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ERP correlates of tactile spatial attention differ under intra- and intermodal conditions

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ABSTRACT

To investigate whether the mechanisms underlying endogenous tactile spatial attention differ under pure tactile compared to mixed modality conditions event-related brain potentials (ERPs) were recorded to bilateral tactile and visual cues and tactile imperative stimuli. In the cue-stimulus interval the anterior directing attention negativity (ADAN) was present contralateral to the side of the attentional shift. Importantly, under pure tactile conditions this component persisted until imperative stimulus onset, while it diminished under intermodal conditions. Furthermore, post-tactile stimulus onset attentional modulations were present for the P100 component and later latencies under intermodal conditions. In contrast, under pure tactile conditions attentional modulations only emerged for the N140 component and later latencies. It is suggested that mechanisms underlying attentional orienting and selection are not entirely supramodal but depend in part on the modalities involved.

The majority of spatial attention research has investigated processes related to the orienting of attention and selection of information within the visual system. In recent years the number of studies investigating the ability to orient attention to locations on the body and to selectively attend to tactile information has increased (see Spence and Gallace, 2007 for review). These studies have shown that also in the tactile modality attention can be oriented voluntarily (endogenously) and reflexively (exogenously) to locations on the body. Electrophysiological and brain imaging studies have reported that early somatosensory processing is modulated by tactile spatial attention (e.g. Michie, 1984; Roland, 1981), while behavioural studies of endogenous tactile attention have found that orienting attention to a location on the body both speeds reaction times (RT) and enhances discrimination of tactile stimuli at that location (see Johansen-Berg and Lloyd, 2000 or Spence, 2002 for reviews).

Endogenous tactile attention can be oriented to a location on the body either in a sustained fashion over longer periods of time or in a transient fashion following informative cues indicating the subsequent stimulus location. Most studies investigating transient endogenous tactile attention have employed either auditory or visual cues to orient participants' attention. Indication that endogenous tactile attention is influenced by the sensory modality of the attention directing cues comes from a recent behavioural study by Chica et al. (2007). In their study participants oriented their attention to tactile target locations following either visual or tactile unilateral cues. Behavioural endogenous attention effects were larger when cue and target were presented in the same sensory modality than when they were presented in different sensory modalities (see also Mondor and Amirault, 1998). Importantly, this result indicates that processes related to endogenous tactile attention, that is attentional orienting to locations on the body and somatosensory stimulus processing, may in part be dependent on the sensory modality of the attention directing cue.

Both brain imaging and electrophysiological studies have begun to investigate the mechanisms underlying attentional orienting. While fMRI studies have revealed an attention network of frontal and parietal activity during the cue-stimulus interval, electrophysiological studies have now started to unravel the temporal pattern of changes in brain activity during the interval between the onset of an attention directing cue and the onset of a subsequent imperative stimulus in cue-locked event-related brain potentials (ERPs). These studies have shown that two successive lateralised ERP components are elicited which are sensitive to the direction of the cued attentional shift (e.g. Hopf and Mangun, 2000; Nobre et al., 2000; Eimer et al., 2002). More specifically, following cue presentation an enhanced negativity is found at frontal electrodes, the so called 'anterior directing attention negativity' (ADAN), when comparing ERPs at electrodes contralateral to the side of attentional shifts to ERPs at ipsilateral electrodes; while during later phases of the cue-stimulus interval an enhanced positivity is

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apparent at posterior electrodes, the so called 'late directing attention positivity' (LDAP), when comparing ERPs at electrodes contralateral to the side of attentional shifts to ERPs at ipsilateral electrodes. Furthermore, it has been suggested that these components reflect functionally distinct attentional control mechanism (Eimer et al., 2003a; Van Velzen et al., 2006).[1] The ADAN has been shown to be sensitive to changes in the position of the hands to opposite hemispaces (Eimer et al., 2001). That is, when the arms are crossed over so that the left hand is placed in right hemispace and the right hand in left hemispace an anterior negativity was now elicited *ipsilateral* to the cued side of external space (but over the hemisphere receiving input from the attended hand). Thus, the ADAN appears to be sensitive to the anatomical identity of the cued hand (and not the attentional shift in external space) and has therefore been suggested to reflect attentional control processes based on somatotopically defined coordinates (see also Eimer et al., 2004). In contrast, the LDAP component does not appear to be sensitive to crossed hand postural changes, instead it has been found to be absent in blind people and in sighted people in complete darkness suggesting that this component is based on representations of visually mediated external space (Van Velzen et al., 2006; see also Harter et al., 1989). Furthermore, this suggests that the availability of visual spatial information influences mechanisms of endogenous spatial orienting.

Although ERP studies have begun to reveal correlates of endogenous attentional control mechanisms when orienting spatial attention to visual, auditory or tactile events (e.g. Eimer et al., 2002), all of the studies to date have employed either visual or auditory, but not tactile, informative cues. However, recent ERP studies (Foxe et al., 2005; Talsma et al., 2008) investigating the effects of congruency between the sensory modality of informative cue and subsequent imperative stimulus in a non-spatial attention task have shown differences in the mechanisms underlying attentional orienting depending on congruency of the sensory modality of cue and stimulus. With respect to tactile spatial attention it is therefore not clear what pattern of ERP correlates of endogenous shifts of attention would be present following tactile attention directing cues and how this pattern of modulation in a pure tactile cue-stimulus presentation differs from mixed modality presentations when, for example, the visual system is engaged through visual informative cues. Such a comparison would provide further insight into the basis of attentional spatial control mechanisms and to what extent these operate in a supramodal or modality specific fashion.

Several studies have reported ERP correlates of transient endogenous spatial attention on tactile stimulus processing. These studies have investigated the timing of spatial attentional modulations of tactile stimulus processing in stimulus-locked waveforms by comparing brain responses elicited by tactile stimuli at currently attended and unattended locations as instructed by previously presented attention directing visual or auditory cues. These studies have reported modulation of the N140 component (present around 140 ms after tactile stimulus onset) followed by a later negativity for tactile stimuli at attended compared to unattended locations (Eimer and Forster, 2003; Eimer et al., 2003b, 2004; Forster and Eimer, 2005; Van Velzen et al., 2006). However, also earlier modulations already present in the time range of the P100 component have been reported (Eimer and Forster, 2003). Importantly, all of these studies are based on attentional orienting across sensory modalities, that is tactile stimuli were preceded by either visual or auditory attention directing cues, and in addition, visual information was always available. It is therefore not clear whether spatial attentional modulations of tactile stimulus processing differ with the engagement of another modality.

The aim of the present study was to investigate ERP correlates of endogenous tactile attentional orienting and stimulus processing under pure tactile conditions where only the tactile system is engaged, and to compare these to ERP correlates of attentional orienting and tactile stimulus processing when the visual system is actively engaged as common in most previous studies. Therefore, we tested the same group of participants in two conditions that differed in the sensory modality of the attention directing cues. In order to match tactile and visual attention directing cue characteristics, tactile vibrations and visual flickers were presented bilaterally to and near both hands, respectively. We investigated the pattern of ERP correlates of attentional orienting in cue-locked waveforms and the timing and amplitude of ERP correlates of tactile stimulus selection in stimulus-locked waveforms. In the cue-locked waveforms we expected to find the ADAN component to be present at frontal electrode sites in both pure tactile and intermodal conditions reflecting attentional control processes based on somatotopic representations of space; followed, only in the intermodal condition, by the LDAP component at occipital–parietal electrode sites reflecting attentional orienting that is mediated by visual space representations. For the post-tactile stimulus interval, we expected to find attentional modulations of early somatosensory components followed by a sustained negativity for tactile stimuli at attended locations. Furthermore, if mechanisms of tactile attentional selection were influenced by visual engagement we expected the timing or the amplitude of these attentional modulations to differ between pure tactile and intermodal conditions.

1. Materials and methods

1.1. Participants

16 paid, healthy volunteers took part in the experiment. Two participants were excluded due to an excess of muscle activity and three due to poor behavioural performance (see below). Thus, 11 participants (6 males and 5 females), aged 22–33 years (average age: 27 years) remained in the sample. All participants were right-handed and had normal or corrected-to-normal vision by self-report. The experiment was approved by the Ethics Committee, City University, London; and all participants gave written informed consent.

1.2. Experimental design

The experiment consisted of 16 experimental blocks of 76 trials each. Each trial started with the presentation of a bilateral cue; either steady versus flickering lights in the visual condition, or continuous versus flutter vibrations in the tactile condition. After an interval of 1100 ms following cue onset, an imperative tactile stimulus was presented. Tactile stimuli were either valid targets that required a response or invalid targets or non-targets that were to be ignored. The inter-trial interval between successive trials was 1000 ms.

1.3. Stimuli and apparatus

Participants sat in a dimly lit sound-attenuated experimental chamber resting their arms on a table in front of them where two small boxes (3 cm × 5 cm × 3 cm), each including one solenoid and one light-emitting diode (LED), were placed. Participants' hands were placed equidistant from the midline with the index fingers 50 cm apart. Tactile stimulation was provided using four 12 V solenoids driving a metal rod with a blunt conical tip to the top segment of the index finger making contact with the fingers whenever a current was passed through the solenoid. Two solenoids were located under the middle fingers and were employed only for the tactile cue presentation and two solenoids were located under the index finger for tactile stimulus presentations. Visual stimuli were presented by two red LEDs placed 47 cm from each other and 1.5 cm from the tactile stimulators on each box. A small white spot drawn on a black cloth that covered the table severed as a fixation point for the intermodal condition only. This was located on the midline centred

[1] While many studies have reported the presence of the ADAN and LDAP component following attention directing cues, some studies have now also shown that attentional orienting can take place in the absence of the ADAN (Green and McDonald, 2006; Green et al., 2005) or LDAP (Van Velzen et al., 2007; Gherri and Eimer, 2008). Therefore, these components appear not to be necessary to control shifts of attention.

between the two boxes at about 32.5 cm from the participants' eyes. White noise (50 dB, measured from the position of participant's head) was presented from two loudspeakers placed 90 cm from the subject's head and 95 cm distant from each other, to mask any sounds made by the tactile stimulators.

Visual and tactile cues were presented bilaterally and consisted of both LEDs or both solenoids being simultaneously and repeatedly switched on and off. Cues lasted 300 ms and two cue types were used to indicate that participants should orient their attention either to the right or to the left hand. The two cue types differed in such a way that one of the cues was perceived as a flickering light/flutter vibration, whereas the other was perceived as a more stable light/continuous vibration. The first cue type consisted of 15 cycles in which both LEDs/solenoids were switched on for 2 ms followed by 18 ms when both LEDs/solenoids were turned off; the other cue type consisted of five cycles in which both LEDs/solenoids were on for 6 ms followed by 54 ms when both LEDs were turned off.

Tactile imperative stimuli were either non-target or target stimuli. Tactile non-targets consisted of one rod tip contacting participants' index finger for 200 ms. Tactile targets were infrequent and had a gap in this continuous contact; so that these were interrupted for 30 ms after a duration of 85 ms.

1.4. Procedure

Participants completed first eight pure tactile blocks and these were followed by eight intermodal blocks. Tactile and intermodal blocks were identical, except the cue modality, and participants were blindfolded throughout the tactile cue blocks and the preceding tactile practice block to prevent engagement of the visual system. In addition, the pure tactile condition was always run first to avoid participants' familiarization with the visual spatial environment that may induce visual Q3 orienting (c.f. Van Velzen et al., 2006). Throughout the intermodal experimental blocks the participants maintained fixation upon the fixation point, and throughout pure tactile experimental blocks they were instructed to keep their eyes as still as possible. Both tactile and intermodal experimental blocks were preceded by one practice block each consisting of a total of 40 trials with 12 valid non-target, 10 valid target, 12 invalid non-target and 6 invalid target trials presented randomly and equiprobably to both hands. Prior to the tactile cue practice block separate tactile cue and a tactile target/non-target presentations were given. In the cue presentation each cue type was presented 4 times and in the target/non-target presentation each type of tactile stimulus (target versus non-target) was presented 8 times. Prior to the intermodal practice block a visual cue presentation was given consisting of each type of visual cue being presented 4 times.

Bilateral cues at the start of each trial indicated the location participants had to attend to. Six participants were instructed to attend to their left hand when the cue was a continuous vibration or a steady light and to attend to their right hand when the cue was a flutter vibration or a flickering light. For five participants this association was reversed.

Bilateral cues were followed by the presentation of an imperative tactile stimulus. Valid tactile targets were tactile gap stimuli delivered to the currently attended hand, which required a foot response, and were delivered in eight trials per block. Invalid tactile targets were tactile gap stimuli on the currently unattended hand, which required no response, and were delivered in four trials per blocks. Targets were presented with equal probability to the right or left hand. On the remaining 64 trials non-target stimuli were presented randomly and with equal probability to the right or left hands of participants; these also required no response. Participants were instructed to respond as quickly and accurately as possible to all validly cued tactile targets. Participants responded by pressing a button with either foot. Six participants used their left foot and the remaining five used their right foot to respond to targets. The response foot was assigned at the beginning of the experiment and was kept constant throughout the experiment. Participants' response time and accuracy was recorded and only the data of participants with a response accuracy of above 75% correct were further analysed.

1.5. EEG recording and data analysis

EEG (electroencephalogram) was recorded with Ag–AgCl electrodes and linked-earlobe reference 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 kΩ and the amplifier bandpass was 0.01–100 Hz. EEG and HEOG were sampled with a 500 Hz digitization rate and, subsequently, off-line digitally filtered with a 40 Hz low pass filter. These were then epoched into 1600 ms periods, starting 100 ms prior to cue onset and ending 400 ms after the onset of the tactile stimulus on each trial. For intermodal and pure tactile experimental blocks separate averages were computed for ERPs recorded in the cue-target interval (relative to a 100 ms baseline preceding cue onset), and for ERPs in response to subsequent tactile stimuli (relative to a 100 ms baseline preceding the onset of these stimuli). Trials with eyeblinks (Fp1 or Fp2 exceeding ±60 μV relative to baseline), horizontal movements (HEOG exceeding ±40 μV relative to baseline) or other artefacts (a voltage exceeding ±60 μV at any electrode relative to baseline) measured in the cue-target interval or within 350 ms after stimulus onset, were excluded from analysis. To detect smaller systematic deviations of eye position, indicating the residual tendencies to move the eyes towards the cued location, averaged HEOG waveforms obtained in the cue-target interval in response to cues directing attention to the left versus right hand were examined separately for each participant for the intermodal and pure tactile conditions. Residual HEOG deviations on left and right cue trials differed less than 4 μV throughout this interval for all participants.

The EEG obtained in the cue-target interval was averaged separately for the visual and tactile conditions and for cues directing attention to the left versus right hand. Because trials containing tactile targets and non-targets were presented in random order, and the presence or absence of a tactile target was therefore completely unpredictable prior to tactile stimulus onset, ERPs recorded during the cue-target interval were collapsed across trials containing a tactile target or non-target. Mean amplitude values were computed at lateral anterior sites (F7/8, F3/4 and FC5/6) and lateral posterior sites (P7/8, P3/4 and O1/2) within successive latency windows (600–900 ms and 900–1100 ms relative to cue onset).[2] These amplitude values were then analysed separately for anterior and posterior electrodes by separate repeated measures ANOVAs for factors electrode site (F7/8, F3/4 versus FC5/6 for anterior; and P7/8, P3/4 versus O1/2 for posterior sites), cue direction (left versus right cue direction) and hemisphere (electrodes over the left versus right hemisphere). A significant cue direction × hemisphere interaction was taken as the presence of lateralized ERP modulations sensitive to the direction of a cued attentional shift.

Post-stimulus ERP analysis was restricted to non-target trials only, in order to avoid contamination by foot responses; in addition, trials immediately following subject's response were excluded from analysis in order to avoid contamination of averaged ERPs by movements-related artefacts. ERPs for tactile non-target stimuli were averaged relative to a 100-ms pre-stimulus baseline for all combination of cue type (valid versus invalid) and stimulated hand (left versus right). Statistical analysis (repeated measures ANOVAs) was conducted for electrode sites close to somatosensory areas where somatosensory ERP components are maximal with the factors condition (pure tactile versus intermodal), cue type (valid versus invalid), hemisphere (contralateral versus ipsilateral to stimulated hand) and electrode site (F3/F4, F5/F6, C3/C4, P3/P4, CP5/CP6). ERP mean amplitudes were computed within successive measurement windows centred on the latencies of early SEP components (in millisecond post-stimulus): P45 (35–55 ms), N80 (60–90 ms), P100 (90–125 ms), and N140 (130–170 ms). Mean amplitudes were also computed in a time interval between 200 and 350 ms post-stimulus in order to investigate longer-latency effects.

2. Results

2.1. Behavioural performance

Participants responded on average 96 ms faster to tactile targets under intermodal compared to pure tactile conditions (512 ms versus 608 ms; $t = 2.3$; $p < 0.05$). False alarms to non-target stimuli were present on less than 1% of all non-target trials in both conditions. Participants missed on average 1.6% of all targets under intermodal conditions and 1.1% of all targets under pure tactile conditions.

2.2. ERP correlates of attentional spatial orienting in the cue-stimulus interval

Fig. 1 shows ERPs to bilateral cues in the intermodal (left panel) and pure tactile (right panel) conditions at anterior and posterior electrodes ipsilateral and contralateral to the cues side. The ADAN appears to be present under both conditions. Under intermodal conditions this component is present at electrodes F3/4 and F7/8 and diminishes around 900 ms after cue onset, in contrast, under pure tactile conditions the ADAN is present at all anterior electrode sites and increases towards the end of the cue-stimulus interval. The LDAP component appears to be absent in both conditions, if anything, it may be present at electrode P7/8.

Statistical analyses of ERPs elicited during leftward and rightward shifts were compared as a function of the recording hemisphere separately for the pure tactile and intermodal conditions. For

[2] The ADAN and LDAP components have been reported to be present in the interval of 300–500 ms and 500–700 ms, respectively, following the onset of simple, short (up to 100 ms) cues (e.g. Harter et al.). However, following cues with more difficult to derive cue meaning, these components have been reported to be delayed (Eimer and Van Velzen, 2002; Green et al., 2005; Jongen et al., 2007).

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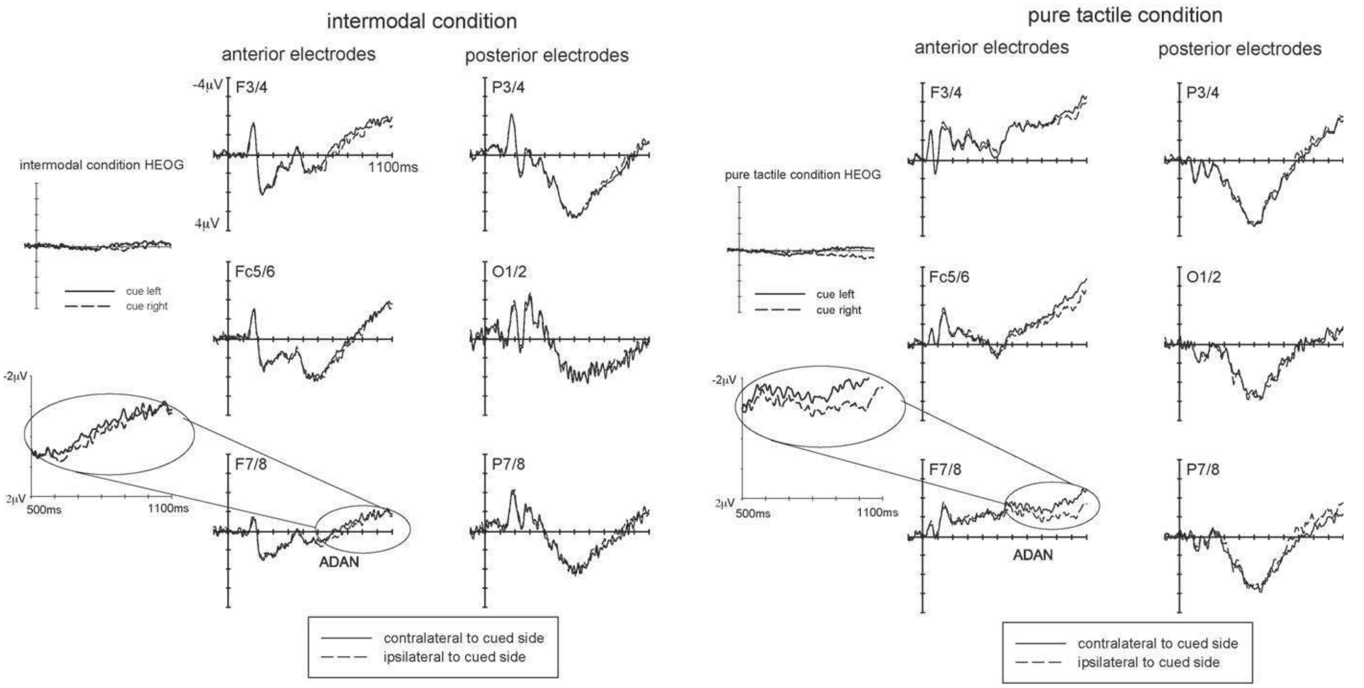

Fig. 1. Grand-averaged ERPs elicited in the 1100 ms following cue onset under intermodal (left panel) and tactile (right panel) conditions at anterior and posterior electrodes ipsilateral and crontalateral to the cued side. To highlight the differences between the two condition insets magnifying ERPs 500–1100 ms post-cue onset at electrode F7/8 are shown. Grand-averaged HEOG waveforms for left and right cues under intermodal and pure tactile conditions are displayed to the left of each panel.

the time interval of 600–900 ms after cue onset a significant cue direction × hemisphere interaction was present for anterior electrode sites following tactile cues ($F(1,10) = 5.01$; $p < 0.05$) reflecting the presence of an enhanced negativity contralateral to the direction of an attentional shift (ADAN). No statistically reliable interaction was present following visual cues, however, follow-up analysis done separately for anterior electrode sites showed a significant cue direction × hemisphere interaction at electrode F3/4 ($F(1,10) = 5.13$; $p < 0.05$) indicating the presence of a localized ADAN also in the intermodal condition. For the following time range until tactile stimulus onset (900–1100 ms after cue onset) a cue direction × hemisphere interaction was again present at anterior electrode sites following tactile cues ($F(1,10) = 16.34$; $p < 0.01$) indicating the continued presence of an enhanced negativity contralateral to the direction of an attentional shift. In contrast, no such interaction was present in the intermodal condition; and overall analysis of anterior electrode sites including the factor condition (pure tactile versus intermodal) showed a close to significant condition × cue direction × hemisphere interaction ($F(1,10) = 4.38$; $p = 0.06$). Taken together these statistical results support the informal observation of an ADAN following tactile attention directing cues that persists until tactile stimulus onset while under intermodal conditions a localized ADAN is present that diminishes prior to tactile stimulus onset. Importantly, there was no statistical evidence of cue direction × hemisphere interactions at posterior electrode sites, even for follow-up analyses separate for each posterior electrode, confirming the absence of a reliable enhanced positivity contralateral to the direction of an attentional shift (i.e. LDAP) in both pure tactile and intermodal conditions.

2.3. *ERP correlates of somatosensory processing and attentional selection*

ERP waveforms elicited in response to tactile non-target stimuli under pure tactile (dashed lines) and intermodal (solid lines) conditions averaged across attention conditions are shown in Fig. 2. A condition effect is clearly visible in the time range of the P100 component with enhanced amplitudes in response to tactile stimuli under intermodal compared to pure tactile conditions; in addition, for later latencies starting around 200 ms a sustained positivity under visual compared to tactile conditions is present. Fig. 3 shows ERPs elicited in response to tactile non-target stimuli at the attended (solid lines) compared to currently unattended hands (dashed lines) separately under pure tactile (top panel) and intermodal (bottom panel) conditions. Waveforms are displayed for electrodes close and over somatosensory cortex contralateral to the side of tactile stimulation. In the pure tactile condition an enhanced negativity in response to tactile stimuli at attended

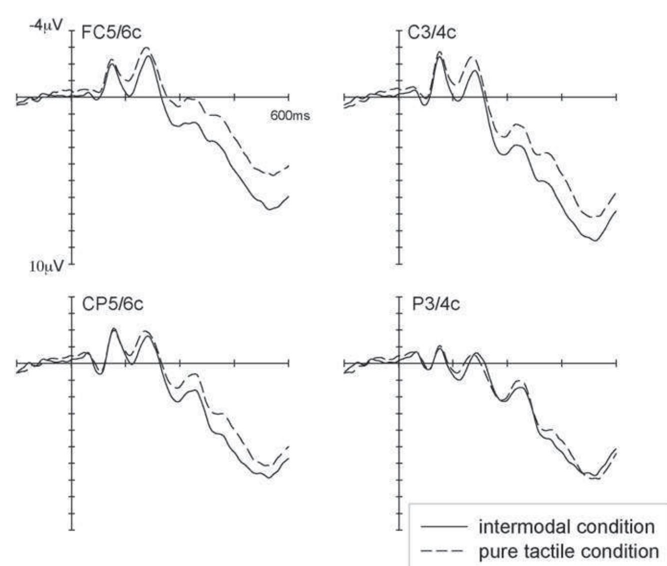

Fig. 2. Grand-averaged ERP waveforms elicited by tactile stimuli under pure tactile (dashed lines) and intermodal (solid lines) conditions at electrodes over the hemisphere contralateral to the stimulation side close to and over somatosensory cortex.

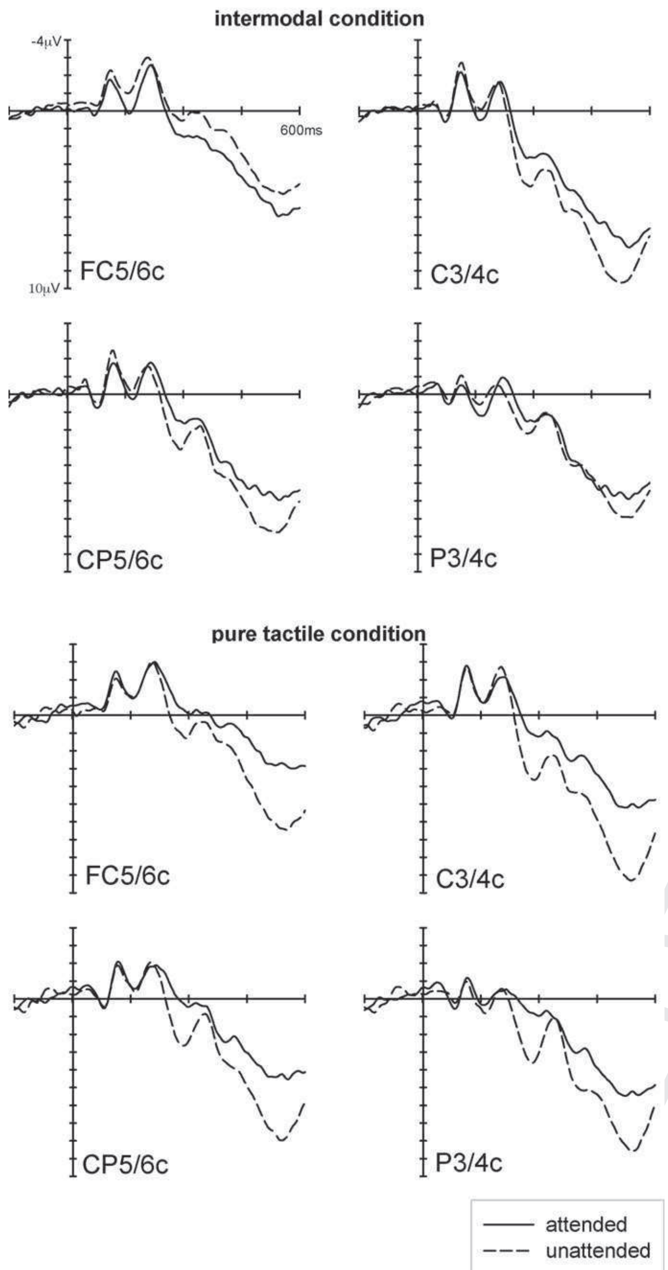

Fig. 3. Grand-averaged ERP waveforms elicited by tactile stimuli at the currently attended (solid lines) and unattended (dashed lines) location under pure tactile (bottom panel) and intermodal (top panel) conditions at electrodes over the hemisphere contralateral to the stimulation side close to and over somatosensory cortex.

locations is present starting at the peak of the N140 component and continues to be present for longer latencies. In contrast, in the intermodal condition attentional modulations of ERP waveforms elicited by tactile stimuli are already present for the time range of the P100 component with an enhanced positivity for tactile stimuli at attended compared to unattended locations. Similar to the pure tactile conditions, an enhanced negativity for ERPs elicited by tactile stimuli at attended compared to unattended locations is present for later latencies.

For the time window of the P100 component (90–125 ms post-stimulus onset) a main effect of condition ($F(1,10) = 9.46$; $p < 0.02$), confirming enhanced ERP amplitudes under intermodal conditions, and, a condition × attention interaction ($F(1,10) = 6.54$; $p < 0.03$) were present. Follow-up analysis separate for the two conditions showed a significant main effect of attention only for the intermodal condition ($F(1,10) = 5.60$; $p < 0.04$) confirming enhancement of the P100 component in response to tactile stimuli at the currently attended compared to the unattended hand only when tactile stimuli were preceded by attention directing visual but not tactile cues. For the time window of the N140 (130–170 ms post-stimulus onset) component neither a main effect of condition or attention, nor a condition × attention interaction reached significance. Follow-up analysis separate for the pure tactile and intermodal conditions showed a significant main effect of attention only for the tactile condition ($F(1,10) = 9.8$; $p < 0.01$) confirming that ERPs in response to tactile stimuli at currently attended compared to unattended locations showed an enhanced N140 component only when preceded by tactile, and not visual, attention directing cues. For the following time window (200–350 ms post-stimulus) a significant main effect of condition ($F(1,10) = 12.35$; $p < 0.01$) was found with more positive ERP amplitudes under visual than tactile conditions. In addition, a main effect of attention ($F(1,10) = 19.40$; $p < 0.01$) was present, but no significant condition × attention interaction, confirming the presence of a sustained negativity for ERPs elicited by tactile stimuli at attended compared to unattended locations under both pure tactile and intermodal conditions (both $F(1,10) \geq 11.23$; $p < 0.01$).

3. Discussion

The aim of the present study was to investigate ERP correlates of pure tactile spatial attention and to compare these to ERP correlates of a mixed modality condition engaging the visual system analogous to presentation conditions in previous tactile attention studies. To investigate the effects of attentional orienting to the site of tactile stimulation ERPs in the cue-stimulus interval were analysed, and to investigate attentional modulations of somatosensory processing ERPs post-tactile stimulus presentation were analysed. The central finding was that correlates of tactile spatial attention differ between purely tactual orientation of attention and the mixed modality condition in which covert endogenous orienting to locations on the body was induced by visual cues. Differences in the pattern of attentional modulations were present during endogenous orienting in the cue-stimulus interval and for post-stimulus selection suggesting that engagement of the visual system alters various stages of endogenous tactile spatial attention.

Several ERP studies have identified two successive lateralised ERP components, the ADAN and LDAP, which are elicited post-cue presentation and are sensitive to the direction of the cued attentional shift (e.g. Hopf and Mangun, 2000; Nobre et al., 2000; Eimer et al., 2002). In line with these previous studies we found the ADAN component to be present with an enhanced negativity at frontal electrodes contralateral to the side of attentional shifts induced under both intermodal and pure tactile conditions. However, under intermodal conditions the ADAN was very localized and diminished during later phases of the cue-stimulus interval. In contrast, under pure tactile conditions the ADAN was clearly present over frontal electrode sites, and furthermore, continued to be present until tactile stimulus onset. While the ADAN was present under both intermodal and pure tactile conditions, differences in duration may reflect additional sensory specific processes following tactile attention directing cues in the pure tactile condition. Thus, this finding is inconsistent with the notion that the ADAN reflects supramodal attentional control processes (e.g. Eimer et al., 2002) rather suggests that the ADAN reflects processes that are, at least in part, modality specific (Green et al., 2005; Green and McDonald, 2006; but see also Seiss et al., 2007). Correspondingly, Green et al. (2008) have recently suggested that the ADAN reflects multiple neural generators that are differentially modulated by task parameters, such as cue modality and response related processes.

The ADAN is usually followed by the LDAP component present over posterior electrode sites contralateral to the side of attentional shifts at later stages of the cue-stimulus interval. However, Van Velzen et al. (2006) have reported that this component is absent following auditory attention directing cues in both blind and sighted people when no visual information is available. In line with this result, we also found the LDAP to be absent under pure tactile conditions when no visual information was available and endogenous attentional orienting was induced by tactile cues. Surprisingly, this component was also absent under conditions when the visual system was engaged through visual attention directing cues. If the LDAP reflects attentional control mechanisms based on representations of visually mediated external space (Harter et al., 1989; Van Velzen et al., 2006) this component should be present when visual spatial information, including vision of the hands and forearms, is available (Gherri and Eimer, 2008). Crucially, in contrast to previous studies that have employed central attention directing cues, we employed bilateral attention directing cues that were presented near the location of the subsequent imperative stimulus. The LDAP is linked to attentional control mechanisms based on representations of visually mediated external space to guide attention to the imperative stimulus location and such a process might be diminished under bilateral cue conditions where the imperative stimulus location is already marked by the preceding cues. This may explain the absence of the LDAP under intramodal bilateral conditions, however further research will need to clarify the role of the relationship between cue and imperative stimulus location in attentional control processes.

In addition to ERP correlates of attentional control processes in the cue-stimulus interval, we also analysed ERP correlates of somatosensory processing post-tactile stimulus presentation. Contrasting ERP waveforms in response to tactile stimuli under intermodal and pure tactile conditions an enhanced positivity for the time range of the P100 component and for later latencies was apparent regardless of the allocation of endogenous spatial attention. Likewise, response times were faster under intermodal than pure tactile conditions. The timing of the ERP waveform differences under inter- and intramodal conditions implies that engagement of the visual system modulates somatosensory processing within secondary somatosensory cortex (Hari et al., 1984; Mima et al., 1998). It should be noted that in the present study under intermodal conditions participants were presented with visual attention directing cues along with visual information of the surrounding space while under pure tactile conditions no visual information was available. Thus any effects of visual engagement on somatosensory processing could be due to either the sensory modality of the cue or the availability of visual information in general, or both; and further experiments are required to tie apart the separate contributions of these factors to the effect of visual engagement on somatosensory processing.

Comparing ERP waveforms in response to tactile stimuli at currently attended and unattended locations, we found that under pure tactile conditions correlates of attentional selection were present starting around 130 ms after tactile stimulus onset with enhancement of the N140 component followed by a sustained negativity for tactile stimuli at attended compared to unattended locations. In contrast, under intermodal conditions ERPs elicited by tactile stimuli at attended locations were already enhanced around 90 ms after tactile stimulus onset, that is in the time range of the P100 component, and, for later latencies a sustained negativity was also present. Furthermore, the early attentional modulations under intermodal conditions were absent under tactile cue conditions as shown by a significant attention by condition interaction. Taken together, this difference in the timing of attentional modulations of early somatosensory processing suggests that visual engagement alters mechanisms of tactile spatial selection.

Chica et al. (2007) have reported behavioural differences in the strength of endogenous attention effects dependent on congruency of the sensory modality of cue and imperative stimulus. Specifically, they found larger attention effects, that is faster responses to stimuli at expected than unexpected locations, under conditions when both cue and imperative stimulus were of the same modality (either visual or tactile) than under mixed modality conditions (one visual the other tactile). In the present study, Q4 behavioural responses were required to infrequent target stimuli at attended locations only, thus not allowing the computation of behavioural attention effects. The ERP data of the present study show earlier attentional modulations of somatosensory processing under mixed modality conditions which may suggest stronger behavioural attention effects under this condition. However, such a translation is questionable; in fact, there is some indication that ERP correlates of attentional modulations at later stages of somatosensory processing reflect more closely behavioural attention effects (Forster and Eimer, 2005).

To our knowledge this is the first ERP study investigating attentional control processes induced by tactile attention directing cues in a pure tactile spatial attention task. We found that under pure tactile conditions following cue presentation ERP correlates of attentional orienting showed the ADAN component over frontal electrode sites contralateral to the induced attentional shift that persisted to be present until onset of the imperative stimulus. Following tactile stimulus onset ERP modulations of spatial attention were present for the N140 followed by a sustained negativity for stimuli at attended locations. Under intermodal conditions this pattern of attentional modulations differed in the cue-stimulus interval as well as post-imperative stimulus presentation. In the cue-stimulus interval the ADAN diminished well before stimulus onset, and attentional modulations post-stimulus presentation were already present for the time range of the P100 component in addition to later latencies modulations. Importantly, in the same time range as the intermodal attentional post-stimulus modulations were present, somatosensory processing was altered under intermodal compared to pure tactile conditions suggesting that tactile stimulus processing and mechanisms underlying attentional selection are affected by visual engagement. Furthermore, these results suggest that the mechanisms underlying endogenous spatial attention, that is attentional orienting as well as stimulus selection, can differ between intramodal and mixed modality conditions and are, therefore, not entirely supramodal.

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