (dashed lines), and also according to the current direction of gaze (left, central or right, shown in separate columns here). Significant unimodal effects of tactile spatial attention on somatosensory potentials were observed for both the somatosensory P100 (100–125 ms) and N140 (155–185 ms) components. These effects were not influenced by the direction of gaze.

external space reference frames thus aligned (see Fig. 1B). Fig. 3 shows ERPs to task-irrelevant visual stimuli according to the direction of endogenous tactile attention during central gaze. Again ERP traces are separated according to whether the stimulus was contralateral or ipsilateral to the relevant electrode (contralateral: panels A and C; ipsilateral: panels B and D). The P1 visual component was particularly pronounced at occipital electrodes (see Fig. 3A and B), while the later N1 component was larger at parietal sites (see Fig. 3C and D).

Direct comparisons of visual ERPs for stimuli presented near the currently attended hand versus near the unattended hand demonstrated crossmodal attentional modulation of both P1 and N1 visual components by endogenous tactile attention. Significant modulation of P1 was observed at ipsilateral occipital electrodes ($T(11) = 2.872$, $P < 0.008$ 1-tailed; see Fig. 3B). N1 modulation was maximal at

contralateral electrodes, with significant effects detected both at parietal ($T(11) = 2.454$, $P < 0.016$ 1-tailed) and occipital ($T(11) = 2.127$, $P < 0.029$ 1-tailed) sites. Thus, here we replicate previous findings that the direction of endogenous tactile spatial attention can affect processing of visual input ([13]). In particular, we show that task-irrelevant visual stimuli presented near the currently attended hand elicited larger P1 and N1 components (sensory-specific visual ERPs) compared with the same stimuli when presented near the unattended hand.

3.4. Spatial nature of crossmodal effects: visual ERPs influenced by tactile attention during deviated gaze

The critical new question for the present experiment concerned the spatial nature of crossmodal spatial interactions between touch and vision. By shifting gaze direction to one or the other side we were able to dissociate anatomical versus external space co-ordinate systems (cf. Fig. 1). Examining responses to visual stimuli at position 2 (with leftward gaze) and position 3 (with rightward gaze) allowed us to test whether directing attention to one hand boosts responses to visual stimuli projecting to the same hemisphere as the attended hand, or it boosts stimuli at the external position corresponding to the location of the attended hand. Note that because we always compared attention to one hand versus attention to the other hand directly, if both types of mapping were equally influential, then any effect of tactile spatial attention should be abolished given that the two mappings lead to opposite predictions.

Fig. 4 shows average visual ERPs for right retinal stimulations during leftward gaze (position 2 in Fig. 1A) and left retinal stimulations during rightward gaze (position 3 in Fig. 1C) as a function of which hand was currently attended for the tactile task. For each graph, the ERPs are averaged considering either the anatomical, same-hemisphere mapping (solid lines), or the external space mapping (dashed lines) of any spatial attentional effect (see also Fig. 5, where these averages are presented for all recorded sites). For example, for stimuli in position 2 during leftward gaze (see Fig. 1), the hemispheric mapping considers ERPs during "attend right hand" trials (this is a right retinal position), while the external space mapping considers "attend left hand" trials (these stimuli are at the same external position as the left hand). Analogously for stimuli in position 3 during rightward gaze, the hemispheric mapping considers ERPs during "attend left hand" trials (these are left retinal stimulations), while the external space mapping considers "attend right hand" trials (these stimuli are at the same external position as the right hand).

The visual P1 component showed an effect of hemispheric versus external space mapping. Right retinal stimulations during leftward gaze (position 2 in Fig. 1A) elicited larger P1 responses after "attend right hand" cues than after "attend left hand" cues, despite these visual stimuli being at the same external location as the left hand (see Fig.

Occipital Electrodes   **Parietal Electrodes**

Fig. 3. Visual evoked potentials: crossmodal effects with central gaze. This figure shows the ERPs in response to task-irrelevant visual stimuli, divided according to whether the stimulus was presented at the same location as the cued hand (solid lines) or at the opposite hand instead (dashed lines). The data shown here concern only trials with central gaze, when anatomical and external space frames of reference were aligned (i.e., left retinal stimulations presented near to the left hand, and right visual retinal stimulations near to the right hand, see also Fig. 1B). Separate ERPs are presented for scalp sites contralateral (A and C) or ipsilateral (B and D) to the visual hemifield that was stimulated. The results indicate that both visual P1 (125–150 ms) and N1 (165–185 ms) amplitudes were affected by the current direction of tactile attention, with larger amplitudes for visual stimuli presented near the currently attended hand. The P1 crossmodal effect was larger at ipsilateral occipital sites (see panel B), while the N1 effect was larger at contralateral parietal sites (see panel C). (*$P < 0.05$, 1-tailed).

Occipital Electrodes   **Parietal Electrodes**

A. Contralateral OL/OR   *C. Contralateral P3/P4*

B. Ipsilateral OL/OR   *D. Ipsilateral P3/P4*

—————— *Vision* projecting to the **same hemisphere** as the attended hand

– – – – *Vision* at the **same external** location as the attended hand

Fig. 4. Visual evoked potentials: crossmodal effects of tactile spatial attention with deviated gaze. Averaged ERPs in response to task-irrelevant visual stimuli at positions 2 and 3 when gaze was deviated to the left or right, respectively (cf. Figs. 1A and 1C). Separate ERPs are presented for scalp-sites contralateral (A and C) or ipsilateral (B and D) to the stimulated visual hemifield. Here the attentional effects are coded following either hemispheric projection or external space mapping. Hemispheric mapping would imply larger deflections for left retinal stimulations (position 3 during rightward gaze) under "attend left hand" conditions and for right retinal stimulations (position 2 during leftward gaze) under "attend right hand" conditions. By contrast, an external space mapping predicts larger deflections for left retinal stimulations (position 3 during rightward gaze) under "attend right hand" condition (as the visual stimulus is then at the same external location as the right hand, see Fig. 1C). Analogously, larger deflections for right retinal stimulation (position 2 during leftward gaze) should be found for "attend left hand" conditions (as this visual stimulus is then at the same external location as the left hand, see Fig. 1C). The data indicate that the P1 component followed a hemispheric mapping for the crossmodal spatial effects (e.g., see panel A), with larger deflections always observed for left retinal stimulation under "attend left hand" conditions (even though left retinal stimuli now appeared at the same external location as the right hand), and for right retinal stimulation under "attend right hand" conditions (even though right retinal stimuli now appeared at the same external location as the left hand). Interestingly, the N1 crossmodal attentional effect was abolished for diverted gaze (e.g., see panels C and D, and compare with the N1 attention effect with central gaze in Fig. 3), consistent with this particular visual component being jointly affected by both hemispheric projections and external location.

1A). Analogously, left retinal stimulations during rightward gaze (position 3 in Fig. 1C) elicited larger P1 responses for "attend left hand" trials than for "attend right hand" trials, despite these stimuli being at the same external location as the right hand. These effects are shown in Fig. 4, where

traces corresponding to the hemispheric mapping (solid lines) demonstrate larger P1 deflections than traces corresponding to the external space mapping (dashed lines). Statistically significant effects were observed at both contralateral occipital sites ($T(11) = 2.490$, $P < 0.030$ 2-tailed; see Fig. 4A) and contralateral parietal sites ($T(11) = 2.347$, $P < 0.039$ 2-tailed; see Fig. 4C). This indicates that these early visual components are affected primarily by the hemispheric correspondence of the attended hand and visual hemifield, more so than by the relative location of the hands and any visual stimulation in external space.

Unlike the attentional effects on P1, the ERP averages for hemispheric and external space mapping for the later N1 component largely overlapped (minimum P value = 0.508, at ipsilateral occipital sites), indicating that on average this component was unaffected by the direction of tactile attention, when gaze was diverted. At contralateral parietal sites (the site of maximal crossmodal influences on N1 during central gaze, see Fig. 3C), we formally assessed the modulatory influence of gaze direction on the visual N1 attentional effect (due to which hand was attended for the tactile task). We tested for an interaction between attended side (left or right hand) and gaze direction (central or diverted) for stimuli presented in positions 2 and 3. This confirmed that gaze direction modulates crossmodal influences of endogenous tactile attention on N1 visual components ($T(11) = 1.3$, $P < 0.05$ 1-tailed), indicating a reduction of this crossmodal effect when gaze was diverted (unlike the outcome for the earlier P1 component). As noted above, such a reduction of the crossmodal attentional effect during diverted gaze (as for the N1 component) might be due to the fact that both hemispheric and external space mappings concurrently influence this component.

4. Discussion

The present study manipulated the direction of gaze while subjects covertly attended to the left or to the right hand to perform a somatosensory discrimination task. To study the effect of endogenous tactile spatial attention on visual processing, on some trials task-irrelevant visual stimuli were presented instead of any tactile stimulus. Critically, the manipulation of gaze direction allowed us to assess whether any crossmodal effects of endogenous tactile attention upon visual ERPs follow a hemispheric or an external space mapping (or some combination).

We found that both P1 and N1 visual components were modulated according to the direction of endogenous tactile spatial attention (see also [12]). While this crossmodal modulation of the P1 visual component followed a purely hemispheric mapping, the modulation of N1 appeared to combine both hemispheric and external space information, with the deviated-gaze conditions eliminating the N1 attention effect as compared with central gaze, a result which did not apply for the earlier P1 component.

Contralateral   *Mid-line*   *Ipsilateral*
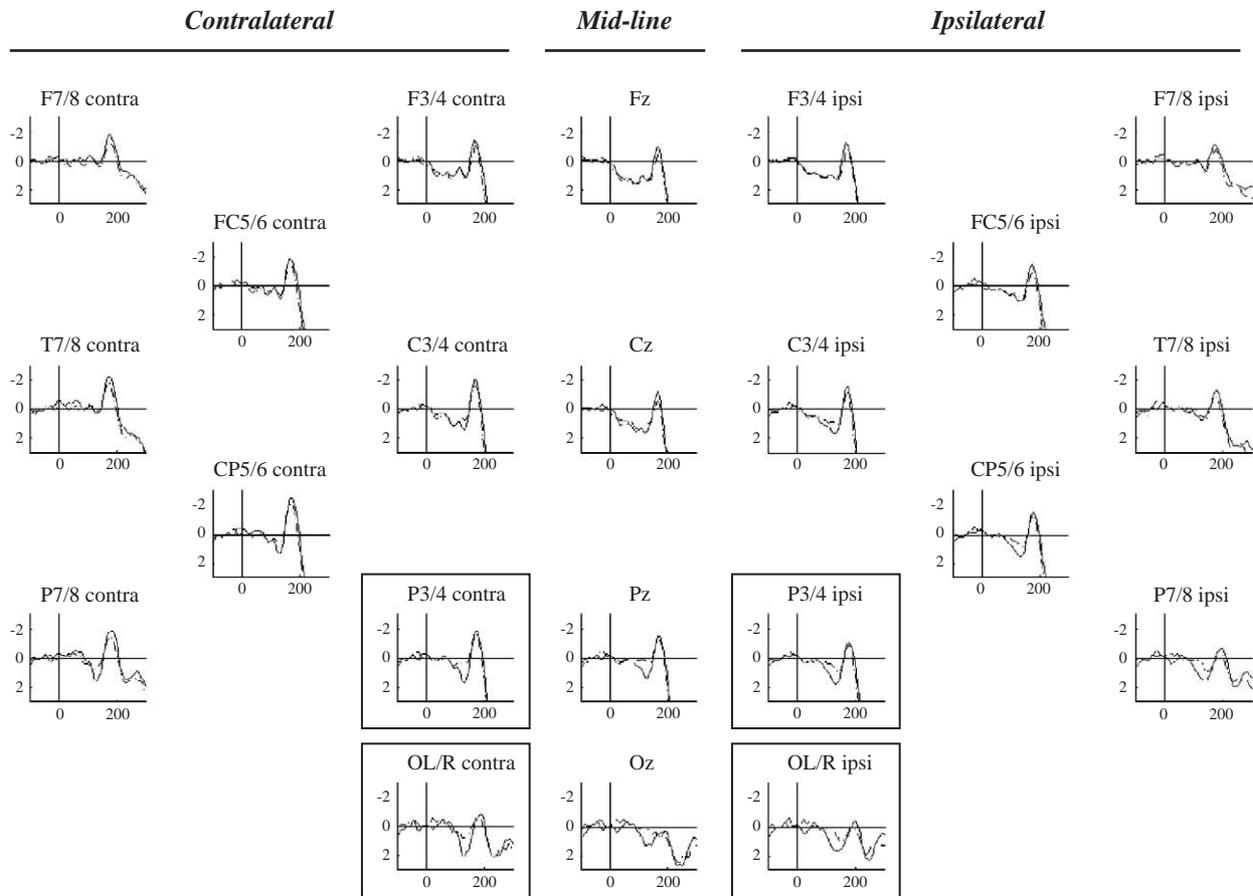
Fig. 5. Direct comparison of hemispheric mapping (solid lines) versus external space mapping (dotted lines) during diverted gaze, for all recording sites. Separate visual ERPs are presented for scalp sites contralateral (plots on the left the this figure), ipsilateral (plots on the right), and midline (center) electrodes. The larger differences were observed at contralateral occipital sites in correspondence of the P1 deflection (see also Fig. 4A). At no scalp site or time window, the external space mapping showed larger deflections than the hemispheric mapping. The boxes highlight the plots reported in Fig. 4. Post-stimulus time in ms, voltage in μV.

In agreement with previous crossmodal ERP studies (e.g., [13]), the direction of tactile spatial attention was found to influence the amplitude of sensory-specific visual components. During central gaze, we observed significant crossmodal effects in two latency windows that were identified as P1 (125–150 ms) and N1 (165–185 ms). While crossmodal modulation of the N1 component by spatial attention has been widely reported in previous studies [13,15,22], crossmodal effects on earlier positive deflections have been more elusive [15,22]. Here we observed significant P1 modulation at ipsilateral occipital electrodes, but trends in the same direction were present also at contralateral sides. The relatively late onset of this component (see Fig. 3A and 3B) might relate to the relatively weak peripheral visual stimuli (11 degrees of eccentricity) and scalp summation of ERPs for several cortical sources (e.g., activation of both ventral and dorsal extrastriate areas for our stimuli that were located on the horizontal meridian). Maximal N1 modulations were found at parietal sites, suggesting a parietal source as one probable generator [8]. The present data with central gaze support the general proposal that crossmodal links in spatial attention do

not only arise because of sensory convergence to multi-modal brain regions, but that instead spatial attention to one modality can influence processing of stimuli in a different modality, at relatively early stages [10,16,26,29], as found here for the P1 component.

While both P1 and N1 visual components were modulated according to the direction of tactile attention during central gaze, diverting gaze away from the central body/head midline had different consequences for the P1 and N1 crossmodal effects. Remarkably, the P1 crossmodal modulation appeared to follow a purely hemispheric mapping, with "attend left hand" conditions always boosting responses to retinally left stimuli, and "attend right hand" conditions always boosting responses to retinally right stimuli (see Fig. 4 and 5). This occurred even though retinally left stimuli were actually located near to the right than left hand in external space during rightward gaze, while retinally right stimuli were in closer spatial proximity to the left hand during leftward gaze. This remarkable outcome appears to disagree with a recent report that endogenous crossmodal spatial effects of tactile endogenous attention upon visual ERPs may always relate to locations in external

space [15]. However, there is an important difference between the present study and Eimer et al.'s experiments [15]. Here we manipulated postural information regarding gaze direction (and thus eye-in-orbit posture), while in the previous Eimer et al. study [15] the postural manipulation consisted of crossing the arms while maintaining central fixation. Note that when the arms are crossed, there is a mismatch not only between hand-centered tactile represen-tations and retinocentric visual representations, but also between tactile representations and any head/body-centered representation of space. When the arms are crossed, the right hand is not only in the left visual hemifield but also in the left hemispace relative to the body. Thus, when somatotopic and head/body-centered representations of space are made incongruent (as when the arms are crossed), somatotopic influences upon vision get re-mapped and crossmodal effects of touch upon vision are observed for visual stimuli at the same external location as the attended hand [15]. However, in the absence of any mismatch between somatotopic and head/body-centered representations (as in the present study, where left and right hands always remained located on the left and right side of the body, respectively), such re-mapping does not arise or is incomplete. In this case crossmodal visuo-tactile effects are primarily determined by hemispheric projections, at least for relatively early visual responses such as the P1 component.

The present finding of purely hemispheric mapping for the early P1 visual component accords with recent proposals that some crossmodal influences on sensory-specific pro-cessing might occur via direct intra-hemispheric projections between unimodal brain areas [17,35]. For example, direct projections from primary auditory areas to regions of the primary visual cortex that represent peripheral locations have been demonstrated in non-human primates [17]. Another pathway that has been put forward as possible anatomical substrate to generate crossmodal responses in relatively early sensory-specific cortices would involve sub-cortical structure (e.g., [19]). Any such influence would presumably not account for subtle changes in posture, and thus could fit with the P1 data presented here. Finally, such hemispheric effects also appear in accord with the more general proposal that the direction of spatial attention can be determined by the relative level of activation of the two hemispheres [23]. Accordingly, directing tactile attention toward one hand should result in the generation of an overall activity bias in favor of the contralateral hemisphere. This should in turn boost also the processing of visual stimuli presented to the same hemisphere.

It is also important to note that, unlike the P1 component, which was found here to be modulated exclusively according to hemispheric mapping when gaze was deviated, the later N1 deflection showed a different outcome. Direct comparison of attentional crossmodal influences with respect to hemispheric versus external space mapping revealed no difference for this component. This suggests

that for the N1 component both hemispheric (e.g., retinal) and eye position signals may be combined to represent spatial locations in an intermediate frame of reference (cf. [33]). Moreover, further analyses confirmed that the amplitude of crossmodal influences on N1 was reliably modulated according to gaze direction, with an N1 attention effect being found under central gaze but eliminated with deviated gaze, consistent with opposing influences of hemispheric and external space mapping in the deviated case. Combined influences of hemispheric projections and of external location would be consistent with the modu-latory effect of eye position now observed in many occipital and parietal areas, both at the single-neuron level in primates [4,6,34,36] and at population level as measured by neuroimaging techniques in humans [7,30]. Given previous reports that some crossmodal effects can com-pletely re-map to reflect solely the position of the stimuli in external space [15,22,27], we also examined ERPs recorded at frontal and temporal sites (see Fig. 5). However, this did not reveal any statistically significant crossmodal effect that would be consistent with a purely external space mapping in the present data set. A possible reason for this might be that we analyzed sensory evoked-potentials associated with the peripheral targets (rather than any cue-related activity that could possibly relate to strategic processes), producing primarily activation at posterior sites.

It should be noted that in the present study subjects could see their hands throughout the ERP recording session. It is therefore possible that visual information might have been used to "tag" the position of the hands in space. However, previous single-cell work in monkeys (e.g., [18]) and fMRI in humans [27] indicate that vision of the hands is not critical for crossmodal re-mapping, suggesting instead a role for extra-retinal information about current posture (presum-ably via proprioception) in modulating spatial interactions between touch and vision. More generally, it is difficult to exclude any contribution of visual attention and/or visual working memory in the present task (e.g., see [2]), because the interpretation of the auditory cue and the shift of tactile attention toward the cued location were under voluntary control of the subject (endogenous attention). It is in principle possible that when instructed to attend to one or to the other hand, subjects shifted visual attention as well as tactile attention, if these are considered as independent attentional processes ([31], but see also [11]). Thus, in this context, the different effect of gaze direction on crossmodal modulation of P1 and N1 could be attributed to a different influence of visual attention on these components [24]. Future studies might explicitly manipulate how visual attention is deployed during a primarily tactile task, investigating the role of visuo-spatial attention during tactile covert spatial orienting (see also [38]).

In addition to crossmodal effects of tactile endogenous spatial attention upon visual ERPs, we also examined any within-modality effects on somatosensory evoked potential (SEPs). We found attentional modulation of P100 and N140

SEP. These somatosensory effects were uninfluenced by current gaze direction (see Fig. 2).

In conclusion, we showed here that the direction of endogenous tactile spatial attention can crossmodally influence the amplitude of both P1 and N1 visual components. Manipulation of gaze direction, and thus of the alignment of visual and somatosensory spatial representations, revealed that crossmodal attentional modulations of the visual P1 component were determined exclusively by hemispheric projections. This suggests that the direction of tactile spatial attention can influence not only somatosensory but also visual sensory-specific representations due to purely hemispheric constraints. In addition, we found that the later visual N1 component combined both hemispheric and external spatial constraints, demonstrating that endogenous spatial attention produces crossmodal effects that have a different spatial nature at different levels of visual processing.

Acknowledgments

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