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Viewing the body modulates neural mechanisms underlying sustained spatial attention in touch

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Abstract

Cross-modal links between vision and touch have been extensively shown with a variety of paradigms. The present event-related potential (ERP) study aimed to clarify whether neural mechanisms underlying sustained tactile-spatial attention may be modulated by visual input, and the sight of the stimulated body part (i.e. hands) in particular. Participants covertly attended to one of their hands throughout a block to detect infrequent tactile target stimuli at that hand while ignoring tactile targets at the unattended hand, and all tactile non-targets. In different blocks, participants performed this task under three viewing conditions: full vision; hands covered from view; and blindfolded. When the participants' hands were visible attention was found to modulate somatosensory ERPs at early latencies (i.e. in the time range of the somatosensory P100 and the N140 components), as well as at later time intervals, from 200 ms after stimulus onset. By contrast, when participants were blindfolded and, crucially, even when only their hands were not visible, attentional modulations were found to arise only at later intervals (i.e. from 200 ms post-stimulus), while earlier somatosensory components were not affected by spatial attention. The behavioural results tallied with these electrophysiological findings, showing faster response times to tactile targets under the full vision condition compared with conditions when participants' hands were covered, and when participants were blindfolded. The results from this study provide the first evidence of the profound impact of vision on mechanisms underlying sustained tactile-spatial attention, which is enhanced by the sight of the body parts (i.e. hands).

Introduction

When we expect to receive a touch on a certain part of our body, we may focus attention on that location, and we may also feel compelled to look at this body part. Covertly directing attention to a location on the body enhances tactile perception at that location (e.g. see Johansen-Berg & Lloyd, 2000; Spence & Gallace, 2007 for reviews). Likewise, increasing evidence has shown that also viewing one's own body improves tactile detection and discrimination in healthy subjects (e.g. Tipper *et al.*, 1998; Kennett *et al.*, 2001; Press *et al.*, 2004) and in brain-damaged patients with somatosensory deficits (Serino *et al.*, 2007), as well as it enhances cortical tactile processing (Taylor-Clark *et al.*, 2002). Furthermore, one positron emission tomography (PET) study has shown that vision can modulate mechanisms underlying sustained covert spatial attention in touch (Macaluso *et al.*, 2000). Macaluso and colleagues reported that when participants had their eyes open and their hands were visible throughout the task, covertly attending to one of their hands resulted in greater activity within the postcentral gyrus, corresponding to secondary somatosensory cortex (SII), and within the intraparietal sulcus (IPS), a region involved in spatial representation across modalities, in response to tactile stimuli

delivered to that hand compared with the other, unattended, hand. By contrast, when participants performed the tactile task with their eyes closed, attentional modulations were only present within the SII, but not in the IPS. This finding suggests that the IPS may be involved in the visual modulation of covert tactile-spatial attention, in line with the view that the highly accurate spatial information vision provides (Rock & Victor, 1964; Eimer, 2004) may facilitate the spatial selection of tactile locations. From Macaluso *et al.*'s (2000) study it is not clear, however, whether it is ambient visual-spatial information or, specifically, the sight of the stimulated body parts (i.e. hands) that plays a crucial role in modulating sustained tactile-spatial attention.

The present study was designed to investigate systematically whether different levels of visual input, namely ambient visual-spatial information and vision of the hands, influence spatial attentional modulations at different stages of somatosensory processing. Electrophysiological studies have consistently reported that sustained tactile-spatial attention modulates somatosensory event-related potentials (ERPs) from early latencies, with greater ERP amplitudes for tactile stimuli at attended relative to unattended locations (e.g. Eimer & Forster, 2003; Zopf *et al.*, 2004). However, no previous ERP study has investigated at which stages of processing the mechanisms underlying covert spatial attention in touch can be modulated by vision.

In line with Macaluso *et al.*'s (2000) findings, we predicted that when visual-spatial information and vision of the hands are available

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to observers, attentional modulations of somatosensory ERPs would occur earlier than in the absence of visual input, that is, when participants are blindfolded. Moreover, we expected that attentional modulations would occur earlier under conditions when participants' hands are visible compared with when these are hidden from view, if vision of the hands has a specific role in modulating attentional effects during tactile-spatial selection.

Materials and methods

Fifteen paid volunteers took part in the experiment. Three had to be excluded for an excess of alpha waves. Thus, 12 participants (five males and seven females), aged between 21 and 38 years (average age: 28.4 years) remained in the sample. All participants were right-handed; and all had normal or corrected-to-normal vision by self-report. All participants gave their written informed consent prior to testing. The experiment was approved by the Ethics Committee, City University London, and was conducted in accordance with the Declaration of Helsinki.

Participants sat in a dimly lit, sound-attenuated experimental chamber. Two small boxes ($3 \times 5 \times 3$ cm), each having one tactile stimulator embedded in its surface, were located on a table in front of the participants, at a distance of about 40 cm from the participants' body. Participants' index fingers were placed on top of each tactile stimulator at a distance of 40 cm from each other, equidistant to the left and right of the participants' midline. On each trial one tactile stimulus was delivered; tactile stimulation was provided using 12-V solenoids (M & E Solve, Rochester, UK; <http://www.me-solve.co.uk>) driving a metal rod with a blunt conical tip to the top segment of the index finger making contact with the finger whenever a current was passed through the solenoid. Tactile non-target stimuli consisted of the rod contacting the participants' index finger for 200 ms (Fig. 1), and were perceived as single taps. Tactile target stimuli were infrequent, and were composed in the same way except that the contact was interrupted for 4 ms halfway through the presentation (Fig. 1); these were perceived as double taps. Tactile stimuli were delivered after 300 ms from the beginning of each trial. From the stimulus onset, participants had 1200 ms to respond. The inter-trial interval before the start of the next trial was randomly set between 200 and 600 ms (see Fig. 1 for a schematic representation of the sequence of events). The software E-Prime (Psychology Software Tools, Pittsburgh, PA, USA; <http://www.psnet.com>) was used for sending trigger signals to the tactile stimulators, for recording response accuracy and latency, and

for sending markers to the electroencephalogram (EEG) recording system (see below).

Each participant completed three experimental conditions. In all three conditions, participants were required to attend either to their left or right hand, in alternating blocks, and to respond to all tactile target stimuli at that hand. The three experimental conditions differed with respect to the viewing condition under which participants performed the task: in the 'Full vision' condition visual-spatial information about the environment as well as the sight of the participants' hands and their forearms were available; in the 'Covered hands' condition only ambient visual-spatial information was available, while the participants' hands as well as their arms were covered and hidden from view; and in the 'Blindfolded' condition participants were blindfolded, and therefore neither ambient visual-spatial information nor vision of the hands and arms was available.

In the 'Full vision' and 'Covered hands' conditions, participants were instructed to keep their gaze on a small white fixation square (0.8 cm^2) drawn on a panel at about the participants' eyes level, positioned at a distance of 75 cm from their body. In the 'Blindfolded' condition participants were instructed to keep their eyes open under the blindfold throughout the experiment, and to keep their gaze straight ahead. White noise (50 dB, measured from the position of the participant's head) was presented from two loudspeakers placed at 110 cm from the participants' head and equidistant to the right and left of the midline, to mask any sounds made by the tactile stimulators. Participants responded to tactile target stimuli by pressing a pedal with either their right or left foot. Half of the participants used their right foot and the other half used their left foot: the foot they had to use to give their responses was assigned at the beginning of the experimental session and was kept constant throughout the three experimental conditions.

At the start of the experimental session, and before an electrodes cap was mounted on their head, participants carried out a pre-experimental block of 48 trials to ensure they could discriminate the tactile stimuli that they would receive during the experiments. Participants had to respond to all tactile target stimuli ('double taps') while ignoring tactile non-target stimuli ('single taps'). Tactile targets were delivered in a random order on half of the trials (i.e. 24 trials) with equal probability to the right and the left hand. Participants started the experimental session only when their accuracy in the pre-test was 75% or above. The data of the pre-experimental blocks were not analysed further. Following the pre-test, each participant completed the experimental conditions 'Full vision', 'Covered hands' and

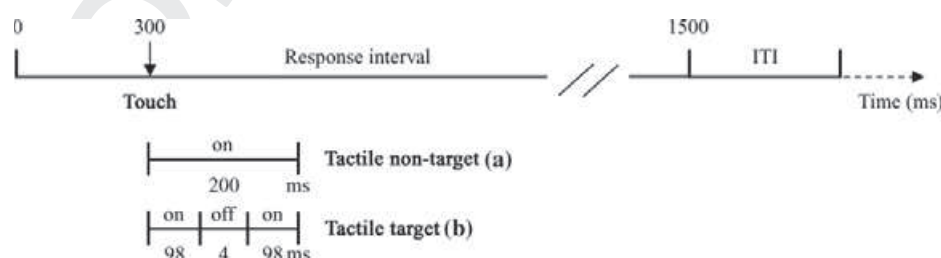


FIG. 1. Schematic representation of the sequence of events. In each trial, a tactile stimulus was delivered after 300 ms from the beginning of the trial, and lasted for 200 ms. Participants had 1200 ms to respond from stimulus onset. The inter-trial interval (ITI) before the start of the next trial was randomly set between 200 and 600 ms. An example of tactile non-target (a) and target (b) stimulus is shown in the figure. Tactile non-targets consisted of the metal rod of a solenoid contacting the participants' index finger ('on') for 200 ms. In each experimental block, 40 tactile non-target stimuli were delivered to the participants' right hand and 40 to the left hand. Tactile targets consisted of the metal rod contacting the participants' index finger for 98 ms ('on'), followed by a 4-ms interval in which this contact was interrupted ('off'), after which the rod contacted the participants' finger again for 98 ms ('on'). In each experimental block, eight tactile target stimuli were delivered to the participants' right hand and eight to the left hand.

'Blindfolded' in counterbalanced order. Each experimental condition consisted of six blocks of 96 trials each. Before the start of each block participants were instructed to attend either to their right or left hand throughout the block in order to respond to infrequent targets ('double taps') at the attended hand. Half of the participants attended to their right hand in the first block of each experimental condition, then to the left hand in the second block, and so on; the other half of participants attended to their left hand first. Eight valid tactile targets (i.e. tactile target stimuli delivered to the attended hand that required a foot response) and eight invalid tactile targets (i.e. target stimuli on the unattended hand that had to be ignored) were delivered in each block. Valid and invalid tactile targets were presented with equal probability to the right or left hand. The remaining 80 trials were non-target trials, which were randomly presented with equal probability to the right and left hand, and required no response.

EEG was recorded from the participants' scalp during each of the three experimental conditions using BRAINVISION recording system (BrainAmp amplifier and BrainVision Recorder software, version 1.02; Brain Products GmbH, Gilching, Germany; <http://www.brainproducts.com>). EEG was recorded with Ag-AgCl electrodes from 28 scalp electrodes (midline electrodes: Fz, Fcz, Cz, Pz; electrodes over the right hemisphere: Fp2, F4, F8, Fc2, Fc6, C4, T8, Cp2, Cp6, P4, P8, O2 and the homologous electrode sites over the left hemisphere). Horizontal electrooculogram (HEOG) was

recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 5 k Ω . EEG and EOG were sampled with a 500-Hz digitization rate. EEG data were analysed using BrainVision Analyzer software (version 1.05; Brain Products GmbH, Gilching, Germany). EEG and EOG were epoched off-line into 700-ms periods, starting 100 ms before and ending 600 ms after the onset of tactile stimuli. ERPs for tactile non-target stimuli were averaged relative to a 100-ms pre-stimulus baseline. Trials with eye blinks (Fp1 or Fp2 exceeding $\pm 60 \mu\text{V}$ relative to baseline), horizontal movements (HEOG exceeding $\pm 30 \mu\text{V}$ relative to baseline, approximately equal to $\pm 2.5^\circ$ of visual angle; see Mangun & Hillyard, 1991) or other artefacts (a voltage exceeding $\pm 60 \mu\text{V}$ relative to baseline at electrodes F4, F8, Fc2, Fc6, C4, Cp2, Cp6, P4, P8, and at homologous electrode sites over the left hemisphere) measured within 600 ms after stimulus onset were excluded from analysis. ERP analysis was restricted to non-target trials only, to avoid contamination of averaged ERPs by movement-related artefacts.

To investigate the effects of tactile-spatial attention on somatosensory ERPs, statistical analyses (repeated-measures ANOVAs) were conducted for recording sites over somatosensory areas, as well as over frontal and parietal areas that are thought to be involved in spatial attention control mechanisms (F3, F4, Fc1, Fc2, Fc5, Fc6, C3, C4, Cp1, Cp2, P3 and P4). ERP mean amplitudes were computed within

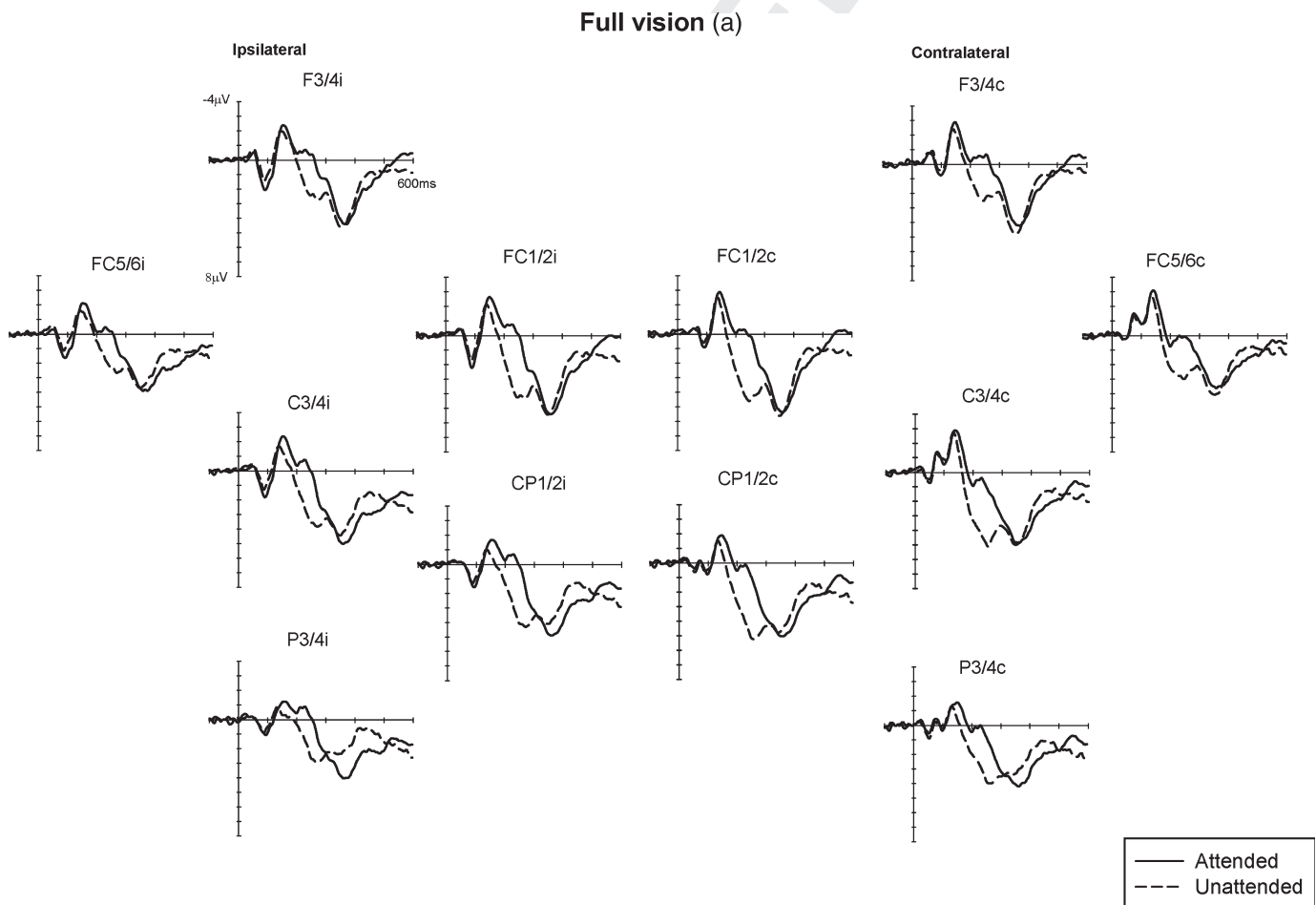


FIG. 2. Grand-averaged somatosensory ERP waveforms elicited in the viewing conditions 'Full vision' (a), 'Covered hands' (b) and 'Blindfolded' (c) in the 600-ms interval following stimulus onset by tactile non-target stimuli at attended (solid lines) and unattended (dashed lines) locations. Somatosensory ERPs are shown for electrodes contralateral (right side of each panel) and ipsilateral (left side) to the site of tactile stimulation.

successive measurement windows centred on the latencies of early somatosensory ERP components: P100 (75–120 ms after stimuli onset) and N140 (135–180 ms after stimuli onset). Mean amplitudes were also computed for the time interval between 200 and 300 ms post-stimulus in order to investigate longer-latency attentional effects.

To investigate effects of tactile-spatial attention on ERPs, separate repeated-measures ANOVAs for the time windows specified above were carried out with the factors: viewing condition ('Full vision' vs. 'Covered hands' vs. 'Blindfolded'); attention (attended vs. unattended); electrode (see above); site (frontal, including F3, F4, Fc1, Fc2, Fc5 and Fc6 vs. centro-parietal, including C3, C4, Cp1, Cp2, P3 and P4); and hemisphere (contralateral vs. ipsilateral to the stimulated hand). To investigate effects of tactile-spatial attention on response speed to tactile target stimuli, a repeated-measures ANOVA was performed on mean reaction times (RTs) to valid tactile targets between the three viewing conditions ('Full vision', 'Covered hands' 'Blindfolded'). Where Mauchly's test indicated violation of sphericity ($P < 0.05$), we verified repeated-measures results with Greenhouse–Geisser adjustments to the degrees of freedom. SPSS for Windows (version 15.0) was used for statistical analysis.

Results

Behavioural data

Participants missed on average $< 1.5\%$ of tactile target stimuli, and there was no significant difference between the percentages of missed

tactile targets between experimental conditions. The rate of false alarms to non-target stimuli was on average below 2%. Trials in which the RTs exceeded ± 2 standard deviations from the mean RT were discarded (leading to the removal of 1.8% of the trials overall).

Participants' RTs to infrequent valid tactile target stimuli were on average 21 ms faster under the 'Full vision' condition (mean = 521.6 ms) compared with the 'Covered hands' condition (mean = 542.6 ms), and 35.3 ms faster compared with the 'Blindfolded' condition (mean = 557 ms). A significant effect of viewing condition was obtained in a repeated-measures ANOVA comparing mean RTs to tactile targets under the three viewing conditions ($F_{1,22} = 8.27$; $P = 0.002$; $\epsilon = 0.761$). Follow-up pair comparisons revealed a reliable difference between 'Full vision' and 'Covered hands' conditions ($t_{1,11} = 2.85$; $P = 0.016$, two-tailed), and between 'Full vision' and 'Blindfolded' conditions ($t_{1,11} = 3.80$; $P = 0.003$, two-tailed), confirming that participants were faster at responding to tactile targets when full visual information was provided compared with when participants' hands were hidden from view or no visual input was available to participants. Although responses were on average 15.6 ms faster in the 'Covered hands' than in the 'Blindfolded' condition, this difference was not reliable ($t_{1,11} = 0.94$; $P = 0.23$, two-tailed).

Spatial attentional modulations of somatosensory ERPs

Figure 2 shows ERPs elicited by tactile stimuli delivered to the attended (solid lines) and the unattended (dashed lines) hand at

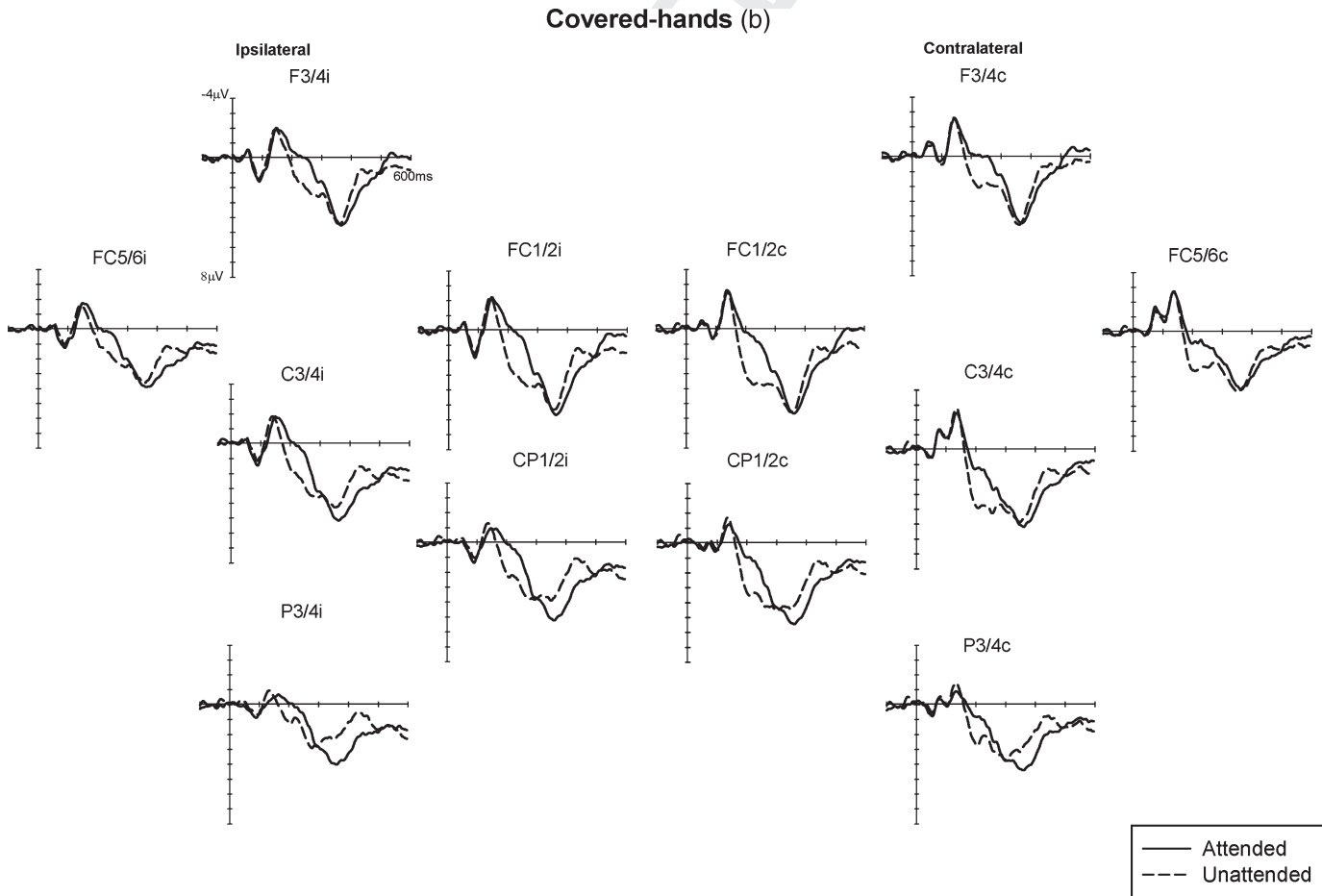


FIG. 2. Continued.

electrodes contralateral (c; right side of each panel) and ipsilateral (I; left side) to the stimulated hand at frontal, central and parietal sites. In Fig. 2A ERP waveforms are displayed for tactile stimuli delivered in the 'Full vision' condition; in Fig. 2B waveforms are shown for the 'Covered hands' condition; and in Fig. 2C for the 'Blindfolded' condition. As can be seen from these waveforms, somatosensory ERPs were modulated by tactile-spatial attention, as reflected by greater amplitudes for ERPs in response to tactile stimuli at the attended relative to the unattended hand. However, spatial attentional modulations appear to be present at different time intervals in the three viewing conditions. In particular, while a sustained negativity was elicited at late time intervals (i.e. beyond 200 ms post-stimulus) by attended-hand compared with unattended-hand stimuli in all three viewing conditions, earlier somatosensory components appear to be modulated by attention in the 'Full vision' condition but not in the other two conditions; although in the 'Covered hands' condition, attentional modulations at frontal, but not at parietal, sites may appear to occur somewhat earlier than 200 ms post-stimulus. These differences in the time course of attentional ERP modulations in the three viewing conditions are further illustrated in Fig. 3. These waveforms were obtained by subtracting ERPs in response to tactile stimuli presented at attended locations from ERPs elicited by tactile stimuli at unattended locations, in each of the three viewing conditions. Difference waveforms are shown for the 'Full vision' (black solid lines), the 'Covered hands' (black dashed lines) and the 'Blindfolded' (grey solid lines) conditions at electrodes contralateral (C; right side of each panel) and ipsilateral (I; left side) to the stimulated hand at

frontal, central and parietal sites. From these difference waveforms, it can be seen that attentional modulations of somatosensory ERPs occurred earlier and were enhanced in the 'Full vision' condition compared with the other two viewing conditions, i.e. 'Covered hands' and 'Blindfolded'.

These informal observations were substantiated by statistical analyses. In the P100 time range (75–120 ms post-stimulus) an attention $\times$ viewing condition $\times$ hemisphere interaction was present ($F_{2,22} = 4.71$; $P = 0.020$; $\epsilon = 0.691$). Follow-up analyses, separate for each viewing condition, revealed a significant attention $\times$ hemisphere interaction for the 'Full vision' condition ($F_{1,11} = 29.26$; $P = 0.001$), indicating that attention effects were present at ipsilateral ($F_{1,11} = 6.13$; $P = 0.031$) but not at contralateral electrodes ($P = 0.29$). No main effects of attention or interactions involving the factor attention were obtained in the analyses carried out for the 'Covered hands' and the 'Blindfolded' conditions (all $P > 0.13$). In the time window of the subsequent N140 component (135–180 ms post-stimulus) a condition $\times$ attention interaction was obtained ($F_{1,22} = 4.92$; $P = 0.023$; $\epsilon = 0.704$). Follow-up analyses for each condition showed in the 'Full vision' condition a main effect of attention ($F_{1,11} = 8.02$; $P = 0.016$) and an attention $\times$ hemisphere interaction ($F_{1,11} = 5.89$; $P = 0.033$), with *post hoc* analyses confirming the presence of attentional modulations at contralateral electrodes ($F_{1,11} = 11.73$; $P = 0.006$) and revealing effects close to significance at ipsilateral electrodes ($F_{1,11} = 4.73$; $P = 0.052$). In the 'Covered hands' and the 'Blindfolded' conditions no main effects of attention or interactions involving the factor attention were obtained

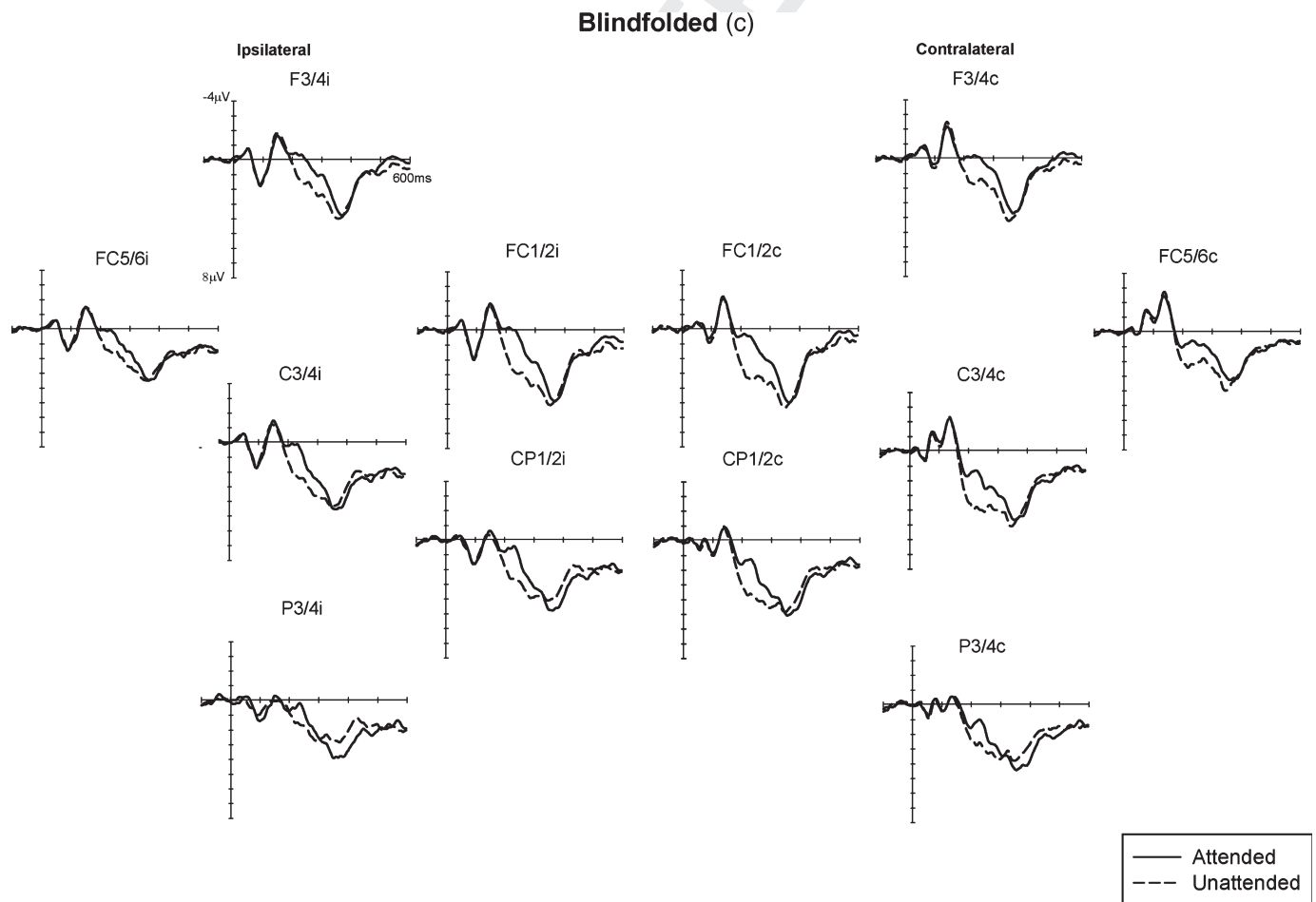


FIG. 2. Continued.

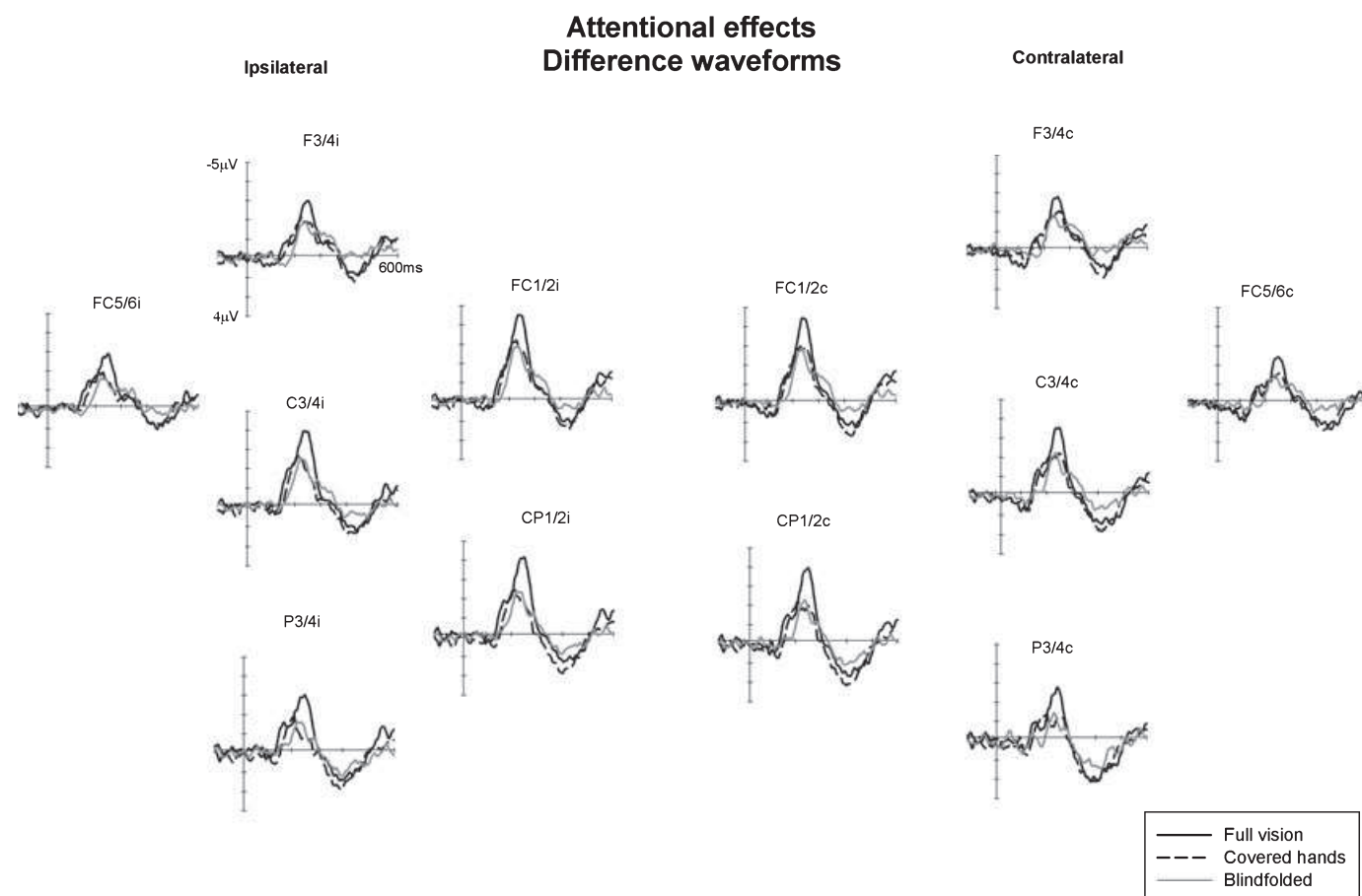


FIG. 3. Difference ERP waveforms obtained by subtracting ERPs in response to tactile non-target stimuli at attended and unattended locations during the 600-ms interval following stimulus onset, in the experimental conditions 'Full vision' (black solid lines), 'Covered hands' (black dashed lines) and 'Blindfolded' (grey solid lines).

in the same time range (all $P > 0.15$). In particular, no interaction between attention and site was found in the 'Covered hand' condition, indicating that no reliable attention effects were present at frontal electrode sites. For the following time window (200–300 ms post-stimulus), a main effect of attention was found ($F_{1,22} = 15.87$; $P = 0.002$; $\epsilon = 0.895$), indicating that in the late time interval spatial attention modulations were present for all three viewing conditions. This was confirmed by separate analyses for each condition (all $F > 5.15$; all $P < 0.05$). An attention $\times$ hemisphere interaction was also obtained in the overall analysis for the same time window ($F_{1,11} = 8.10$; $P = 0.016$), and follow-up analyses revealed a main effect of attention for both contralateral ($F_{1,11} = 18.08$; $P = 0.001$) and ipsilateral electrodes ($F_{1,11} = 13.64$; $P = 0.004$).

Discussion

The aim of the present ERP study was to investigate whether vision modulates mechanisms underlying sustained covert spatial attention to tactile stimuli. In particular, we aimed to clarify whether different levels of visual input (ambient visual-spatial information vs. the sight of the hands) modulate neural mechanisms of spatial attentional selection at different stages of somatosensory processing. For this purpose, participants performed a tactile attention task under three viewing conditions: full vision; with hands covered from view; and

blindfolded. The task required observers to attend to one of the hands throughout a block while maintaining central fixation, in order to detect all tactile target stimuli among non-target stimuli at the currently attended hand.

We found that when participants' hands were visible, attentional ERP modulations occurred earlier compared with when no visual input was given, that is, when participants were blindfolded and, crucially, also compared with when participants' hands were hidden from view and only ambient visual-spatial information was provided. In particular, when full visual information was available, attentional modulations of somatosensory ERPs were found in the time range of the P100 component and of the subsequent N140 component, followed by a sustained negativity for tactile stimuli delivered at attended compared with unattended locations. By contrast, in the other two viewing conditions attentional effects only emerged at later time intervals, about 200 ms after the onset of tactile stimuli, with a sustained negativity for attended compared with unattended stimuli. In addition, the behavioural results were in line with these ERP findings, showing shorter response latencies to tactile target stimuli at the attended hand under full vision condition compared with conditions when the hands were not visible, or when participants were blindfolded.

Taken together, the results from the present study show that vision of the body can influence the mechanisms underlying attentional selection within the somatosensory modality. These results are in line with those of a recent PET study (Macaluso *et al.*, 2000), which

showed that the presence of visual input increased activity related to sustained tactile-spatial attention within the IPS, a brain region involved in spatial representation and attention across modalities. Importantly, in that study participants performed a tactile attention task with their eyes open and closed, in different blocks; therefore, the visual modulations of tactile attention effects found by Macaluso and colleagues could be attributed to either the availability of ambient visual-spatial information or to the sight of the hands in particular, or both. The present study shows for the first time that seeing one's own body (i.e. the hands) while covertly attending to specific locations on its surface is a crucial factor in facilitating sustained attentional processes within the somatosensory modality.

Furthermore, our findings demonstrate that visual information about the hands affects sustained tactile-spatial attention at early stages of processing, as early somatosensory ERP components (namely the P100 and the N140) were found to be modulated by attention under full visual input. These particular somatosensory components have been shown to originate in secondary somatosensory areas (SII; Hari *et al.*, 1984; Frot & Mauguière, 1999). This is in contrast to Macaluso *et al.*'s (2000) study, where visual modulations of tactile attention effects were only observed in multimodal intraparietal regions but not in early somatosensory areas such as SI and SII. One important difference that might have contributed to the different results in the two studies is whether tactile stimulation was unilateral or bilateral. In our study participants received tactile stimuli on one hand at a time and had to discriminate their physical properties, which has been shown to take place in primary and secondary somatosensory cortices (Murray & Mishkin, 1984; Krupa *et al.*, 2004; Fitzgerald *et al.*, 2006). By contrast, in the study by Macaluso and colleagues' tactile stimulation was always bilateral and tactile targets at the attended hand had to be reported. This task requires perceptual inhibition of stimuli concurrently presented at the unattended location, which is likely to involve higher-order areas, such as the posterior parietal cortex, for the resolution of interference and efficient spatial attentional processing (Nassauer & Halperin, 2003; Geng & Behrmann, 2006; Nee & Jonides, 2007; Nee *et al.*, 2007).

While few formal investigations have been concerned with the effects of visual information about the body on tactile-spatial localization, an ever-growing number of studies have shown that 'overt' vision of a body site improves tactile acuity at that particular site in healthy and brain-damaged subjects (e.g. Kennett *et al.*, 2001; Press *et al.*, 2004; Serino *et al.*, 2007), and enhances early somatosensory ERP components (Taylor-Clark *et al.*, 2002). This effect has been termed visual enhancement of touch (VET), and it has been suggested to result from descending signals from multisensory areas that may 'pre-activate' the primary SII during vision of the body (Kennett *et al.*, 2001; Fiorio & Haggard, 2005). In our study, a main effect of viewing condition (i.e. irrespective of attention) was not obtained, suggesting that our findings cannot be explained by a mechanism such as VET, although it is possible that the easiness of the task may have prevented such an effect (see Press *et al.*, 2004).

Unlike VET, which has been argued not to result from general attentional enhancement (see Kennett *et al.*, 2001; Fiorio & Haggard, 2005), our finding that early attentional ERP effects are modulated by the sight of the stimulated body parts suggests that interactions between attention and multisensory processing can influence responses in early somatosensory areas. Evidence from previous studies has shown that tactile-spatial attention and vision of the body can (independently and jointly) modulate the activity of somatosensory areas. Previous functional magnetic resonance imaging (fMRI) and PET studies have suggested that attentional modulations

within early somatosensory areas may rely on feedback projections from associative areas of the fronto-parietal network involved in spatial attention processing, such as the dorsolateral prefrontal cortex and the posterior parietal cortex (Roland, 1981, 1982; Macaluso *et al.*, 2000, 2002; Staines *et al.*, 2002; Schaefer *et al.*, 2005). In addition, single-cell recordings in animals (Graziano & Gross, 1993; Duhamel *et al.*, 1998), and neuropsychological and fMRI studies in humans (Làdavas, 2002; Làdavas & Farnè, 2004; Macaluso & Driver, 2005; Macaluso, 2006) have suggested that heteromodal brain regions in frontal and parietal cortices may be involved in cross-modal effects between vision and touch. Attentional and cross-modal areas in frontal and parietal cortices (e.g. the dorsolateral prefrontal cortex involved in attentional processing, and the IPS, a multimodal region that may be involved in multisensory body representation) have been shown to be interconnected via feedforward and feedback projections (Lu *et al.*, 1994; Takada *et al.*, 2004; Tomassini *et al.*, 2007) within a network of attentional and multimodal systems (Calvert *et al.*, 2004). In line with this, visual modulations of touch suggesting interactions with attentional factors have been reported in healthy observers (Forster & Eimer, 2005) and in the neuropsychological literature (Làdavas *et al.*, 2000). For example, in right-brain-damaged patients with spatial attention impairment tactile perception has been shown to be modulated by visual stimuli presented near the patients' stimulated hand, specifically under conditions when that hand was visible (Làdavas *et al.*, 2000).

Taken together, the evidence presented above supports the account that cross-modal interactions (i.e. sight of the stimulated hands) modulate tactile-spatial attention effects within early somatosensory areas via feedback projections from frontal and parietal areas that are involved in the control of spatial attention and multisensory representation of the body. However, the exact neural mechanisms underlying the effect found in our study remain to be clarified. On the one hand, this modulatory effect could result from 'independent' influences from higher-order areas involved in attention and multisensory body representation on the somatosensory cortex. On the other hand, interactions between multisensory processing and attention might occur within fronto-parietal areas (see above) before these project back to somatosensory areas. Although both these accounts may be plausible in explaining our findings, two aspects of our results may be in favour of the latter account. First, we did not find an effect of viewing condition independent of attention. In addition, there was no reliable three-way interaction between viewing condition, attention and site (frontal vs. parietal). Although it does not allow us to draw more specific conclusions about the neural circuit underlying the effects found in this study, this is in accordance with the hypothesis of an involvement of both frontal and parietal cortices in the visual modulation of mechanisms of tactile selection.

Finally, it is interesting to note that vision of the hands, rather than ambient visual information alone, was found to be the crucial factor in determining attentional modulations at early somatosensory cortical stages in our study. Ambient visual-spatial information might have been expected to affect tactile-spatial processing because it provides observers with information about the external spatial framework within which tactile events occur, over and above that provided by proprioception. It is thought that tactile events, the location of which can be represented in terms of anatomical and external spatial coordinates, are automatically remapped into an external spatial framework, which is dominated by vision (e.g. Pavani *et al.*, 2000; Kitazawa, 2002). Such remapping is established by the visual system during development, as it occurs in sighted and late blind observers, but not in the congenitally blind (Röder *et al.*, 2004). Moreover,

remapping of touch into an external spatial coordinate system is substantially reduced when the hands are placed at locations for which visual information is limited or is not usually available (i.e. behind observers' back; Kobor *et al.*, 2006). Visual information about the external environment might thus be expected to aid tactile selection by facilitating the remapping of tactile locations into external coordinates. However, in our study facilitation occurred only when visual information included the sight of the hands. Therefore, our findings suggest that visual-spatial information per se may not be what drives the dominance of the tactile external coordinate system over a purely anatomical one, but that this dominance is strongly tied to the sight of the hands within it.

In conclusion, this study shows that mechanisms of sustained covert spatial attention within the somatosensory modality may operate in a multimodal fashion. In particular, our results demonstrate that attentional effects can occur at earlier stages of somatosensory cortical processing when visual information about the hands is available. We suggest that the sight of the body (i.e. the hands) plays a crucial role in spatial attentional selection of the currently task-relevant hand by providing spatial information about the body and the space around it. Future investigations with more advanced neuroimaging techniques such as diffusion tensor imaging, in combination with fMRI, could help clarify the specific neural pathway involved in interactions between spatial attention and the sight of the body as those observed in the present study.

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Abbreviations

EEG, electroencephalogram; ERPs, event-related potentials; fMRI, functional magnetic resonance imaging; HEOG, horizontal electrooculogram; IPS, intraparietal sulcus; PET, positron emission tomography; RT, reaction times; SII, somatosensory cortex; VET, visual enhancement of touch.

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