

Shifts of attention in the early blind: An ERP study of attentional control processes in the absence of visual spatial information

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Received 30 November 2005; received in revised form 9 March 2006; accepted 19 March 2006

Available online 9 May 2006

Abstract

To investigate the role of visual spatial information in the control of spatial attention, event-related brain potentials (ERPs) were recorded during a tactile attention task for a group of totally blind participants who were either congenitally blind or had lost vision during infancy, and for an age-matched, sighted control group who performed the task in the dark. Participants had to shift attention to the left or right hand (as indicated by an auditory cue presented at the start of each trial) in order to detect infrequent tactile targets delivered to this hand. Effects of tactile attention on the processing of tactile events, as reflected by attentional modulations of somatosensory ERPs to tactile stimuli, were very similar for early blind and sighted participants, suggesting that the capacity to selectively process tactile information from one hand versus the other does not differ systematically between the blind and the sighted. ERPs measured during the cue–target interval revealed an anterior directing attention negativity (ADAN) that was present for the early blind group as well as for the sighted control group. In contrast, the subsequent posterior late direction attention negativity (LDAP) was absent in both groups. These results suggest that these two components reflect functionally distinct attentional control mechanisms which differ in their dependence on the availability of visually coded representations of external space.

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Keywords: Attention; Blindness; Control; Touch; Event-related brain potential

1. Introduction

Covert shifts of spatial attention can affect the perceptual processing of stimuli that are located within the current focus of attention. Evidence for such attentional modulations of sensory processing has been provided by event-related brain potential (ERP) studies, which have demonstrated that amplitudes of early modality-specific ERP components are enhanced when visual (e.g., Mangun & Hillyard, 1991), auditory (e.g., Näätänen, 1982) or tactile (e.g., Michie, Bearpark, Crawford, & Glue, 1987) stimuli are presented at attended relative to unattended locations. In contrast, the covert attentional control processes that are elicited in anticipation of task-relevant stimuli at specific locations, and which are responsible for spatially specific effects of attention, have only recently become the object of experimental investi-

gation. Such control processes can be studied by using fMRI or ERP measures of brain activity in response to attentional cues that direct attention to one side versus the other, prior to the presentation of any sensory events at attended versus unattended locations (see Corbetta & Shulman, 2002, for a review of fMRI evidence for attentional control circuits).

While most ERP studies have examined attentional control processes triggered during covert anticipatory shifts of visual spatial attention (e.g., Harter, Miller, Price, LaLonde, & Keyes, 1989; Yamaguchi, Tsuchiya, & Kobayashi, 1994; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000), some recent studies have now begun to look for ERP correlates of covert attentional orienting towards the anticipated side of relevant auditory or tactile events (Eimer, Van Velzen, & Driver, 2002; Eimer, Forster, & Van Velzen, 2003a; Eimer, Van Velzen, Forster, & Driver, 2003b; Eimer, Forster, Fieger, & Harbich, 2004; Eimer & Van Velzen, 2002). These experiments have uncovered two lateralised ERP components that are elicited during the cue–target interval and which are sensitive to the

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direction of a cued attentional shift. An enhanced negativity at frontal electrodes contralateral to the side of attentional shifts between 300 and 500 ms after cue onset ('anterior directing attention negativity', ADAN) was followed by an enhanced contralateral positivity at posterior electrodes ('late directing attention positivity', LDAP), which emerged during later phases of the cue–target interval. Interestingly, these effects were not just triggered during shifts of visual attention, but also when attention was directed towards anticipated task-relevant auditory or tactile events (e.g., Eimer et al., 2002).¹

The functional interpretation of such lateralised ERP components that are elicited during covert attentional shifts is currently under debate. Based on the observation that these components are very similar during attentional shifts towards task-relevant visual, auditory or tactile events, we have previously suggested (Eimer & Driver, 2001; Eimer et al., 2002) that they reflect the activity of multimodal attentional control processes, which determine the spatial parameters of attentional shifts in a supramodal fashion, regardless of sensory modality (see also Farah, Wong, Monheit, & Morrow, 1989, for similar arguments). While the ADAN may reflect processes within a multimodal 'anterior attention system' (Posner & Petersen, 1990), the posterior LDAP might be linked to the activation of posterior parietal areas, which are known to be involved both in the orienting of spatial attention (e.g., LaBerge, 1995) and in the integration of information from different sense modalities (e.g., Andersen, Snyder, Bradley, & Xing, 1997). In contrast, others (e.g., Harter et al., 1989) have argued that the posterior LDAP component reflects the spatially selective activation of modality-specific visual areas in anticipation of task-relevant visual events. This hypothesis might appear inconsistent with recent observations that this component is elicited not only when attention is allocated to the expected location of visual stimuli, but also during shifts of tactile or auditory attention (Eimer et al., 2002, 2003a; Eimer & Van Velzen, 2002; see also Green, Teder-Sälerjärvi, & McDonald, 2005), since there is no obvious reason to assume that visual areas should be selectively activated in anticipation of auditory or tactile events. However, if one assumes that the control of attentional shifts is generally dominated by visual spatial information, even when other modalities are task-relevant, the possibility that ADAN and/or LDAP might predominantly reflect visual attentional control becomes more plausible. Vision provides superior spatial acuity relative to hearing or touch, thus allowing for more precise tuning of spatial attention. In view of this, it could also be used to control shifts of attention to anticipated locations of auditory or tactile events. If visual information was used to guide the spatial selection of auditory or tactile stimuli, lateralised ERP components elicited during attentional shifts towards anticipated tactile or auditory events might

primarily reflect shifts of attention within visual space, rather than the activity of a genuinely multimodal attentional control system.

On a more general level, the question under debate is which spatial reference frames are used when shifts of attention are programmed and executed. Attentional orienting might be based, primarily or exclusively, on visually mediated representations of external space, even when modalities other than vision are currently task-relevant. Alternatively, the control of spatial attention might be based on multiple frames of reference, including coordinates of visually represented external space, body-centred space, somatotopic space, or, in the case of genuinely supramodal attentional control, amodal spatial coordinates. Thus, it is clearly important to investigate whether the lateralised ERP components that are triggered during cued shifts of spatial attention (ADAN and LDAP) reflect attentional control processes that are based on a single shared spatial frame of reference, or whether these components are linked to separable control mechanisms that differ in terms of their spatial coordinates.

Some initial evidence for the latter hypothesis comes from previous ERP studies demonstrating dissociations between the ADAN and LDAP. In one experiment (Eimer et al., 2003a) participants directed attention to their left versus right hand (as indicated by a central precue on every trial), and ERPs were recorded during the cue–target interval under conditions where hands were either uncrossed or crossed. This manipulation of hand posture had a marked effect on the ADAN component. When considered in terms of the direction of attentional shifts in external space, the ADAN was delayed and reversed polarity with crossed relative to uncrossed hands, suggesting that the attentional control processes reflected by the ADAN may be primarily based on somatotopic spatial coordinates, and not on visually defined external space. In contrast, when considered in terms of external space, the LDAP component was completely unaffected by crossing the hands, thus indicating that the control processes reflected by this component operate primarily on the basis of representations of visually mediated external space. Another study (Eimer et al., 2004) supported these conclusions by demonstrating that when participants were cued to direct attention to the left or right hand for a tactile task, the distance between hands in external space modulated the LDAP (which was more pronounced when hands were wide apart), but left the ADAN component entirely unaffected.

One way to investigate the hypothesis that the LDAP (but not the ADAN) reflects the visually mediated control of attention shifts is to eliminate continuously available ambient visible sources of information about task-relevant stimulus locations. When visual spatial information about the visible positions of hands and arms, or the visible location of tactile and auditory stimulators, is eliminated either by blindfolding participants or by running an experiment in the dark, and visual cues are no longer available to aid and possibly dominate the spatial selection of tactile or auditory events, lateralised ERP components linked to attentional control based on coordinates of visual space should be absent, whereas components that are based on other non-visual spatial reference frames should remain unaffected.

¹ An earlier negative deflection at posterior electrodes contralateral to the direction of the induced attentional shift ('early directing attention negativity'), which was observed in some ERP studies (Harter et al., 1989; Nobre et al., 2000; Yamaguchi et al., 1994) is likely to be a lateralised visual response triggered by non-symmetrical visual cues (such as left-pointing and right-pointing arrows), rather than a genuine reflection of covert attentional control processes (see Van Velzen and Eimer, 2003, for supportive evidence).

Table 1
Description of early blind participants

No.	Age	Gender	Handedness	Visual perception	Age of onset	Cause of blindness
1	60	Male	Right	None	18 months	Eye glass damage
2	54	Female	Right	None	Birth	Retinopathy of prematurity
3	63	Male	Right	Diffuse light	Birth	Nervus opticus atrophy
4	54	Male	Right	None	Birth	Retinopathy of prematurity
5	23	Female	Neither	Diffuse light	Birth	Retinopathy of prematurity
6	23	Female	Neither	Diffuse light	Birth	Retinopathy of prematurity
7	29	Female	Right	None	2 years	Detached retina
8	54	Female	Right	None	Birth	Retinopathy of prematurity
9	55	Male	Neither	None	Birth	Retinopathy of prematurity
10	50	Male	Right	None	13 months	Detached retina

We first tested this prediction in a study (Eimer et al., 2003b) where participants had to shift their attention towards their left or right hand (as indicated by an auditory cue presented at the start of each trial) in anticipation of task-relevant tactile events, either in a normally lit environment or in darkness. The ADAN component, which was present under normal illumination conditions, remained virtually unchanged in darkness. Although the LDAP was also reliably present in both conditions, its amplitude was reduced in the dark. The finding that the ADAN does not seem to depend on the continuous availability of visual spatial information is in line with the idea that this component reflects the control of attention within somatotopic or body-centred space. However, the observation that the LDAP was reduced, but still reliably present in the dark, does not allow any firm conclusions with respect to its dependence on visual spatial representations. One account of the presence of an attenuated LDAP during shifts of attention in the dark assumes that the brain might still utilize stored visual representations of external space, or visual imagery, in the control of tactile attention shifts in the dark. In our previous experiment (Eimer et al., 2003b), all participants had received several training blocks under normal illumination conditions, with half of them being tested first in a lit experimental room before being tested in the dark. Thus, they may have been able to use stored visual representations of the spatial layout of the task situation when directing tactile attention in the dark. Consistent with this explanation, LDAP amplitudes were found to be even smaller in a follow-up experiment where all blocks were conducted in darkness (although training blocks were still run in a lit environment; see Eimer et al., 2003b, for more details).

The main aim of the present experiment was to further clarify the role of visual spatial information during attentional orienting and its impact on lateralised ERP components triggered during shifts of spatial attention. ERP correlates of tactile attention shifts were measured in 10 early blind participants who were either blind from birth or had lost all vision within the first 2 years of life (see Table 1 for details). Due to the lack of visual input during perceptual and cognitive development, congenitally or early blind participants clearly cannot employ a visually defined spatial frame of reference, or visual imagery, to guide shifts of attention towards anticipated task-relevant tactile events. Investigating whether lateralised ERP components (ADAN and LDAP) are present during cued shifts of

tactile attention in early blind participants² therefore provides a strong test as to whether one or both of these components reflect attentional control processes that are primarily guided by visual information. Control processes that depend on visually defined spatial coordinates should be entirely absent during attentional orienting in the early blind. In contrast, control processes (and their ERP correlates) which operate independently of visual information should remain present.

In addition to measuring ERPs during tactile attention shifts for early blind participants, we also tested a group of 10 age-matched sighted control participants. Both sighted and blind participants had to detect and respond to infrequent tactile target stimuli when these were delivered to the currently task-relevant hand, whilst ignoring tactile stimuli when these were presented to the other irrelevant hand. Experimental blocks were conducted in a completely dark experimental booth. Similar to our previous study (Eimer et al., 2003b), a trial-by-trial cueing paradigm was employed where the relevant hand was indicated at the beginning of each trial by an auditory cue. In contrast to this previous study, sighted control participants received task instructions and all training blocks needed to familiarize them with task procedures in the dark. This was to eliminate the possibility that, during training, they would build up visual representations of the spatial layout of the experimental set-up, which might be utilized to guide shifts of tactile attention in the dark.

One set of analyses was conducted for ERP components elicited in the cue–target interval in response to auditory cues directing tactile attention to the left versus right hand. Based on our earlier finding with sighted participants, which had shown that the ADAN component appears to be entirely unaffected by the absence of ambient visual information (Eimer et al., 2003b), we expected this component to be present for the sighted control group. The new question was whether an ADAN would also be elicited in the early blind group. If this component was linked to attentional control processes that depend at least in part upon the availability of visual input during perceptual and cognitive

² In studies on visual impairments, the label ‘congenitally totally blind’ is sometimes also applied to people who lost their sight in infancy (up to the age of 2 years), whereas ‘early blind’ is often used when vision was lost in early childhood. Since the present group contained seven genuinely congenitally blind participants, and three participants with loss of sight within the first 2 years of life, we chose to use the more conservative term ‘early blind’.

development, it might be attenuated or even absent in the early blind. The other question concerned the fate of the posterior LDAP. If this component reflected the activity of attentional control mechanisms that rely on the present or past availability of visual spatial input, this component should be entirely absent during attentional orienting in early blind participants. For the sighted control group, the question was whether an LDAP would still be elicited during shifts of tactile attention even though participants had no opportunity to build up and store visual spatial representations of the task situation.

Another set of analyses was conducted for somatosensory ERP components triggered in early blind and sighted participants in response to tactile non-target stimuli presented to the cued (attended) or uncued (unattended) hand. With sighted participants, directing tactile attention to one hand versus the other has been found to result in an enhancement of the somatosensory N140 component, which is usually followed by a sustained attentional negativity beyond 200 ms post-stimulus (Eimer & Forster, 2003). There is substantial evidence that the early loss of visual information can result in compensatory improvements of spatial perception in the remaining intact modalities (see Röder & Neville, 2003, for a review). For example, Röder et al. (1999b) have demonstrated superior auditory localization abilities for congenitally blind adults when attending to sounds in peripheral auditory space. Such compensatory changes might in principle be reflected by earlier, or more pronounced effects of spatial attention on somatosensory ERPs for the early blind as compared to the sighted group. However, the few previous ERP studies to date that have investigated this issue found little evidence for an improvement of spatially selective attentional processing in the early blind, relative to sighted people. When comparing sighted and blind participants in terms of the effects of sustained spatial attention on auditory ERPs (Liotti, Ryder, & Woldorff, 1998), or on somatosensory as well as auditory ERPs (Hötting, Rösler, & Röder, 2004), no indication of earlier or more pronounced attentional modulations of early modality-specific ERP components were observed for the blind. The present experiment investigated this issue by contrasting the effects of tactile-spatial attention on somatosensory ERPs for early blind and sighted participants under transient attention conditions where attentional orienting was cued on a trial-by-trial basis.

2. Materials and methods

2.1. Participants

Twenty paid volunteers took part in this study. Ten participants were either congenitally blind or had lost sight within 2 years after birth (see Table 1 for further details). The other 10 participants were sighted and reported normal or corrected-to-normal vision. The blind group included five male and five female participants, aged between 23 and 63 years (average age 46.5 years). The age-matched sighted control group also included five males and five females, aged between 22 and 69 years (average age 47.2 years).

2.2. Stimuli and apparatus

Participants sat in a soundproof and completely dark experimental chamber, with a head-mounted microphone positioned in front of their mouth. Two tones differing in pitch (low: 1000 Hz; high: 1500 Hz; each at 72 dB SPL) served as cue

stimuli (see below). On each trial, one of these auditory stimuli was presented from a loudspeaker located directly in front of the participant at a distance of about 15 cm from the participant's eyes. Participants placed their hands on a table, at a distance of about 26 cm between the left and right index finger and the body midline. Tactile stimuli were presented using two 6 V solenoids, driving a metal rod with a blunt conical tip to the radial side of the middle phalanx of the left and right index fingers, making contact with a finger whenever a current was passed through the solenoid. The solenoids were attached to the fingers with white medical tape. White noise (65 dB SPL, measured from the position of the participants' head) was continuously present to mask any sounds made by the tactile stimulators. Tactile stimuli were vibrations, and these were generated by presenting a sequence of 20 rapidly delivered brief pulses. The stimulus onset asynchrony between successive pulses was 10 ms, corresponding to a stimulation frequency of 100 Hz. Tactile vibrations differed with respect to their intensity. To present 'weak' vibrations, which served as target stimuli, the contact time between rod and skin was set to 2 ms, followed by an 8 ms interpulse interval. To present 'strong' vibrations, which were non-target stimuli, contact time was set to 3 ms, followed by a 7 ms interpulse interval. Subjectively, these manipulations resulted in perceived vibrations with identical frequency, but different intensities. The duration of each vibratory stimulus was 200 ms.

2.3. Procedure

Sixteen experimental blocks, each consisting of 72 trials, were run. Each trial started with a 50 ms presentation of an auditory cue stimulus, followed after an interval of 650 ms by a peripheral tactile stimulus (200 ms duration). Inter-trial interval was 1000 ms. Participants were instructed to respond vocally (by saying "yes") whenever a tactile target (a soft vibration) was presented to the relevant hand (left or right). Which hand was relevant changed from trial to trial, and was indicated by the pitch of the auditory cue (low versus high). For five blind and five sighted participants, a high tone signalled that the left hand was relevant, while a low tone indicated that the right hand was relevant. This pitch-to-hand mapping was reversed for the other five blind and five sighted participants. The two auditory cues were presented in random order and with equal probability. In 48 trials per block, a tactile non-target stimulus (i.e., a strong vibration requiring no response) was presented with equal probability to the left or right hand. These non-targets were preceded with equal probability by either a high-pitch or low-pitch cue, resulting in a total of 12 non-target trials per block for each combination of cued hand (left versus right) and stimulus location (left versus right). In the remaining 24 trials per block, tactile target stimuli (soft vibrations) were presented with equal probability on the left or right hand. Sixteen of these trials (eight left and eight right) contained a tactile target stimulus at the relevant hand (as indicated by the preceding auditory cue), and only these stimuli required a vocal response. In the remaining eight trials (four left and four right), tactile targets were presented at the uncued hand and responses had to be withheld to these stimuli.

Participants were instructed to respond as quickly as possible only to soft tactile vibrations at the cued hand, and to ignore all non-targets at that hand, as well as all tactile stimuli presented to the uncued hand. A minimum of two training blocks were run prior to the first experimental block. These training blocks were identical to the experimental blocks, also being delivered in absolute darkness, to prevent sighted participants from utilizing (or memorizing) visual spatial cues when performing the tactile task.

2.4. Recording and data analysis

EEG was recorded with Ag-AgCl electrodes and linked-earlobe reference from Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8 and Oz (according to the 10–20 system), and from OL and OR (located halfway between O1 and P7, and O2 and P8, respectively). Horizontal EOG (HEOG) was recorded bipolarly from the outer canthi of both eyes. The impedance for all electrodes was kept below 5 k Ω . The amplifier band-pass was 0.1–40 Hz. EEG and EOG were sampled with a digitisation rate of 200 Hz and stored on disk. For each vocal response, voice onset times were measured using a voice key.

EEG and HEOG were epoched off-line into 1300 ms periods, starting 100 ms prior to cue onset and ending 500 ms after the onset of the peripheral stimulus on

each trial. 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 peripheral stimuli (relative to a 100 ms baseline preceding the onset of these stimuli). Trials with eyeblinks (Fpz exceeding $\pm 60 \mu\text{V}$ relative to baseline), horizontal eye movements (HEOG exceeding $\pm 30 \mu\text{V}$ relative to baseline) or other artefacts (a voltage exceeding $\pm 60 \mu\text{V}$ at any electrode location relative to baseline) were excluded from analysis. To detect smaller systematic deviations of eye position, indicating 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. Residual HEOG deviations remained below $\pm 3 \mu\text{V}$ throughout this interval for all early blind and sighted participants.

The EEG obtained in the cue–target interval in response to auditory cue stimuli was averaged separately for cues directing attention to the left versus right hand, respectively. Because trials containing tactile targets and non-targets were presented in random order, and the presence versus 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. Based on our previous work investigating ERP correlates of covert attention shifts in the cue–target interval (Eimer et al., 2002, 2003a, 2003b, 2004; Eimer & Van Velzen, 2002), mean amplitude values were computed at lateral anterior sites (F7/8, F3/4 and FC5/6), lateral central sites (T7/8, C3/4 and CP5/6) and lateral posterior sites (P7/8, P3/4 and OL/R) within two successive latency windows (300–500 and 500–700 ms relative to cue onset). These amplitude values were then analysed separately for lateral anterior, central and posterior electrodes, and separately by repeated measures ANOVAs for the between-subject factor group (blind versus sighted), and the within-subject factors electrode site (F7/8 versus F3/4 versus FC5/6, for anterior sites; T7/8

versus C3/4 versus CP5/6, for central sites and P7/8 versus P3/4 versus OL/R, for posterior sites), cued direction (leftward versus rightward shift of attention) and hemisphere (left versus right). Additional analyses were also conducted separately for the blind and sighted group, respectively. In all of these analyses, the presence of lateralised ERP modulations sensitive to the direction of a cued attentional shift will be reflected by significant hemisphere \times cued direction interactions.

The EEG obtained in response to peripheral tactile stimuli was averaged for non-target stimuli only (i.e., strong vibrations, which required no behavioural response), to avoid contamination by vocal responses, and to equate trials with respect to response-related factors, such as the difference between response execution versus response inhibition. Trials where false-positive vocal responses were recorded on non-target trials (occurring on only 0.6% of these trials for the blind group, and on 0.8% for the sighted group) were also excluded from analysis. Separate averages were computed for all combinations of cued direction and stimulus side (left versus right). Mean amplitude values were computed for measurement windows centred on the peak latencies of the somatosensory P100 and N140 components (90–120 and 130–170 ms post-stimulus, respectively). Sustained attentional ERP modulations at longer latencies were investigated within a latency window between 200 and 350 ms after stimulus onset. Analyses of somatosensory ERPs were conducted separately for lateral sites (F3/F4, C3/C4 and P3/P4) contralateral and ipsilateral to the side of the stimulated hand, as well as for midline electrodes (Fz, Cz and Pz), for the factors group, electrode site (frontal versus central versus parietal), attention (stimulus at cued location versus uncued location) and stimulus side. Again, separate analyses were also conducted for the blind and sighted groups, respectively. Where appropriate, Greenhouse–Geisser adjustments to the degrees of freedom were performed and the adjusted *p*-values are reported.

ERPs elicited in the cue-target interval Blind participants

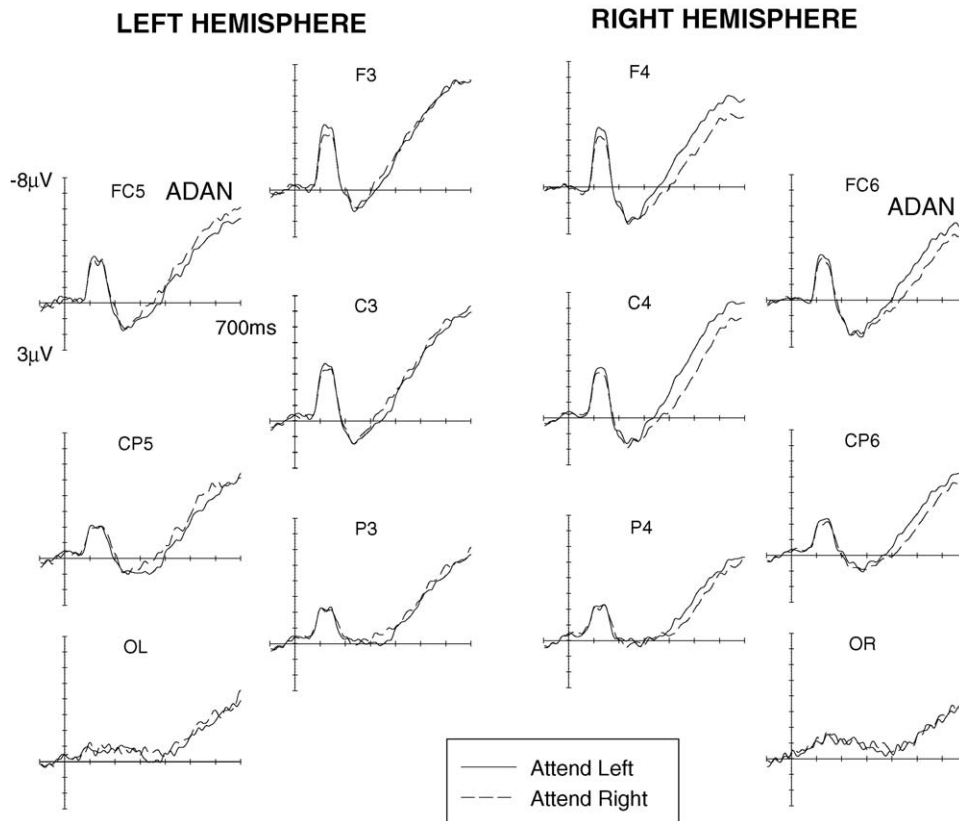


Fig. 1. Grand-averaged ERPs elicited for congenitally blind participants over the left and right hemisphere in the interval between cue onset and onset of the subsequent peripheral tactile stimulus. ERPs in response to auditory cues directing attention to the left side (solid lines), and cues directing attention to the right side (dashed lines) are shown separately. An anterior directing attention negativity (ADAN) was elicited at frontal and centroparietal sites.

3. Results

3.1. Behavioural performance

Mean vocal response times to cued tactile targets were 545 ms in the blind group, and 595 ms in the sighted group. This difference failed to reach significance ($t(18) < 1$). In the blind group, responses to tactile targets presented to the right hand were faster than responses to left hand targets (533 ms versus 557 ms), and this difference was significant ($t(9) = 2.3$; $p < .05$). No such difference was present for the sighted controls (595 and 594 ms for left and right targets).

False alarms to tactile non-target stimuli were present on 0.6% (blind group) and 0.8% (sighted group) of all non-target trials, and this difference was not significant. Blind participants missed 6.3% of all targets presented at cued locations, and produced false alarms on 6.9% of all trials where tactile targets were presented at uncued locations, as compared to 9.2% misses and 2.1% false alarms for the sighted group. Based on these data, sensitivity measures (d') and measures of response bias (C) were computed for both groups (derived from signal detection theory, and described in Macmillan & Creelman, 1991). Whereas d' did not differ significantly between the two groups, C was sig-

nificantly larger for sighted as compared to blind participants ($t(18) = 4.3$; $p < .001$), demonstrating that the blind used a more liberal response criterion.

3.2. ERP correlates of tactile-spatial orienting in the interval between auditory cues and peripheral tactile stimuli

Figs. 1 (blind group) and 2 (sighted control group) show ERPs elicited at lateral electrodes over the left and right hemisphere in the interval between cue onset and onset of the subsequent tactile stimulus, displayed separately for auditory cues directing tactile attention to the left side (solid lines) and to the right side (dashed lines). As can be seen from these figures, the pattern of ERP lateralisations sensitive to the direction of a cued attentional shift was remarkably similar across both groups. For blind as well as sighted participants, a negativity contralateral to the direction of an attentional shift (anterior directing attention negativity) was maximal at frontocentral electrodes, but also seemed to be present at more posterior sites (CP5/6). Importantly, no contralateral late directing attention positivity appeared to be present for either group.

The presence and time course of the ADAN component, its similarity across blind and sighted participants, and the absence

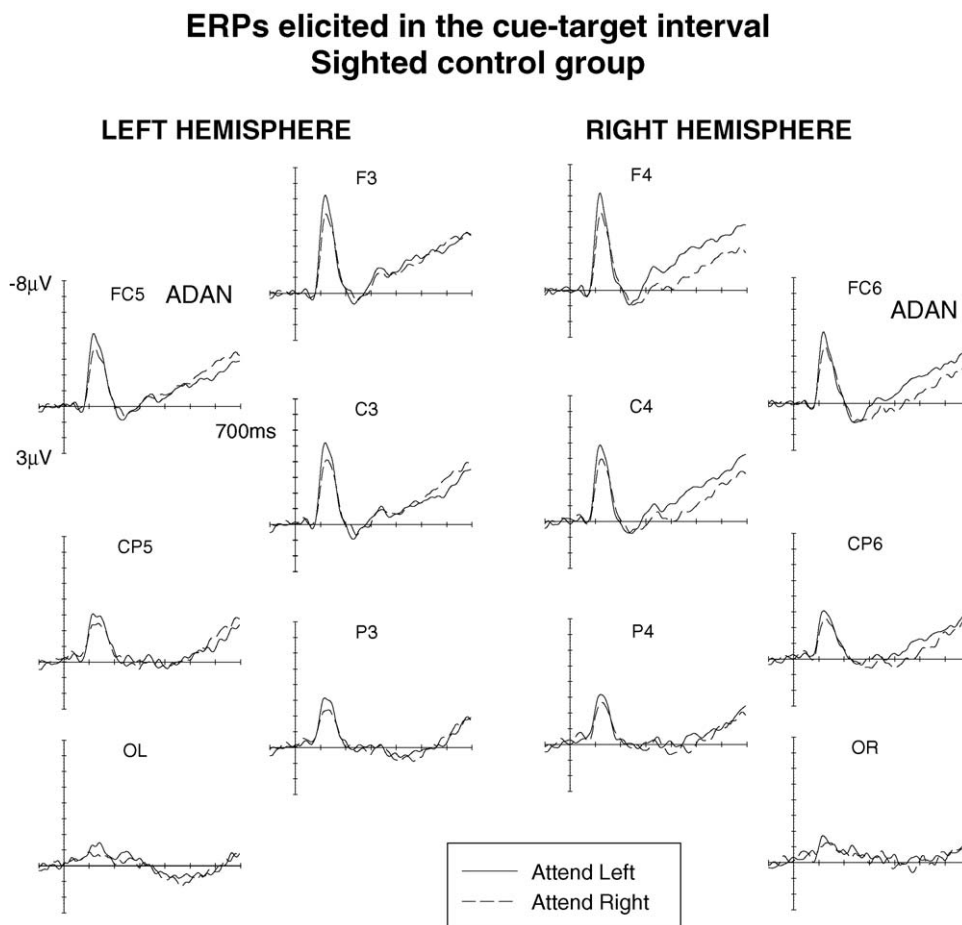


Fig. 2. Grand-averaged ERPs elicited for the sighted control group over the left and right hemisphere in the interval between cue onset and onset of the subsequent peripheral tactile stimulus, in response to auditory cues directing attention to the left side (solid lines), and cues directing attention to the right side (dashed lines). As for the blind group, an anterior directing attention negativity (ADAN) was present.

of a posterior LDAP component in both groups is further illustrated in Fig. 3, which shows difference waveforms obtained at lateral anterior (top panels), central (middle panels) and posterior electrode pairs (bottom panels), for the blind group (solid lines) and the sighted group (dashed lines). These difference waves were obtained by first subtracting ERPs recorded during attentional shifts to the right from ERPs elicited during leftward attentional shifts, and then subtracting the resulting difference waveforms at right electrodes from the difference waveforms emerging at corresponding electrodes over the left hemisphere. In the resulting double subtraction waveforms, an overall negativity contralateral to the direction of attentional shifts (ADAN) is reflected by positive amplitude values (downward-going deflections). Any contralateral positivity (LDAP) would have been reflected by negative values (upward deflections). Fig. 3 shows that an ADAN component was elicited at about 300 ms following cue onset in both groups. With the possible exception of F7/8, where the ADAN seems more pronounced in the sighted control group, overall this component appears to be similar in amplitude for both groups and remained present at lateral anterior and central sites throughout the cue–target interval. In contrast, there was no evidence that a posterior LDAP component was elicited

during later stages of the cue–target interval in either the blind or sighted group.

Statistical analyses confirmed these informal observations. ERPs elicited during leftward and rightward attention shifts were compared directly as a function of the recording hemisphere, prior to the double subtraction visualised in Fig. 3. No systematic ERP modulations sensitive to the direction of attentional shifts were observed within the first 300 ms following cue onset. In the 300–500 ms post-cue interval, significant hemisphere × cued direction interactions were present at anterior sites ($F(1,18)=20.4$; $p<.001$), as well as at central sites ($F(1,18)=18.1$; $p<.001$), reflecting the enhanced negativity contralateral to the direction of an attentional shift (ADAN) visible in Figs. 1–3. Importantly, there were no indications of any group × hemisphere × cued direction interactions at lateral anterior or central sites (both $F(1,18)<1$), indicating that there were no systematic differences between ADAN components triggered during shifts of tactile attention in the blind and sighted groups. Analyses conducted separately for each group confirmed the presence of significant hemisphere × cued direction interactions at lateral anterior and lateral central recording electrodes in both groups (all $F(1,9)>8.1$; all $p<.02$). No over-

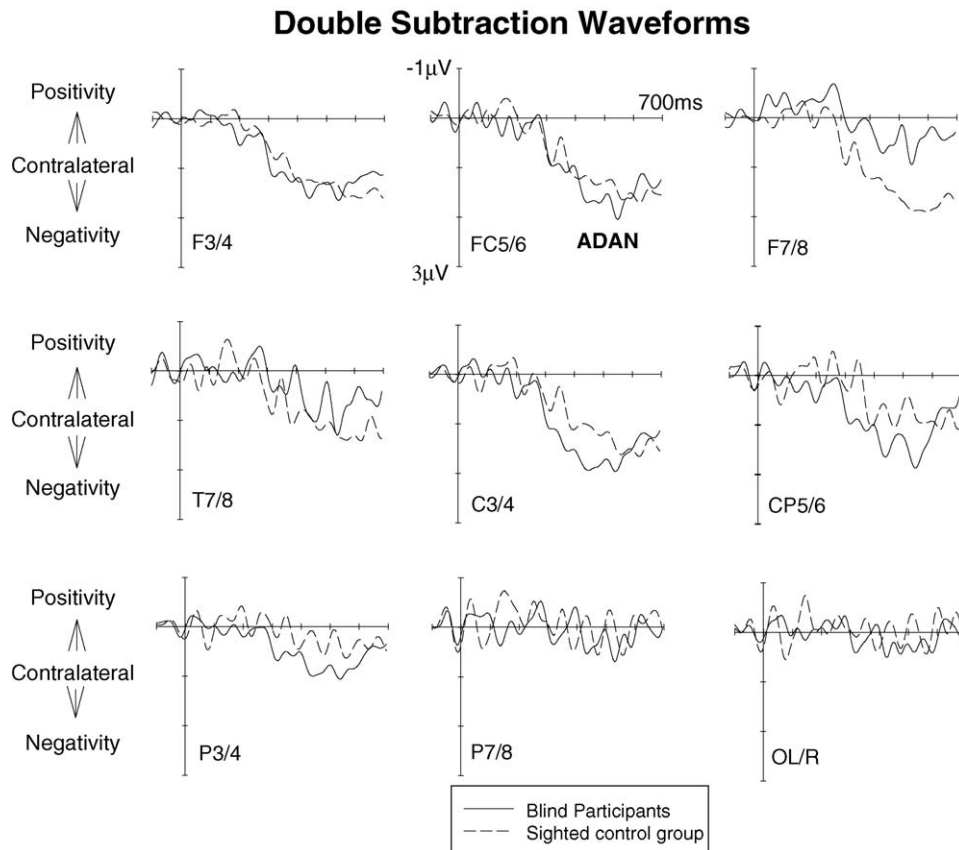


Fig. 3. Difference waveforms obtained at lateral anterior (top), central (middle) and posterior (bottom) electrodes in the 700 ms interval between cue onset and onset of the subsequent peripheral tactile stimulus, illustrating the time course of lateralised ERP modulations sensitive to the direction of attentional shifts for blind participants (solid lines) and for the sighted control group (dashed lines). Difference waveforms were generated by first subtracting ERPs in response to cues directing attention to the right from ERPs in response to cues directing attention to the left; and then subtracting the resulting difference waves at right electrodes from the difference waveform obtained for the corresponding left-hemisphere electrode. Enlarged negativities contralateral to the direction of attentional shifts are reflected by positive amplitude values (downward-going deflections). Enhanced contralateral positivities would have been reflected by negative values (upward-going deflections). Waveforms show a sustained anterior directing attention negativity (ADAN) for both groups, but no evidence for any posterior late directing attention positivity (LDAP) in either group.

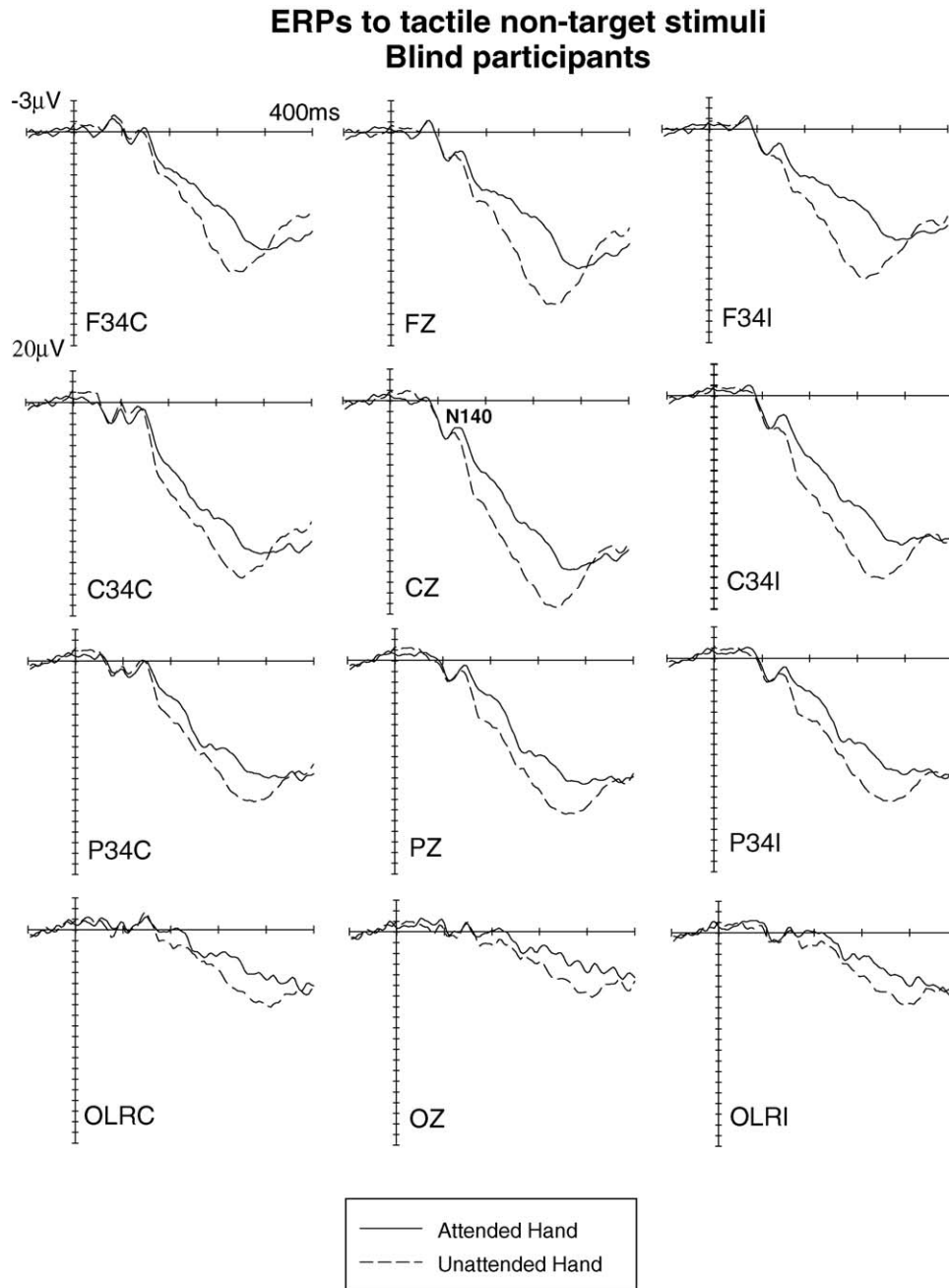


Fig. 4. Grand-averaged somatosensory ERPs elicited for congenitally blind participants at midline electrodes, and at sites contralateral (C) and ipsilateral (I) to the side of stimulus presentation, in response to tactile non-target stimuli at cued locations (solid lines) and uncued locations (dashed lines) in the 500 ms interval following stimulus onset.

all significant hemisphere \times cued direction interaction, or any group \times hemisphere \times cued direction interaction was present in the 300–500 ms interval at lateral posterior electrodes.

A similar pattern of results was found in the subsequent 500–700 ms post-cue interval (corresponding to the final 200 ms prior to the onset of a lateral tactile stimulus). Again, significant hemisphere \times cued direction interactions were present at lateral anterior ($F(1,18) = 42.7$; $p < .001$) as well as at lateral central electrodes ($F(1,18) = 28.8$; $p < .001$), demonstrating that the ADAN remained present during the later phase of the cue–target interval. As was the case for 300–500 ms time window, no

sign of any group \times hemisphere \times cued direction interaction was found at these electrode sites (both $F(1,18) < 1.8$). Again this strongly suggests that ADAN amplitudes did not differ systematically across the blind and sighted groups.³ Analyses

³ A four-way interaction (group \times hemisphere \times cued direction \times electrode site) was obtained at lateral anterior electrodes in the 500–700 ms measurement interval ($F(2,36) = 4.5$; $p < .03$; $\epsilon = .846$). Follow-up analyses revealed the presence of a significant group \times hemisphere \times cued direction interaction at F7/8 only. As can also be seen in Fig. 3, the late phase of the ADAN component tended to be larger for sighted relative to blind participants at this electrode pair.

conducted separately for each group confirmed that significant hemisphere × cued direction interactions were present at lateral anterior sites as well as at lateral central sites in both groups (all $F(1,9) > 11.5$; all $p < .01$).

Importantly, in contrast to previous investigations of cued shifts of spatial attention with sighted participants, there was no statistical evidence whatsoever for the presence of a posterior LDAP component during this 500–700 ms measurement interval. At lateral posterior electrodes, the overall hemisphere × cued direction interaction failed to reach significance ($F(1,18) < 1.5$). A hemisphere × cued direction × electrode site interaction ($F(2,36) = 7.1$; $p < .02$; $\epsilon = .837$) was accompanied

by a significant hemisphere × cued direction interaction at P3/4 ($F(1,18) = 9.4$; $p < .01$), reflecting the fact that the ADAN continued to be present, albeit in attenuated fashion, at this electrode pair (see Fig. 3). Importantly, however, there was no trace of any hemisphere × cued direction interaction at lateral posterior electrode pairs P3/4 and OL/R (both $F(1,18) < 1$), where the LDAP component was reliably found in previous studies of spatial orienting in sighted participants. In addition, not only were group × hemisphere × cued direction interactions not found at either of these electrode pairs (both $F(1,18) < 1$), but also follow-up analyses conducted separately for the blind and sighted groups failed to find any indication of hemisphere × cued direc-

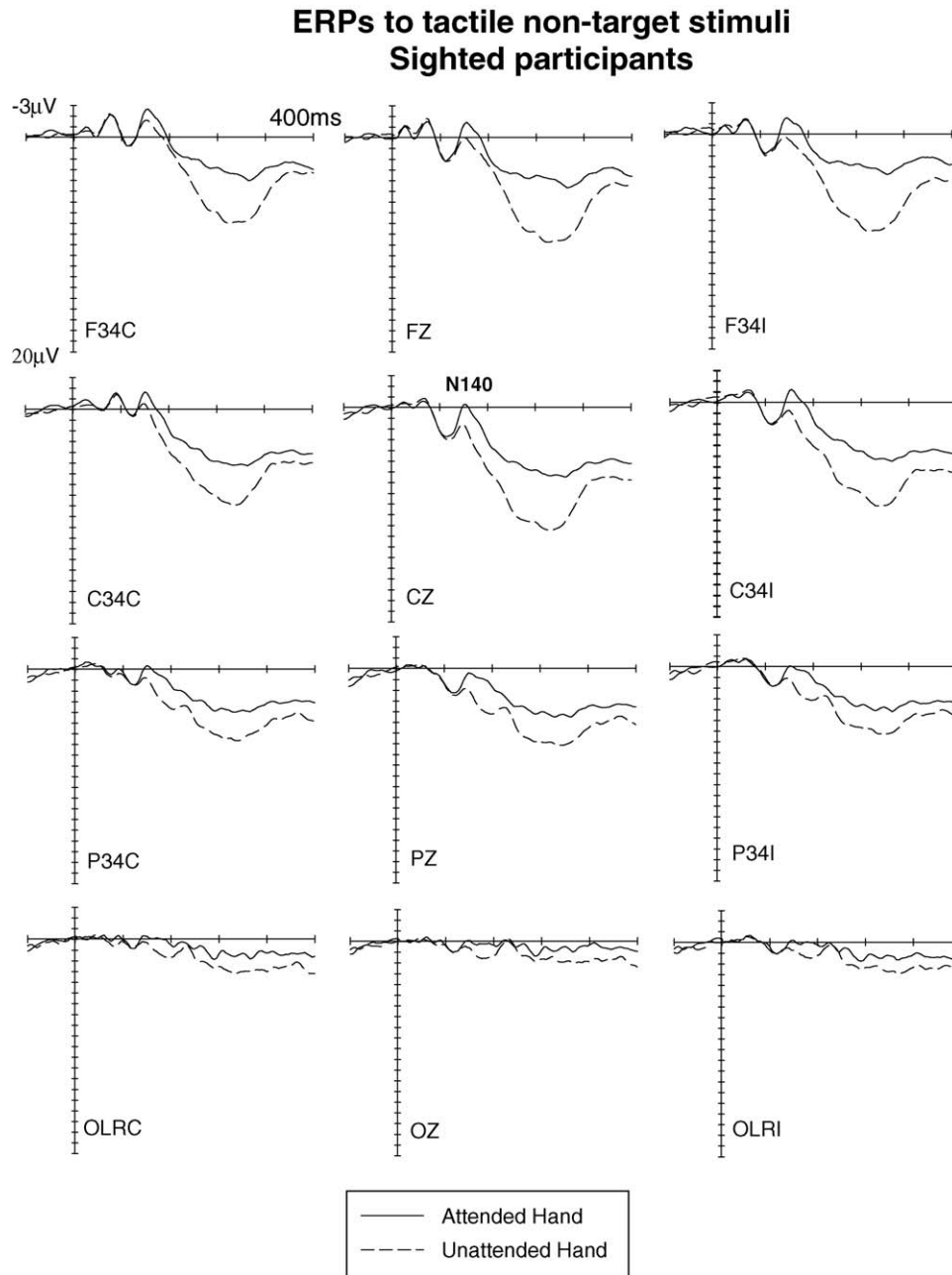


Fig. 5. Grand-averaged somatosensory ERPs elicited for the sighted control group at midline electrodes, and at sites contralateral (C) and ipsilateral (I) to the side of stimulus presentation, in response to tactile non-target stimuli at cued locations (solid lines) and uncued locations (dashed lines) in the 500 ms interval following stimulus onset.

tion interactions at P3/4 and OL/R, thereby strongly suggesting that the LDAP component was not only absent in the early blind group, but also for the sighted controls.

3.3. Effects of spatial attention on somatosensory ERPs

ERPs elicited in response to tactile non-target stimuli at cued locations (solid lines) and uncued locations (dashed lines) are shown in Fig. 4 for blind participants, and in Fig. 5 for the sighted control group. Waveforms are displayed separately for midline electrodes and for electrode sites contralateral (left panels) and ipsilateral (right panels) to the side of tactile stimulation. In both groups, somatosensory N140 components appear to be enhanced when tactile stimuli were presented to the attended hand relative to tactile stimuli presented to the unattended hand. In addition, a sustained enhanced negativity in response to attended relative to unattended tactile stimuli was elicited in a similar fashion for sighted and early blind participants.

No significant main effects of attention or group \times attention interactions were present for the P100 component (90–120 ms post-stimulus). In the N140 latency range (130–170 ms post-stimulus), main effects of attention were obtained at contralateral and ipsilateral electrodes as well as at midline sites (all $F(1,18) > 13.8$; all $p < .05$), demonstrating that directing tactile attention to one hand versus the other modulated N140 amplitudes. A main effect of group was significant at ipsilateral electrodes ($F(1,18) = 6.5$; $p < .02$), but failed to reach significance at contralateral and midline sites. This reflects the fact that somatosensory ERPs in the N140 time range tended to be generally more positive for the blind relative to the sighted group (see Figs. 4 and 5). However, and more importantly, no group \times attention interactions were present in the N140 time window (all $F(1,18) < 1$), suggesting that analogous attentional N140 modulations were elicited in the blind and sighted groups. Follow-up analyses conducted separately for both groups revealed reliable effects of attention on N140 amplitudes at ipsilateral, contralateral, and midline sites for the sighted group (all $F(1,9) = 5.1$; all $p < .001$), and reliable attentional effects at ipsilateral sites ($F(1,9) = 11.1$; $p < .01$) and at midline electrodes ($F(1,9) = 5.7$; $p < .05$) for the blind group.

In the 200–350 ms measurement window, main effects of attention were obtained at contralateral, ipsilateral, as well as midline sites (all $F(1,18) > 39.5$; all $p < .001$), reflecting the sustained enhanced negativity for attended relative to unattended tactile stimuli shown in Figs. 4 and 5. Main effects of group were also present at these sites (all $F(1,18) > 7.1$; all $p < .02$), as ERPs were generally more positive in the blind as compared to the sighted group during this time window. However, analogous to the results found for the N140 component, there was no indication of any group \times attention interaction (all $F(1,18) < 1$) suggesting that attentional ERP modulations triggered between 200 and 350 ms post-stimulus were comparable in size across blind and sighted participants. Figs. 4 and 5 suggest that at longer latencies, this attentional negativity might extend to more posterior (occipital) sites, particularly in the early blind group. To investigate this, additional post hoc analyses were conducted for ERP waveforms obtained at Oz, OL and OR between 300

and 400 ms after stimulus onset. A main effect of attention was obtained for the blind group ($F(1,9) = 9.0$; $p < .02$), although this effect was not significant for sighted participants ($F(1,9) = 2.5$; $p < .15$). However, this difference was not substantiated by an overall significant group \times attention interaction.

4. Discussion

The main aim of the present ERP experiment was to investigate the role of visual spatial information in the control of tactile attention shifts. ERP correlates of tactile attention were measured under conditions where visual spatial information was permanently or temporarily unavailable. Ten participants who were either blind from birth or had lost all vision during the first 2 years of life and 10 age-matched controls were instructed to direct attention to their left or right hand (as indicated by an auditory attention cue presented at the start of each trial), in order to detect infrequent tactile targets when these were delivered to this relevant hand. This task was performed in a dark experimental booth. Processes involved in the control of attentional orienting were investigated by measuring ERPs during the cue–target interval, and effects of spatial attention on somatosensory processing were studied by comparing somatosensory ERPs to tactile non-target stimuli at attended versus unattended locations.

Attentional control processes (and their electrophysiological correlates) that are based on visually mediated representations of external space should depend critically on the availability of visual spatial information or visual imagery, and therefore should be entirely absent during attentional orienting in the early blind. In contrast, control processes that operate independently of visually mediated spatial information should be preserved in the early blind. The pattern of ERP results obtained for the early blind group during covert shifts of spatial attention in the present experiment was clear-cut. Whereas an anterior directing attention negativity was clearly present, there was no evidence whatsoever for any posterior late direction attention positivity. Essentially the same pattern of results was also obtained for the age-matched sighted control participants, who performed the tactile attention task in complete darkness. Again, the ADAN component was present, but the LDAP was absent.

This dissociation between ADAN and LDAP components is in line with the hypothesis that these two components are linked to separable attentional control mechanisms that differ in terms of their spatial reference frame. The presence of an ADAN in the early blind strongly suggests that this component is linked to attentional control processes that are entirely independent of any visually mediated spatial representation, and is thus consistent with our earlier suggestion that this component might predominantly reflect the control of attention within a somatotopically defined spatial reference frame (Eimer et al., 2003a). Attentional control mechanisms based on somatotopically defined spatial coordinates are unlikely to be affected by the early loss of visual spatial information. The lack of an LDAP in the present study for either group diverges markedly from the findings from previous ERP investigations where sighted participants were cued to shift attention towards the location of task-relevant tactile events in

a lit environment (e.g., Eimer et al., 2002, 2003a, 2004). The absence of the LDAP also contrasts with earlier studies where ERP correlates of visual or auditory attention shifts were measured (e.g., Hopf & Mangun, 2000; Nobre et al., 2000; Green et al., 2005). In all of these studies, LDAP components were reliably and consistently elicited in the cue–target interval. Given these earlier results, the absence of the LDAP in the early blind as well as in the sighted control group is remarkable, and thus suggests that the attentional control processes reflected by this component are strongly dependent upon visually defined external spatial reference frames.

To provide additional evidence for this conclusion, we tested a further eight right handed and normally sighted participants (five females, three males, aged between 20 and 69 years, mean age 40 years) using procedures identical to the experiment reported above, except for the fact that all blocks were delivered under normal illumination conditions. Fig. 6 shows difference waveforms analogous to those shown in Fig. 3 for lateral anterior electrodes F3/4 (top) and lateral occipital electrodes OL/R (bottom),

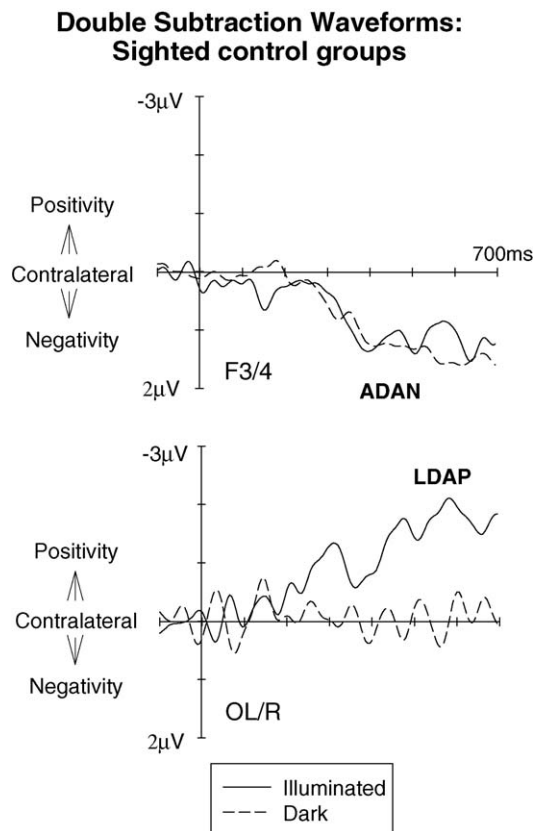


Fig. 6. Difference waveforms obtained at lateral anterior electrodes F3/4 (top) and at lateral occipital electrodes OL/R (bottom) in the 700 ms interval between cue onset and onset of the subsequent peripheral tactile stimulus, generated in the same way as the difference waves shown in Fig. 3, with positive amplitude values reflecting an enlarged negativity contralateral to the direction of a cued attentional shift, and negative values reflecting an enhanced contralateral positivity. Results for a group of eight sighted control participants who performed the tactile attention task under a normal illumination conditions (solid lines) are contrasted with the results obtained for sighted participants in the main experiment, who performed the same task in darkness (dashed lines). While the ADAN was present in both groups, the LDAP component was only triggered for the former group.

obtained for the eight sighted participants tested in this control experiment (solid lines), and for the 10 sighted participants tested for the main experiment in the dark (dashed lines). While there was no obvious difference between these two groups for the ADAN component, the posterior LDAP was clearly present when participants were tested in a lit environment. This contrasts markedly with the results from the main study, where the LDAP was entirely absent (see Fig. 6, bottom). To substantiate these observations, ERPs obtained for these eight new participants in response to cues directing tactile attention to the left versus right side were analysed, using identical statistical procedures to the ones described above. Significant hemisphere \times cued direction interactions were present in the 300–500 ms post-cue interval at lateral anterior electrodes ($F(1,7) = 8.0$; $p < .03$), reflecting the presence of the ADAN component. More importantly, highly significant hemisphere \times cued direction interactions were now also present during the 500–700 post-cue interval at lateral occipital electrodes OL/R ($F(1,7) = 13.6$; $p < .001$). This result confirms findings from previous studies (Eimer & Van Velzen, 2002; Eimer et al., 2003b) that the LDAP is elicited during shifts of tactile attention induced by centrally presented symbolic auditory cues under conditions where visual spatial information is continuously available.

The hypothesis that ADAN and LDAP reflect functionally distinct attentional control mechanisms, which mediate the control of attention shifts within anatomically defined (somatotopic) and external (visually mediated) frames of reference, respectively, is also in line with the results of two previous studies demonstrating dissociations between the ADAN and LDAP. Manipulating the distance between hands in external space was found to affect LDAP, but not ADAN amplitudes (Eimer et al., 2004), whereas crossing the hands (and thus inducing a conflict between external and somatotopically defined reference frames) resulted in a polarity reversal of the ADAN when considered in terms of external space (Eimer et al., 2003a). However, results from another recent study (Eimer et al., 2003b) appear to contradict the present finding that the LDAP component was completely absent not only in the early blind, but also in the sighted control group. In this study, an attenuated, but statistically significant LDAP was found when sighted participants directed their attention to task-relevant locations of tactile events in the dark. The presence of a residual LDAP in this experiment could indicate that participants were still able to use stored visual spatial information when directing attention to their left or right hand. Half of them completed the tactile attention task under normal illumination conditions before performing the same task in the dark, all were familiarized with task conditions in a lit environment, and some had participated in previous attention experiments in the same lab, and were thus familiar with its general spatial layout. Together, these factors may have been sufficient to enable these participants to employ stored visual spatial representations when directing attention to the left versus right hand in the dark, and this might have been reflected by a residual LDAP component. In contrast, all sighted control participants in the present experiment were newly recruited, and were not allowed any task practice under normal illumination conditions, in order to eliminate the possibility that they

would use visual imagery when performing the tactile task in the dark.

The conclusion that the LDAP component appears to be closely linked to attentional control mechanisms that operate on the basis of visually mediated representations of external visual space differs from our earlier claim (Eimer et al., 2002) that attentional orienting is mediated by purely multimodal (i.e., modality-unspecific) control systems. The fact that the LDAP was absent during shifts of tactile attention in the early blind and for sighted control participants in the dark suggests that visual spatial information is critical for the attentional control processes reflected by this component. Whenever visual information is available, shifts of attention towards relevant tactile events in the sighted appear to be partially based on control processes that specify task-relevant external locations of tactile events in visually defined spatial coordinates, and thus give rise to an LDAP component. When task-specific visual spatial information is either permanently absent (in the early blind) or temporarily unavailable (as for the sighted control group in the present experiment), and visual spatial coordinates thus cannot be used to anchor shifts of attention in external space, such control processes are not activated, and the LDAP is absent.

It is remarkable that in spite of the absence of visual spatial information during attentional orienting, and the resulting absence of an LDAP in the cue–target interval, attentional modulations of somatosensory ERPs observed in the present experiment in the early blind group and in the sighted control group were very similar to the effects of tactile-spatial attention shifts obtained under normal illumination conditions in previous ERP studies with sighted participants (cf., Michie et al., 1987; Eimer & Forster, 2003). In both groups, tactile stimuli delivered to the attended hand elicited enhanced somatosensory N140 components as well as a subsequent sustained attentional negativity when compared to tactile stimuli presented to the unattended hand. The presence of such attentional modulations of somatosensory ERPs indicates that the capacity to selectively process tactile information from the task-relevant cued hand was largely unaffected by the lack of visual spatial information in either group. Furthermore, there were no statistically significant differences in the effects of spatial attention on somatosensory ERPs between the early blind and sighted groups. This is in line with previous investigations (Liotti et al., 1998; Hötting et al., 2004) that also failed to demonstrate any systematic differences in attentional modulations of auditory and somatosensory ERP components between the blind and the sighted. If the early loss of visual information had resulted in compensatory improvements in the level of spatial selectivity within touch, one would expect to find earlier, or more pronounced attentional modulations of somatosensory ERP waveforms for early blind as compared to sighted participants. The fact that this was not observed in the present experiment indicates that under conditions where attention is directed to one hand versus the other, similar somatosensory processing stages are selectively modulated by tactile-spatial attention in the early blind and in the sighted.

There is, however, also some previous evidence for topographic differences of attentional ERP modulations between

blind and sighted groups in other tasks requiring selective stimulus processing. For example, Alho et al. (1993) found that the attentional processing negativity elicited by attended auditory events was distributed more posterior in the blind than in the sighted. Other studies (Kujala et al., 1995; Röder, Rösler, & Neville, 1999a) demonstrated similar topographic differences between blind and sighted groups in response to deviant auditory or tactile events. These results have generally been interpreted as evidence for cortical reorganisation processes in the early blind, with posterior brain areas normally involved in vision now participating in the selective processing of auditory and tactile events. In the present study, significant attentional modulations of somatosensory ERPs were found beyond 300 ms post-stimulus at occipital recording sites for the early blind group, but not for the sighted control group. While this observation could point towards cortical reorganisation processes, the difference in the absolute size of occipital attention effects between groups was relatively small (see Figs. 4 and 5), and did not result in a significant group \times attention interaction.

There were also some potentially interesting performance differences between blind and sighted participants. While the blind responded faster when tactile target stimuli were presented to the right versus left hand, no such hand-specific RT difference was found for the sighted group. This right hand advantage in the predominantly right handed blind group could be linked to the dominance of the right index finger in Braille reading. It has been shown that Braille reading can produce neuroplastic changes (e.g., Pascual-Leone & Torres, 1993; Sadato et al., 1996; Buchel, Price, Frackowiak, & Friston, 1998), although current evidence as to whether or not such changes also result in improved tactile acuity is mixed (e.g., Van Boven, Hamilton, Kauffman, Keenan, & Pascual-Leone, 2000; Grant, Thiagarajah, & Sathian, 2000). Nevertheless, when sighted adults are deprived of vision for an extended period, and thus forced to rely on non-visual information alone, their ability to discriminate Braille patterns with their dominant hand improves more rapidly (Kauffman, Théoret, & Pascual-Leone, 2002; see also Weisser, Stilla, Peltier, Hu, & Sathian, 2005). Although this and other previous studies of tactile perception in blind or visually deprived sighted participants have focussed on accuracy rather than response speed, it is entirely plausible that increased practice in tactile discrimination with the dominant hand through Braille reading could also result in faster discrimination between tactile targets and non-targets.

One further difference between early blind and sighted participants was that the former adopted a more liberal response criterion when reporting the presence versus absence of tactile target stimuli. This observation may be related to the previous finding that blind Braille readers mislocalize tactile events presented to specific fingers more often than sighted controls (Sterr, Green, & Elbert, 2003), which also suggests that the blind and the sighted adopt different strategies in tactile discrimination tasks. Sighted participants may use more conservative response criteria when localizing events on the basis of somatosensory information, because visual input is often also available to guide their task performance. In contrast, the blind rely on touch as the primary source for constructing meaningful representations of

the surrounding environment through active exploration and the combination of serially acquired tactile information. Because this is very time-consuming, blind individuals may sometimes use more liberal decision criteria, in order to compensate for the extra time required by tactile exploration.

In spite of such performance differences, the overall pattern of ERP results obtained for the early blind group and the group of age-matched sighted control participants was remarkably similar. There were no statistically reliable differences between the two groups either in terms of lateralised ERP components triggered during the cue–target interval, or in terms of attentional modulations of somatosensory ERP waveforms. This suggests that the processes involved in the control of tactile attention shifts and the effects of tactile-spatial attention are very similar in the early blind and in sighted participants when they are directing tactile attention in the dark. Whilst the absence of the posterior LDAP component in both groups indicates that this component is linked to the guidance of attention shifts in visually mediated space, the lack of visual spatial coordinates in the present study did not appear to have a detrimental effect on attentional selectivity in somatosensory processing. Finally, it needs to be noted that these conclusions are based on results obtained under conditions where the attentional selection task was relatively easy. Selecting the left versus right hand in anticipation of task-relevant events delivered to this hand does not impose very high demands on spatially selective somatosensory processing. It is possible that when these demands are increased, for example, by presenting all stimuli to the same hand or to the same finger, systematic ERP differences between early blind and sighted participants might emerge.

In summary, the present study has provided new evidence for a functional dissociation between attentional control processes that give rise to lateralised ERP components during covert spatial orienting. The processes reflected by the ADAN component appear to be entirely independent of a visual spatial reference frame, as they are activated during shifts of attention in the early blind. In contrast, the availability of visual spatial representations clearly plays a critical role for the posterior LDAP component, which is likely to reflect processes that guide attentional shifts towards task-relevant locations within visually defined coordinates of external space.

Acknowledgements

This research was supported by a grant from the Wellcome Trust (UK). M.E. holds a Royal Society–Wolfson Research Merit Award.

References

- Alho, K., Kujala, T., Paavilainen, P., Summala, H., & Näätänen, R. (1993). Auditory processing in visual brain areas of the early blind: Evidence from event-related potentials. *Electroencephalography and Clinical Neurophysiology*, *86*, 418–427.
- Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representations of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience*, *20*, 303–330.

- Buchel, C., Price, C., Frackowiak, R. S. J., & Friston, K. (1998). Different activation patterns in the visual cortex of late and congenitally blind subjects. *Brain*, *121*, 409–419.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.
- Eimer, M., & Driver, J. (2001). Crossmodal links in endogenous and exogenous spatial attention: Evidence from event-related brain potential studies. *Neuroscience and Biobehavioral Reviews*, *25*, 497–511.
- Eimer, M., & Forster, B. (2003). Modulations of early somatosensory ERP components by transient and sustained spatial attention. *Experimental Brain Research*, *151*, 24–31.
- Eimer, M., Forster, B., Fieger, A., & Harbich, S. (2004). Effects of hand posture on preparatory control processes and sensory modulations in tactile-spatial attention. *Clinical Neurophysiology*, *115*, 596–608.
- Eimer, M., Forster, B., & Van Velzen, J. (2003). Anterior and posterior attentional control systems use different spatial reference frames: ERP evidence from covert tactile-spatial orienting. *Psychophysiology*, *40*, 924–933.
- Eimer, M., Van Velzen, J., Forster, B., & Driver, J. (2003). Shifts of attention in light and in darkness: An ERP study of supramodal attentional control and crossmodal links in spatial attention. *Cognitive Brain Research*, *15*, 308–323.
- Eimer, M., & Van Velzen, J. (2002). Crossmodal links in spatial attention are mediated by supramodal control processes: Evidence from event-related potentials. *Psychophysiology*, *39*, 437–449.
- Eimer, M., Van Velzen, J., & Driver, J. (2002). Crossmodal interactions between audition, touch and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *Journal of Cognitive Neuroscience*, *14*, 254–271.
- Farah, M. J., Wong, A. B., Monheit, M. A., & Morrow, L. A. (1989). Parietal lobe mechanisms of spatial attention: Modality-specific or supramodal? *Neuropsychologia*, *27*, 461–470.
- Grant, A. C., Thiagarajah, M. C., & Sathian, K. (2000). Tactile perception in blind Braille readers: A psychophysical study of acuity and hyperacuity using gratings and dot patterns. *Perception and Psychophysics*, *62*, 301–312.
- Green, J. J., Teder-Sälerjärvi, W. A., & McDonald, J. J. (2005). Control mechanisms mediating shifts of attention in auditory and visual space: A spatio-temporal ERP analysis. *Experimental Brain Research*, *166*, 358–369.
- Harter, M. R., Miller, S. L., Price, N. J., LaLonde, M. E., & Keyes, A. L. (1989). Neural processes involved in directing attention. *Journal of Cognitive Neuroscience*, *1*, 223–237.
- Hötting, K., Rösler, F., & Röder, B. (2004). Altered auditory–tactile interactions in congenitally blind humans: An event-related potential study. *Experimental Brain Research*, *159*, 370–381.
- Hopf, J. M., & Mangun, G. R. (2000). Shifting visual attention in space: An electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology*, *111*, 1241–1257.
- Kauffman, T., Théoret, H., & Pascual-Leone, A. (2002). Braille character discrimination in blindfolded human subjects. *Neuroreport*, *13*, 571–574.
- Kujala, T., Alho, K., Kekoni, J., Hämäläinen, H., Reinikainen, K., Salonen, O., et al. (1995). Auditory and somatosensory event-related brain potentials in early blind humans. *Experimental Brain Research*, *104*, 519–526.
- LaBerge, D. (1995). *Attentional processing*. Cambridge, MA: Harvard University Press.
- Liotti, M., Ryder, K., & Woldorff, M. G. (1998). Auditory attention in the congenitally blind: Where, when, and what gets reorganized? *Neuroreport*, *9*, 1007–1012.
- Macmillan, N. A., & Creelman, C. D. (1991). *Detection theory: A user's guide*. Cambridge: Cambridge University Press.
- Mangun, G. R., & Hillyard, S. A. (1991). Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception and Performance*, *17*, 1057–1074.
- Michie, P. T., Bearpark, H. M., Crawford, J. M., & Glue, L. C. T. (1987). The effects of spatial selective attention on the somatosensory event-related potential. *Psychophysiology*, *24*, 449–463.

- Näätänen, R. (1982). Processing negativity: An evoked-potential reflection of selective attention. *Psychological Bulletin*, *92*, 605–640.
- Nobre, A. C., Sebestyen, G. N., & Miniussi, C. (2000). The dynamics of shifting visuospatial attention revealed by event-related brain potentials. *Neuropsychologia*, *38*, 964–974.
- Pascual-Leone, A., & Torres, F. (1993). Plasticity of the sensorimotor cortex representation of the reading finger in Braille readers. *Brain*, *116*, 39–52.
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42.
- Röder, B., & Neville, H. J. (2003). Developmental functional plasticity. In J. Grafman & I. Robertson (Eds.), *Plasticity and rehabilitation. Handbook of neuropsychology*: vol. 9, (vol. 9, (pp. 231–270). Amsterdam: Elsevier.
- Röder, B., Rösler, F., & Neville, H. J. (1999). Effects of interstimulus interval on auditory event-related potentials in congenitally blind and normally sighted humans. *Neuroscience Letters*, *264*, 53–56.
- Röder, B., Teder-Salejärvi, W., Sterr, A., Rösler, F., Hillyard, S. A., & Neville, H. J. (1999). Improved auditory spatial tuning in blind humans. *Nature*, *400*, 162–166.
- Sadato, N., Pascual-Leone, A., Grafman, J., Ibanez, V., Delber, M. P., Dold, G., et al. (1996). Activation of the primary visual cortex by Braille reading in blind subjects. *Nature*, *380*, 526–528.
- Sterr, A., Green, L., & Elbert, T. (2003). Blind Braille readers mislocate tactile stimuli. *Biological Psychology*, *63*, 117–127.
- Van Boven, R. W., Hamilton, R. H., Kauffman, T., Keenan, J. P., & Pascual-Leone, A. (2000). Tactile spatial resolution in blind Braille readers. *Neurology*, *54*, 2230–2236.
- Van Velzen, J., & Eimer, M. (2003). Early posterior ERP components do not reflect the control of attentional shifts towards expected peripheral events. *Psychophysiology*, *40*, 827–831.
- Weisser, V., Stilla, R., Peltier, S., Hu, X. P., & Sathian, K. (2005). Short-term visual deprivation alters neural processing of tactile form. *Experimental Brain Research*, *166*, 572–582.
- Yamaguchi, S., Tsuchiya, H., & Kobayashi, S. (1994). Electroencephalographic activity associated with shifts of visuospatial attention. *Brain*, *117*, 553–562.