

Research report

Shifts of attention in light and in darkness: an ERP study of supramodal attentional control and crossmodal links in spatial attention

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Abstract

Crossmodal links in spatial attention, uncovered by recent behavioural and electrophysiological studies, have been interpreted as evidence for supramodal processes controlling shifts of attention. However, previous experiments have usually been conducted in illuminated environments. Continuously available visuo-spatial information might result in shifts of attention being primarily guided by visible information, even when another modality is task-relevant. The present ERP study evaluated this. A symbolic auditory cue directed attention to the left or right hand. Participants had to detect infrequent tactile targets delivered to the cued hand, while ignoring any visual stimuli. Stimuli were presented either in a lit environment or in darkness. Although continuous ambient visuo-spatial information was eliminated in the latter condition, processing of task-irrelevant visual events was still modulated by spatial attention for the tactile task. Moreover, ERP correlates of attentional shifts in the cue–target interval were similar for both illumination conditions. This was further confirmed in a follow-up experiment where the darkness condition was repeated without any peripheral visual stimulation ever occurring. These findings demonstrate that the ERP correlates of crossmodal attention (both preparatory effects in the cue–target interval, and also modulations of stimulus-evoked components) do not depend on selection being guided by ambient visible information in a lit environment. They suggest instead that spatial shifts of attention are controlled supramodally.

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1. Introduction

When people endogenously direct their covert spatial attention to a particular location, sensory processing can be enhanced there relative to other locations, as revealed by both psychophysical and neurobiological measures (see Ref. [3] for a recent review). For instance, an extensive literature concerning event-related potentials (ERPs) recorded from the scalp has shown that relatively early, modality-specific sensory components show larger amplitudes for stimuli presented at covertly attended versus unattended locations (e.g., Ref. [17]). Such results have been shown for endogenous spatial attention in visual (e.g.,

Refs. [5,24]), auditory (e.g., Refs. [1,27]) or tactile experiments (e.g., Refs. [14,26]).

While the majority of ERP studies on covert spatial attention have focused on such sensory modulations, a few studies have also examined preparatory control states (arising prior to onset of stimulation) that may induce such sensory modulations, reflecting an anticipatory attentional shift. For instance, Harter et al. [15] measured ERPs during shifts of covert visual attention to a left or right location. These were triggered by a central arrow cue indicating the side of an upcoming visual event. An early negative deflection at posterior electrodes contralateral to the direction of the induced attentional shift was observed (early directing attention negativity, or EDAN; see also Refs. [28,34,35]). An enhanced contralateral positivity at posterior electrodes (late directing attention positivity, LDAP) emerged during later phases of the cue–target interval. In

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addition, Mangun [23] (see also Ref. [19]) and Nobre et al. [28] observed enhanced negativities at frontal electrodes contralateral to the direction of attentional shifts, between 300 and 500 ms after onset of the central cue (anterior directing attention negativity, ADAN). All these effects (i.e., the EDAN, LDAP, and ADAN) were assumed to reflect successive phases in the control of covert *visual* orienting.

Although spatial attention has traditionally been studied separately for different sensory modalities, there is now a growing literature on *crossmodal* interactions in exogenous (involuntary) and endogenous (voluntary) spatial attention (see Refs. [4,6,9,33]). For example, masked visual stimuli are detected more accurately when preceded by irrelevant auditory events at the same location [25]. For the case of endogenous spatial attention, crossmodal interactions have now been demonstrated with psychophysical measures plus electrophysiological measures such as ERPs. For instance, Spence and Driver [30] (see also Ref. [31]) found that when covert attention was directed to one side in anticipation of a visual target, auditory (or tactile) performance was enhanced at that location as well as visual performance, even if the auditory or tactile targets were more likely to appear elsewhere. Electrophysiological studies using ERP methods have also revealed crossmodal interactions in endogenous spatial attention, providing evidence on the levels of processing and timing of the neural responses affected by these crossmodal interactions (see Refs. [7,8,10–12,16,32]). The ERP results to date have consistently suggested that relatively early stages of visual, auditory, and tactile information processing (i.e., stages traditionally considered to reflect ‘unimodal’ sensory processing) can be affected by crossmodal interactions in endogenous spatial attention (see Refs. [6,9] for more detailed reviews of these findings and their implications, and [21,22] for further evidence from recent brain imaging studies).

Such crossmodal modulations raise questions concerning attentional control mechanisms responsible for allocating attention to specific locations. The possibility that spatial attention might be controlled supramodally was raised by Ward [33] for exogenous attention. Effects of endogenous attentional shifts within one modality upon sensory-specific ERP components for stimuli in another modality might analogously be taken to suggest that locations are initially selected at a multimodal level of spatial representation (see Ref. [13]), with this selection then feeding down to influence ‘unimodal’ sensory processes for incoming stimuli. Alternatively, initial spatial selection might arise primarily within a given task-relevant modality, and then spread to other modalities [30].

As noted above, relatively few ERP studies have examined the attentional control processes arising in anticipation of a stimulus, rather than sensory modulations in response to the stimulus when it does appear. Moreover, these studies have examined such control processes almost exclusively within vision, under conditions where visual

targets were anticipated at a specific location (see Refs. [15,19,23,28,34,35]). However, Eimer et al. [12] recently whether preparatory ERP components might operate multimodally. Since this study provides the foundation for the present experiment, we describe it in some detail. Covert attention was directed to the right or left by a central visual precue in order to judge either auditory or tactile targets at just the cued side. The relevant modality (audition or touch) differed between blocks, and any stimuli in other modalities were to be entirely ignored. Lateralised ERP modulations sensitive to the direction of spatial orienting were found in the cue–target interval. An enhanced anterior negativity contralateral to the cued side (ADAN [19,23,28]) was followed by an enhanced contralateral positivity at posterior sites (LDAP [15,28,34,35]). Importantly, these effects were very similar regardless of whether attention had to be directed to the location of relevant auditory events, or to the location of relevant tactile events instead, in other blocks (see also Ref. [12]). Moreover, these lateralised ERP modulations also closely resembled ERP modulations previously observed during shifts of visual attention [15,18,23,28]. This finding that ERP modulations sensitive to the direction of spatial orienting are highly similar during shifts of attention in anticipation of relevant visual, auditory, or tactile stimuli, appears to support the notion of the task-relevant location being selected by supramodal control processes.

Based on these results, Eimer et al. [12] suggested that the ADAN may reflect supramodal processes within an ‘anterior attention system’ [29] controlling spatial parameters of attentional shifts, regardless of sensory modality. The posterior LDAP was hypothesized to reflect activity in posterior parietal areas, involved not only in the orienting of spatial attention [20] but also in the integration of information from different sensory modalities (e.g., Ref. [2]). However, to date such proposals were based on the results of just a single ERP study [12] which requires further corroboration and extension. Moreover, these suggestions departed from previous proposals based on studies of control processes in purely visual paradigms. For instance, Harter et al. [15] argued that the posterior LDAP component reflects a spatially selective activation of *modality-specific visual* areas, in anticipation of relevant visual events at the specified location. Initially, such a proposal might appear inconsistent with the recent observation [12] that an LDAP is elicited not only when attention is allocated to the expected location of visual stimuli, but also during analogous shifts of tactile or auditory attention. Why should visual areas be selectively activated in anticipation of auditory or tactile events at specific locations?

A possible answer to this question arises when considering that all the experiments to date were implemented in lit environments, where the locations of possible auditory and tactile targets were *visible*. That is, the ambient visual array provided visible sources of information about relevant stimulus locations, even for anticipated stimuli in

non-visual modalities (e.g., the locations of visible loudspeakers for audition, or the positions of the hands and arms for touch). As this visuo-spatial information was continuously available throughout the experiment, participants might have relied primarily on visual representations when directing attention to the left or right side, even when their task was to detect just auditory or tactile events at the task-relevant location. Vision can provide better spatial acuity than other modalities, and thus might in principle allow more accurate ‘anchoring’ of spatial attention.

Under conditions where continuous visible information could be used to anchor spatial selection in this way, any ERP modulations sensitive to the direction of an attentional shift might then reflect shifts of attention within *visible* space, rather than the activity of a supramodal attentional control system. If so, then the LDAP might indeed reflect preparatory activation of modality-specific visual areas (as originally proposed by Harter et al. [15]), even though it can still be observed in anticipation of a tactile or auditory target, at least within a lit environment [12]. Finally, the modality of the attention-directing cue might also have an impact, and such cues have typically been visual in previous ERP studies of attentional control processes (including Ref. [12]).

Note that the possibility of attention-shifts being guided by continuously available visual representations of spatial locations, even when attention is directed in anticipation of auditory or tactile targets, does not only apply to ERP studies. It also has potential implications for previous studies of crossmodal attention that used behavioral or neuroimaging methods, rather than ERPs. When lit environments were used, it remains possible that some of the crossmodal effects observed might have had their origin in participants’ use of the visual modality to select the relevant location, even when the primary task concerned a different modality.

In the present study, we manipulated whether the experimental environment was lit or dark, while using ERP measures to assess several questions. First, are the preparatory components (ADAN and LDAP) that can be found during anticipatory attention shifts [12] even for non-visual modalities (here touch) still found even when eliminating ambient visuo-spatial information? Second, do crossmodal influences upon sensory components for a task-irrelevant modality (here vision) arise from the direction of covert attention in the primary modality (here, touch), even when ambient visuo-spatial information is removed?

Participants had to direct their attention to the hand indicated symbolically by an auditory precue at the beginning of each trial, in order to detect and respond to infrequent tactile ‘oddballs’ among tactile standards at just the cued hand. Tactile stimuli at the uncued hand were simply to be ignored. In our main experiment, visual events could also appear near either hand, instead of a tactile event, and these were to be ignored regardless of their location. In a follow-up experiment, these visual

events were eliminated. Unlike previous ERP studies of attentional control processes, auditory rather than visual precues were used, so that we could determine whether the ADAN and/or LDAP specifically require the use of visual cues.

Critically, in one experimental half, the experimental chamber was in darkness, so that no continuous ambient visual information was available. Moreover, the occasional peripheral visual stimuli that were briefly presented as task-irrelevant stimuli were so dim that they did not illuminate the hands or the rest of the environment (see below). Hence, we assumed that in this Darkness condition, no currently visible information was available for directing the anticipatory attentional shift in the tactile task during the cue–target interval, or for producing any subsequent crossmodal interactions. In Section 4, we consider possible challenges to this claim (involving short-term-memory for the location of peripheral visual events), and briefly present a follow-up experiment that eliminated all such visual events, to exclude these challenges. In the other experimental half, the experimental chamber was illuminated to provide continuous ambient visual input concerning the location of the hands and the surrounding environment, as in all our previous studies (and as in many crossmodal experiments by other groups).

To assess preparatory control processes, ERPs were measured during the cue–target interval following onset of the central auditory cue. To assess any consequent sensory modulations, ERPs were measured in response to standard non-target tactile stimuli on either hand, and also to task-irrelevant visual stimuli on either side. Separate ERPs were computed for the Darkness and Illuminated conditions, and the critical questions concerned whether or not the illumination manipulation would produce systematically different ERP effects.

For ERPs elicited in the cue–target interval in the Illuminated condition, we expected lateralised ERP modulations sensitive to the direction of an attentional shift (ADAN, LDAP) that would confirm our previous findings [12], despite auditory rather than visual precues now being used. The critical new question was whether these effects would remain during attentional shifts towards anticipated tactile events in darkness, where no ambient visual information was continuously available to anchor selection of relevant peripheral tactile locations. If the LDAP and ADAN reflect the allocation of attention only when guided by continuously visible information from the spatial environment, then systematically different ERP modulations should be observed during attentional shifts in the Illuminated versus Darkness conditions. By contrast, if the ERP effects during the cue–target interval reflect supramodal control systems for spatial attention (as argued in Ref. [12]), then these should be largely unaffected by the difference between illumination conditions.

For ERPs elicited in response to lateral stimuli presented subsequent to the auditory cue, we could examine any modulation of sensory responses by covert spatial atten-

tion, both for the task-relevant tactile modality, and also for the task-irrelevant visual modality. In a previous ERP study within a lit environment [8], where attention was directed to the location of relevant tactile events on one visible hand or the other, while any visual events could be completely ignored, spatially selective attentional modulations were found for both somatosensory and visual ERPs. The latter visual effects were taken as evidence for crossmodal links in spatial attention, from touch to vision; but, as noted above, they might be reconsidered as reflecting selection of currently *visible* locations for the tactile task, if they turned out to be specific to illuminated environments.

We expected to replicate the spatially selective modulation of visual ERP components during a tactile attention task in the Illuminated condition. The new question was whether analogous spatially selective modulations of visual ERPs could also be observed when all stimuli were presented in an otherwise dark environment. If such modulations were the result of attentional shifts operating specifically for currently visible locations, they should be eliminated in the Darkness condition, as ambient visual-spatial information was no longer continuously available to guide such selection. By contrast, if they reflect tactile-visual interactions that arise regardless of ambient visual

information from the environment, the crossmodal influence should be replicated even in the dark condition.

2. Materials and methods

2.1. Participants

Thirteen paid volunteers participated. One had to be excluded because of inadequate fixation in the cue-target interval (see below). Thus 12 participants (nine females), aged 19–50 years (mean age: 25.8 years), remained. Eleven were right-handed by self-report, one left-handed; all reported normal or corrected vision.

2.2. Stimuli and apparatus

Fig. 1 shows the experimental setup. Participants sat in a soundproof experimental chamber that was either dimly lit (Illuminated condition) or dark (Darkness condition). A head-mounted microphone was positioned in front of the mouth. In the Illuminated condition, participants had to keep their gaze focused at a small white fixation cross that was continuously present on a computer screen throughout the experimental blocks, as in our previous studies. In the

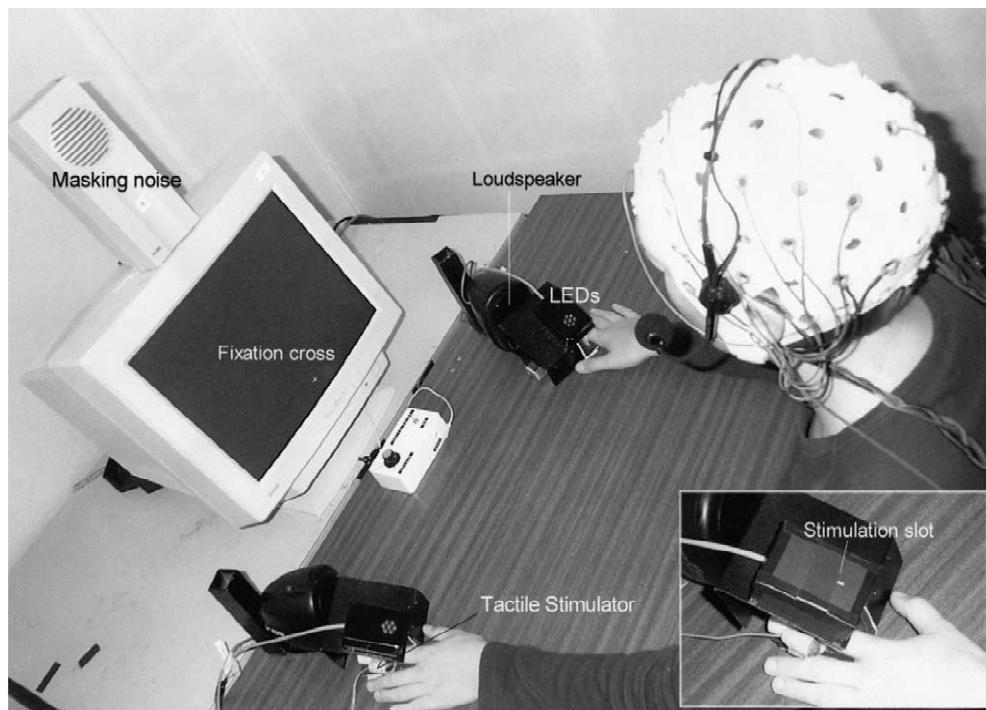


Fig. 1. The experimental setup used in the Illuminated condition of the present study. EEG was recorded while single visual or tactile stimuli were presented on the left or right side. Visual stimuli were brief flashes of LEDs, and tactile stimuli were delivered by stimulators attached to the left or right index finger. Participants had to direct attention to the side indicated symbolically by an auditory cue presented at the beginning of each trial, in order to detect tactile oddball targets at the cued hand. The setup was equivalent in the Darkness condition, except that the experimental chamber was completely dark, the fixation cross was replaced by a very dim LED, and the peripheral LEDs were covered by black cardboard boxes containing a small aperture (insert, bottom right) to reduce their intensity.

Darkness condition, this monitor was switched off, and a dim red LED positioned at the same location as the fixation cross now served as a ‘pin-hole’ fixation point. One of two tones differing in pitch (low, 1000 Hz; high, 1500 Hz, each at 72 dB SPL) was presented simultaneously from two loudspeakers located on the left and right side (it thus appeared to come from a central auditory location). One of these two pitches was used as the cue stimulus on each trial.

Tactile stimuli were presented using two 12-V solenoids that drove a metal rod with a blunt conical tip to the outside of the index fingers, making contact with the middle segment of the participants’ index fingers whenever a current was passed through the solenoid. The timing of stimulus events and EEG trigger signals took into account that there was a 5-ms delay between current onset and initial contact between rod and finger. The rods and fingers were occluded, so that participants could not see the rod movements even in the Illuminated condition (see Figure 1). White noise (62 dB SPL) was presented continuously from a central loudspeaker, positioned on top of the computer screen, throughout the experimental blocks to mask any sounds made by operation of the tactile stimulators. Visual stimuli were presented by illuminating an ensemble of green LEDs on the left or right side. Each ensemble consisted of six LEDs arranged in a circle plus one central LED element. The angular size of each LED was 0.65° , the diameter of the circle was 2.4° . In order to prevent these visual stimuli from partially illuminating the hands and the rest of the environment in the Darkness condition (and also to minimise afterimages), the luminance of the LED ensembles was reduced in the Darkness condition by covering LED ensembles with a black cardboard box. This box contained a small aperture (4×1.5 mm) which was covered with semi-transparent fabric (see insert in Fig. 1, bottom right). The luminance of these visual stimuli, as measured with a SpectraScan PR650 (Micron Techniques), was 184 cd/m^2 in the Illuminated condition, but only 2.45 cd/m^2 in the Darkness condition. The two tactile stimulators, the two LED ensembles, and the two peripheral loudspeakers were placed on a table in close spatial register, at 25° to the left or right of central fixation, at a viewing distance of about 45 cm from the participant’s eyes (Fig. 1).

Each auditory cue stimulus was presented for 50 ms. Tactile non-target (i.e., standard) stimuli consisted of one rod tip contacting an index finger for 200 ms. Tactile target (i.e., oddball) stimuli had a gap, where contact was interrupted for 10 ms after a duration of 95 ms. Visual stimuli consisted of one LED ensemble being illuminated for 200 ms. Vocal response onset times were measured with a voice key.

2.3. Procedure

The experiment consisted of 18 experimental blocks of

68 trials. Each trial started with a 50-ms presentation of an auditory cue stimulus, followed after an interval of 650 ms by a peripheral visual or tactile stimulus (200-ms duration). The intertrial interval was 1000 ms. The Illuminated and Darkness conditions consisted of eight and 10 successive blocks, respectively. The order in which these two conditions were delivered was counterbalanced across participants. Two additional blocks were included in the Darkness condition because pilot work showed that eye-blinks and eye-movements were more frequent (leading to more excluded trials) in darkness. Moreover, because the intensity of the peripheral visual stimuli had to be reduced in the Darkness condition (see above), these additional blocks were also intended to improve signal-to-noise ratio for the visual ERPs.

In both illumination conditions, participants were instructed to respond vocally (by saying ‘yes’) whenever a tactile oddball target (i.e., gap) stimulus was presented at the relevant hand (left or right). Which hand was relevant changed from trial to trial, as indicated by the pitch of the tone cue (low versus high). Pitch-to-hand mapping was counterbalanced across participants. The two cues were presented in random order and with equal probability. In 56 trials per block, a visual stimulus or a tactile non-target stimulus (i.e., a standard with no gap, requiring no response) was presented with equal probability on the left or right side. Each of these stimuli was preceded with equal probability by either of the two cues, resulting in a total of seven trials per block for each combination of cued hand (left versus right), stimulus modality (vision versus touch), and stimulus location (left versus right). In the remaining 12 trials per block, tactile target stimuli (i.e., oddballs with gaps) were presented with equal probability on the left or right side. Eight of these trials (four left, four 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 four trials (two left, two right), tactile gap 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 tactile targets at just the cued hand, and to ignore any tactile stimuli at the uncued hand as well as any visual stimuli regardless of their location. They were also told to maintain central eye fixation throughout the blocks. Several training blocks were run prior to the first experimental block of both the Illuminated and Darkness condition. Eye movements were closely monitored during these training blocks. Whenever the horizontal EOG revealed that participants did not maintain central eye fixation, they were reminded again of the necessity of holding central fixation throughout the experimental block. Additional training blocks were run until fixation control was regarded as satisfactory. To ensure that participants were dark-adapted prior to the start of EEG recording in the Darkness condition, training blocks were delivered for

at least 10 min before the first experimental block was started.

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 bandpass was 0.1 to 40 Hz. EEG and EOG were sampled with a digitisation rate of 200 Hz and stored on disk. Voice onset times were measured for each vocal response to the rare tactile oddball targets.

EEG and HEOG were epoched off-line into 1400-ms periods, starting 100 ms prior to cue onset and ending 600 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 ± 60 μ V relative to baseline), horizontal eye movements (HEOG exceeding ± 30 μ V relative to baseline), or other artefacts (a voltage exceeding ± 60 μ V at any electrode location relative to baseline) were excluded from analysis. Averaged HEOG waveforms in response to cues directing attention to the left versus right side were scored for systematic deviations of eye position, indicating any residual tendencies to move the eyes towards the cued location. A residual HEOG deviation exceeding ± 2 μ V led to the disqualification of one participant.

The EEG obtained in the cue–target interval was averaged for all combinations of illumination (Illuminated versus Darkness) and cued direction (left versus right). Based on our previous work on attention shifts in the cue–target interval [12], mean amplitude values were computed at lateral anterior sites (F7/8, F3/4, FC5/6), lateral central sites (T7/8, C3/4, CP5/6), and lateral posterior sites (P7/8, P3/4, OL/R) within two successive latency windows (300–500 and 500–700 ms relative to cue onset), and these values were analysed separately for anterior, central, and posterior electrodes by repeated measures ANOVAs for the factors of illumination, electrode site, cued direction, and hemisphere (left versus right).

The EEG obtained in response to peripheral tactile and visual stimuli was averaged for non-target stimuli only (i.e., with no gaps, requiring no behavioural response), to avoid contamination by vocal responses. Trials where false-positive vocal responses were recorded on non-target

trials (only 0.2% of such trials) were also excluded from analysis. Separate averages were computed for visual and tactile non-target stimuli for all combinations of illumination, cued direction, and stimulus side (left versus right), resulting in 16 average waveforms for each participants. Based on our previous work on visual and somatosensory modulations (e.g., Ref. [8]), mean amplitude values were computed for sensory-specific visual and somatosensory ERPs within different latency windows measured relative to onset of the peripheral stimulus (visual P1, 100–140 ms; visual N1, 170–210 ms; somatosensory N140, 130–180 ms). Later attentional effects were analysed between 180 and 260 ms (for somatosensory ERPs; see Refs. [7,8,26]) and between 220 and 300 ms (for visual ERPs; see Refs. [5,24]). Mean amplitude values for visual and somatosensory ERPs at lateral anterior sites, lateral central sites, lateral posterior sites and at midline electrodes (Fz, Cz, Pz) were submitted to separate ANOVAs with the factors of illumination, electrode site, spatial attention (stimulus at cued location versus uncued location), stimulus side, and hemisphere (this latter factor was omitted in the analysis of midline electrodes). When appropriate, Greenhouse–Geisser adjustments to the degrees of freedom were performed, and the adjusted *P* values are reported. Non-significant terms, and results due trivially to stimulus and anatomical laterality, are not reported. Whenever interactions between attention and electrode site were found (for brevity, these are not all reported in full), additional analyses were conducted for single electrode sites. For vocal responses to the rare tactile targets, repeated measures ANOVAs were performed on response latencies and on arcsin-transformed error rates, with the factors of illumination and target location (left versus right).

3. Results

3.1. Behavioural performance

The latency of vocal responses to tactile targets (measured relative to the onset of the target-defining gap) was unaffected by illumination (558 vs. 556 ms in the Illuminated and Darkness conditions, respectively; $F < 1$). Responses to targets presented to the right hand were faster than those on the left hand (547 vs. 567 ms; $F(1,11) = 7.5$; $P < 0.02$), possibly reflecting the fact that vocal responses are predominantly controlled by the left hemisphere to which the right hand initially projects. Participants missed 8.3 and 5.5% of all targets at cued locations in the Illuminated and Darkness condition, respectively, and this difference was not significant. The rate of False Alarms to tactile gap targets at uncued locations (3.1 vs. 2.9%) likewise did not differ between illumination conditions. False Alarms to tactile non-target stimuli (without gaps) and to visual stimuli occurred on less than 0.2% of trials.

3.2. ERP correlates of spatial orienting in the cue–target interval

Figs. 2 and 3 show ERPs elicited at lateral anterior, central, and posterior electrodes in the interval between cue onset and onset of the subsequent peripheral stimulus, under conditions where the experimental chamber was illuminated (Fig. 2) or dark (Fig. 3). Waveforms in response to auditory cues directing tactile attention to the left versus right hand are shown separately. ERP lateralisations sensitive to the direction of attentional shifts are visible in both sets of waveforms. A negativity contralateral to the direction of an attentional shift (anterior directing attention negativity; ADAN) was elicited at frontal electrodes, similar to our previous findings [12] (see also Refs. [28,23]). At lateral posterior electrodes, a contralateral positivity was present (late directing attention positivity; LDAP), again very similar to earlier observations from crossmodal [12] and unimodal visual studies [15]. Critically, these lateralised effects in the cue–target interval appeared present not only when the chamber was illuminated (Fig. 2), so that ambient visual–spatial information

was continuously available, but also when the chamber was in darkness (Fig. 3).

The presence of ERP lateralisations sensitive to the direction of attentional shifts can be seen most clearly in the difference waveforms shown for anterior and posterior electrodes in Fig. 4. These difference-waves were generated 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. As a result of these double subtractions, a net negativity contralateral to the direction of attentional shifts (ADAN) is reflected by positive amplitude values (downward-going deflections; Fig. 4, top), and a net positivity at contralateral sites (LDAP) is reflected by negative values (upward deflections; Fig. 4, bottom). Fig. 4 indicates that a frontal ADAN and a posterior LDAP were elicited during attentional shifts to the location of anticipated tactile events on the relevant hand, both when these shifts took place in an illuminated environment with the hand visible (solid lines) and in darkness (dashed lines).

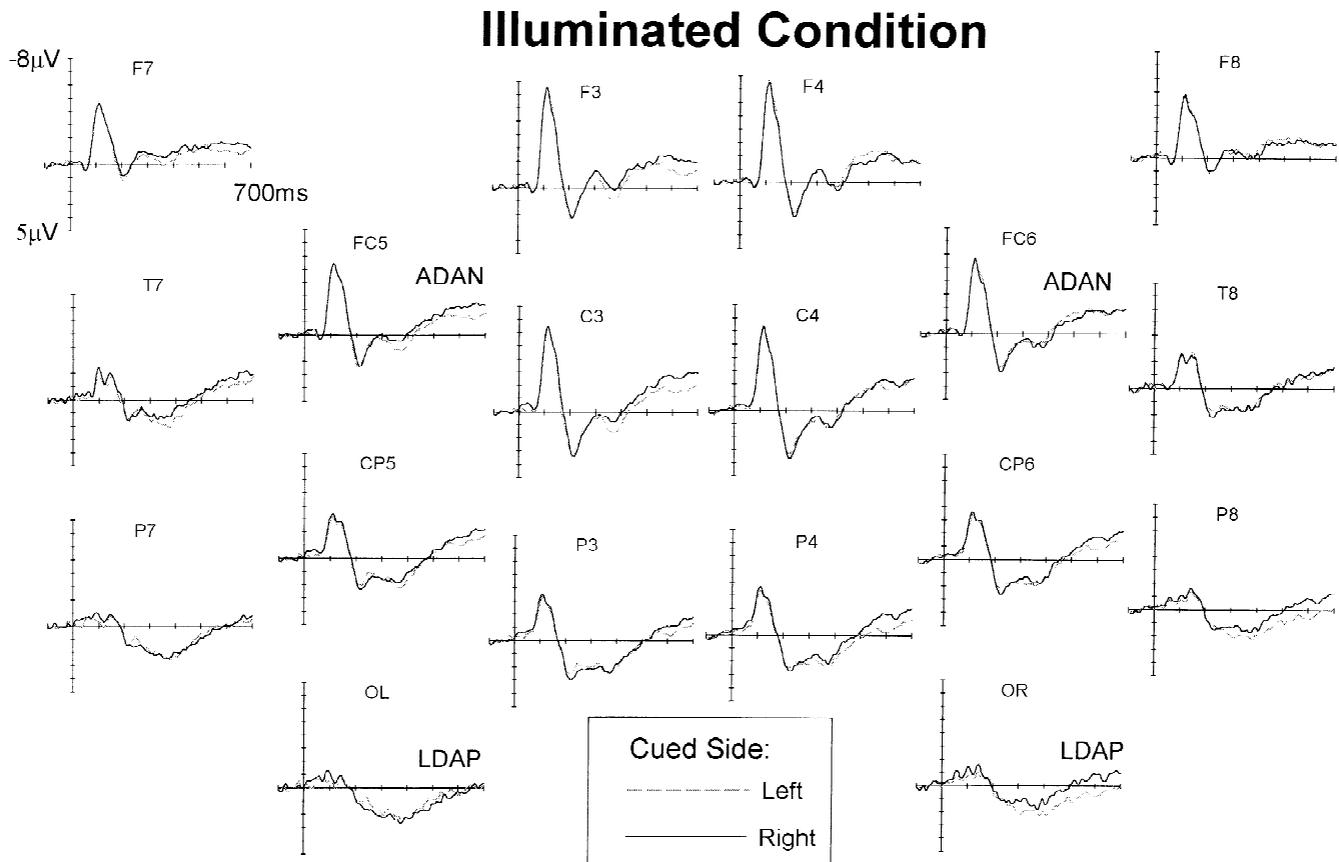


Fig. 2. Grand-averaged ERPs elicited in the Illuminated condition at anterior, central, and posterior lateral electrodes, in the interval between cue onset and onset of the subsequent peripheral stimulus, for auditory cues directing attention to the left side (dashed lines), and cues directing attention to the right side (solid lines). ERPs show a frontocentral negativity (anterior directing attention negativity; ADAN) and a posterior positivity (late directing attention positivity; LDAP) contralateral to the direction of the cued attentional shift.

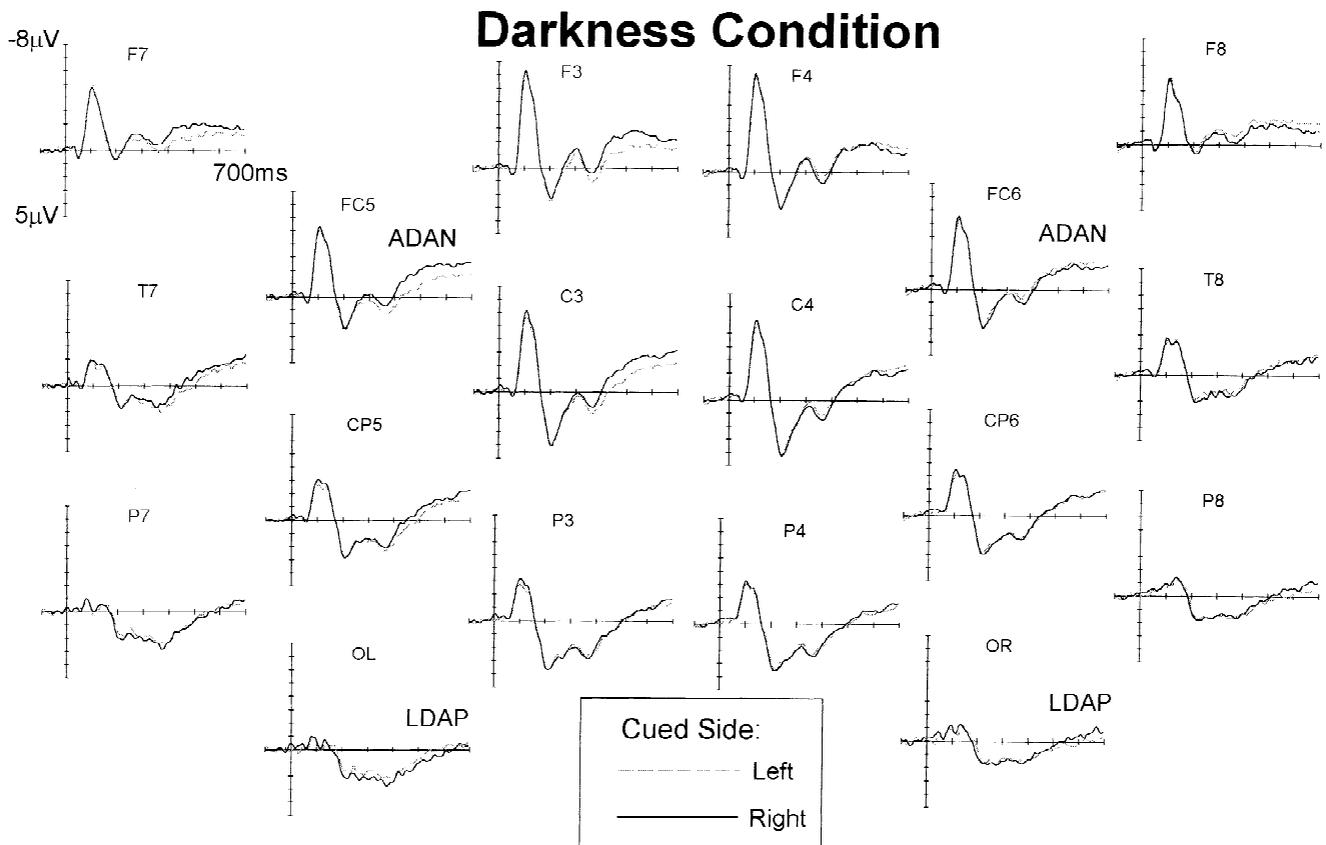


Fig. 3. Grand-averaged ERPs elicited in the Darkness condition at anterior, central, and posterior lateral electrodes, in the interval between cue onset and onset of the subsequent peripheral stimulus, for auditory cues directing attention to the left side (dashed lines), and cues directing attention to the right side (solid lines). As in Fig. 2 (which showed analogous data for the Illuminated condition), a frontocentral negativity (anterior directing attention negativity; ADAN) and a posterior positivity (late directing attention positivity; LDAP) are present contralateral to the direction of the cued attentional shift.

Statistical analyses were used to confirm that the ADAN and LDAP effects shown in these figures were indeed produced by reliably different ERP responses triggered in response to auditory cues directing attention to the left or right side. Note that these analyses compared leftward and rightward attention-shifts directly, as a function of the site and hemisphere of the electrode, prior to the double subtraction visualised in Fig. 4. 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, a significant hemisphere \times cued direction interaction was present at anterior sites ($F(1,11)=22.0$; $P<0.001$), reflecting increased negativities contralateral to the direction of an attentional shift (i.e., an ADAN). Although Fig. 4 (top) suggests that this ADAN was somewhat larger in amplitude during attentional shifts in darkness than for attentional shifts in the illuminated condition, the three-way interaction (illumination \times hemisphere \times cued direction) was not significant. Follow-up analyses revealed significant hemisphere \times cued direction interactions for both illumination conditions ($F(1,11)=9.0$ and 26.4 ; $P<0.012$ and 0.001 , for Illumination and Darkness, respectively). No reliable hemisphere \times cued direction interac-

tions were observed at lateral posterior and central electrodes during this time interval.

In the subsequent 500–700-ms post-cue interval (corresponding to the final 200 ms prior to the onset of a lateral tactile or visual stimulus), the hemisphere \times cued direction interaction at lateral posterior electrodes was almost significant ($F(1,11)=4.8$; $P<0.051$), and a three-way interaction (recording site \times hemisphere \times cued direction: $F(2,22)=10.3$; $P<0.003$; $\epsilon=0.722$) was obtained, suggesting that a reliable LDAP may have been present at some lateral posterior sites. Follow-up analyses confirmed a significant hemisphere \times cued direction interaction at lateral occipital electrodes OL/R ($F(1,11)=9.2$; $P<0.011$). Although Figs. 4 (bottom) gives the appearance of this occipital LDAP being somewhat larger in the Illuminated condition, no significant illumination \times hemisphere \times cued direction interaction was in fact obtained at OL/R, and further analyses confirmed that the LDAP effect was reliable for both illumination conditions (hemisphere \times cued direction: $F(1,11)=8.8$ and 6.7 , both $P<0.025$, for Illuminated and Darkness, respectively). A significant hemisphere \times cued direction interaction was also present at P7/8 ($F(1,11)=5.3$; $P<0.05$), but not at P3/4.

In addition to this posterior LDAP, a significant

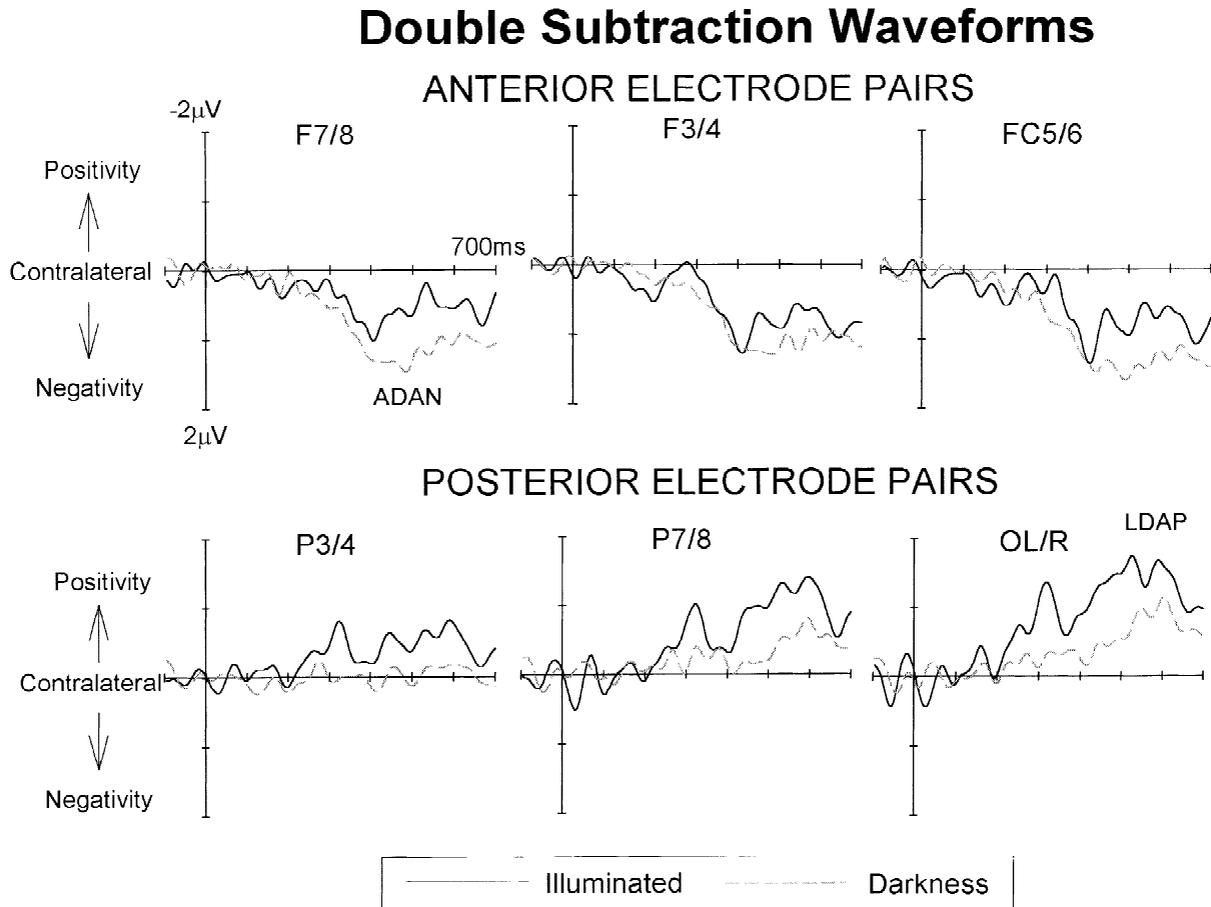


Fig. 4. Difference waveforms obtained at lateral anterior (top) and posterior (bottom) electrodes in the 700-ms interval between cue onset and onset of the subsequent peripheral stimulus in the Illuminated condition (solid lines) or Darkness condition (dashed lines), reflecting lateralised ERP modulations sensitive to the direction of attentional shifts. 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), and larger positivities at contralateral sites are reflected by negative values (upward-going deflections; see text for further details). The resulting waveforms show that both an anterior directing attention negativity (ADAN) at contralateral anterior sites and a late directing attention positivity (LDAP) at contralateral posterior electrodes were elicited in both Illuminated and Darkness conditions.

hemisphere \times cued direction interaction was also obtained at lateral anterior electrodes in the final 200 ms of the cue–target interval ($F(1,11)=13.4$; $P<0.004$). This interaction reflects the fact that the frontal ADAN did not return to baseline during late phases of the cue–target interval (unlike our previous study using visual cues [12]), but remained present up to the onset of lateral sensory events. This can be seen most clearly in the double-subtraction waveforms of Fig. 4 (top). In addition, this figure also suggests that this ‘late’ period of the ADAN may have been somewhat more pronounced during attentional shifts in darkness. This was confirmed by a significant illumination \times hemisphere \times cued direction interaction ($F(1,11)=5.2$; $P<0.05$). However, follow-up analyses demonstrated that the ‘late’ ADAN was reliable not only during darkness, but also for attentional shifts in the Illuminated condition (hemisphere \times cued direction: $F(1,11)=6.5$ and 17.7 , $P<0.03$ and 0.001 , for Illuminated

and Darkness, respectively). No reliable hemisphere \times cued direction interactions reflecting either ADAN or LDAP effects were observed at lateral central electrodes in the final 200 ms of the cue–target interval.

3.3. Crossmodal effects of spatial orienting to the cued hand upon visual ERPs

ERPs elicited in response to task-irrelevant peripheral visual events at cued and uncued locations are shown in Fig. 5 (Illuminated condition) and Fig. 6 (Darkness condition). Waveforms are displayed separately for electrodes contralateral (C) and ipsilateral (I) to the side of stimulation, and for midline electrodes. As would be expected, sensory-specific visual P1 and N1 components were somewhat smaller and delayed in the Darkness condition, reflecting the fact that the absolute intensity of the visual stimuli presented in darkness was much lower

Visual ERPs - Illuminated Condition

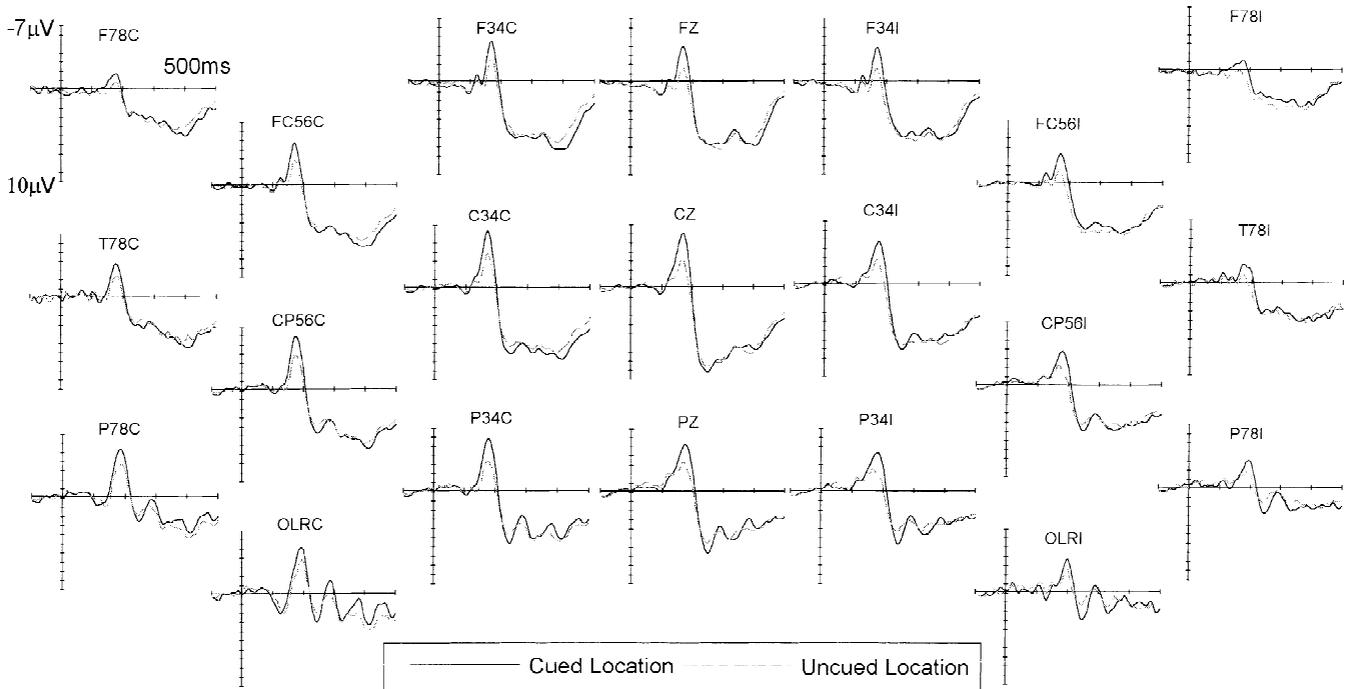


Fig. 5. Grand-averaged visual ERPs elicited in the Illuminated condition at midline electrodes, and at sites contralateral (C; left panels) and ipsilateral (I; right panels) to the side of stimulus presentation, by task-irrelevant visual stimuli at cued locations (solid lines) and uncued locations (dashed lines) in the 500-ms interval following onset of the visual stimulus.

Visual ERPs - Darkness Condition

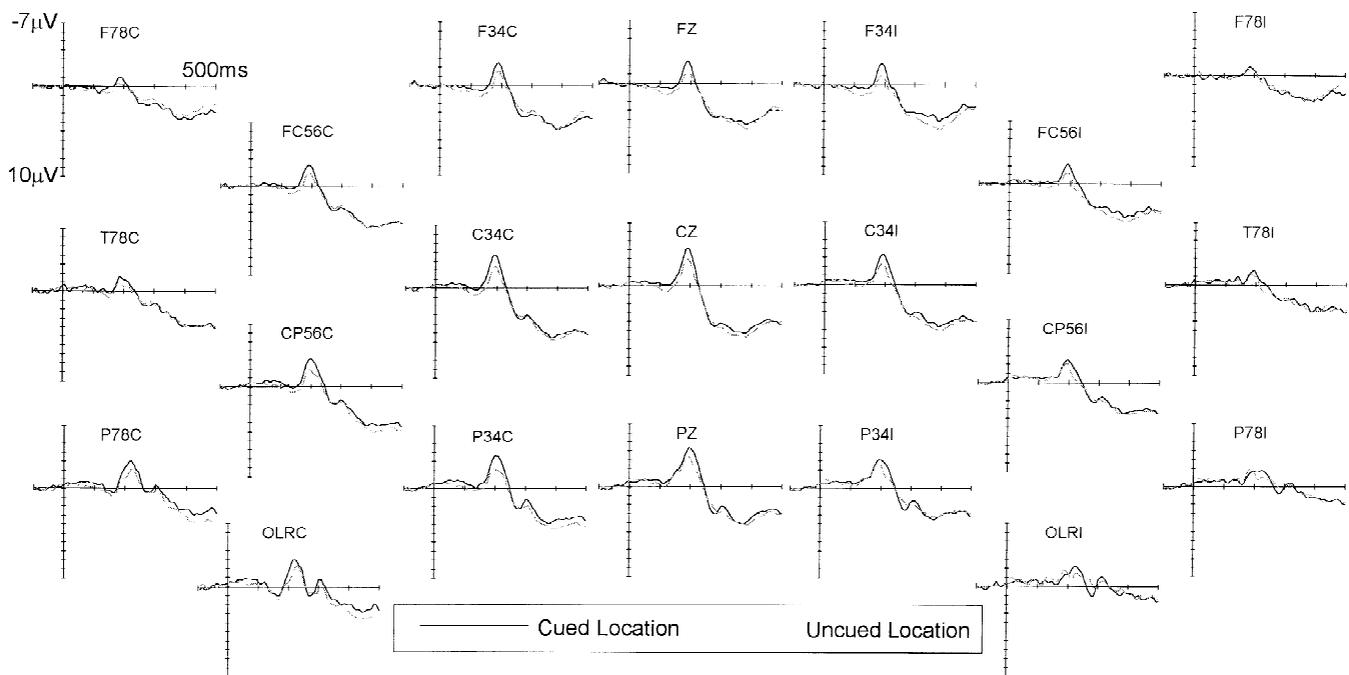


Fig. 6. Grand-averaged visual ERPs elicited in the Darkness condition at midline electrodes, and at sites contralateral (C; left panels) and ipsilateral (I; right panels) to the side of stimulus presentation, by task-irrelevant visual stimuli at cued locations (solid lines) and uncued locations (dashed lines) in the 500-ms interval following onset of the visual stimulus.

than in the Illuminated condition (recall that this had been introduced to avoid these stimuli illuminating the rest of the environment when turned on in darkness, and to minimise after-images; see Section 2). More importantly, there were clear effects of spatial attention (i.e., of which hand had been cued as relevant for the tactile task) on visual N1 components, with larger N1 amplitudes in response to visual stimuli near the task-relevant hand. Figs. 5 and 6 suggest that these attentional modulations were present not only in the Illuminated condition, but also when peripheral visual stimuli appeared in Darkness. These observations were confirmed by statistical analyses. No effect of spatial attention was found for the P1 component (100–140-ms post-stimulus) at lateral occipital electrodes, but reliable spatial attention effects were observed for the N1 component (170–210-ms post-stimulus) at lateral posterior electrodes ($F(1,11)=20.4$; $P<0.001$), reflecting enhanced N1 amplitudes for visual stimuli at tactually relevant locations. An illumination \times spatial attention interaction ($F(1,11)=5.4$; $P<0.05$) indicated that this attentional effect was somewhat larger in the Illuminated condition. However, subsequent analyses revealed that effects of spatial attention on posterior N1 amplitudes were significant not only in the Illuminated condition ($F(1,11)=19.7$; $P<0.001$), but importantly were significant also for visual stimuli presented in darkness ($F(1,11)=5.1$; $P<0.05$).¹ This is an important finding, since it indicates a crossmodal influences from which hand is relevant for a tactile task upon visual ERPs, even when the experiment is conducted in a dark environment so that the relevant tactile location is not visible prior to stimulation.

Significant attentional N1 modulations were also observed at lateral anterior and central electrodes, as well as at midline sites (all $F(1,11)>23.4$; all $P<0.001$), reflecting enhanced N1 components for visual stimuli at cued locations. No significant illumination \times spatial attention interactions were found in any of these analyses, indicating that these modulations were of similar size in the Illuminated and Darkness conditions (see Figs. 5 and 6). To confirm that directing attention to the location of relevant tactile events in darkness critically affected visual N1 components at anterior, central, and midline electrodes, separate analyses were conducted for visual ERPs obtained in the Darkness condition. Significant attention effects were obtained for all three electrode groups (all $F(1,11)>$

18.6; all $P<0.001$). No effects of spatial attention on visual ERPs were present at any recording site beyond the N1 component (220–300 ms latency window).²

3.4. Effects of spatial orienting to the relevant hand on somatosensory ERPs

ERPs elicited in response to tactile non-target stimuli at cued and uncued locations are shown in Fig. 7 for midline electrodes and lateral electrode sites, separately for the Illuminated condition (left) and the Darkness condition (right). Effects of spatial attention to the relevant hand on somatosensory ERPs were clearly present in both task conditions, as would be expected. The somatosensory N140 component appears modulated by spatial attention in the Darkness condition (Fig. 7, right), although this effect seems somewhat smaller in the Illuminated condition (Fig. 7, left). Subsequent attentional negativities were present in both task conditions, although they appeared more pronounced when stimuli were delivered in darkness. These informal observations were substantiated by statistical analyses. In the N140 latency range (130–180-ms post-stimulus), effects of spatial attention approached significance at lateral central sites ($F(1,11)>3.5$; $P<0.09$). Follow-up analyses conducted separately for the Illuminated and Darkness conditions revealed no reliable effects of spatial attention on N140 amplitudes in the Illuminated condition. However, significant attentional enhancements of N140 amplitudes at lateral central electrodes were present in the Darkness condition ($F(1,11)=5.0$; $P<0.05$), and this effect was close to conventional significance at lateral anterior sites ($F(1,11)=4.6$; $P<0.06$).

In the subsequent analysis window (180–260-ms post-stimulus), main effects of spatial attention were obtained at lateral anterior and central electrodes as well as midline sites (all $F(1,11)>10.2$; all $P<0.01$), reflecting enhanced negativities for tactile stimuli at the cued versus uncued hand (Fig. 7). Significant illumination \times spatial attention interactions were obtained for all three electrode groups ($F(1,11)>5.3$; all $P<0.05$), indicating that these attentional negativities were more pronounced for tactile stimuli presented in darkness. Follow-up analyses conducted separately for both conditions revealed reliable attentional negativities at lateral anterior, central, and midline electrodes in the Darkness condition (all $F(1,11)>17.1$; all $P<0.002$); and also for lateral central and midline electrodes in the Illuminated condition (both $F(1,11)>5.4$; both $P<0.05$).

¹Follow-up analyses, conducted for ERPs obtained in the Darkness condition separately for each posterior electrode pair, revealed significant attentional N1 modulations at P3/4, but this effect failed to reach significance at OL/R and T7/8. To account for the fact that N1 components were substantially delayed in the Darkness relative to the Illuminated condition, due to the reduced visual stimulus intensity, additional analyses were performed for a later N1 time interval (200–240 ms post-stimulus), which was centred on the peak amplitudes of posterior N1 components as elicited in the Dark condition (see Fig. 6). These analyses revealed reliable attentional N1 modulations at all posterior electrode pairs (all $F(1,11)>4.9$; all $P<0.05$).

²To confirm that no reliable attentional modulations of visual ERPs were present at longer latencies, an additional analysis was conducted on ERP mean amplitudes obtained in the 300–400-ms latency range. No main effects of spatial attention or any illumination \times spatial attention interactions approached significance at any electrode site.

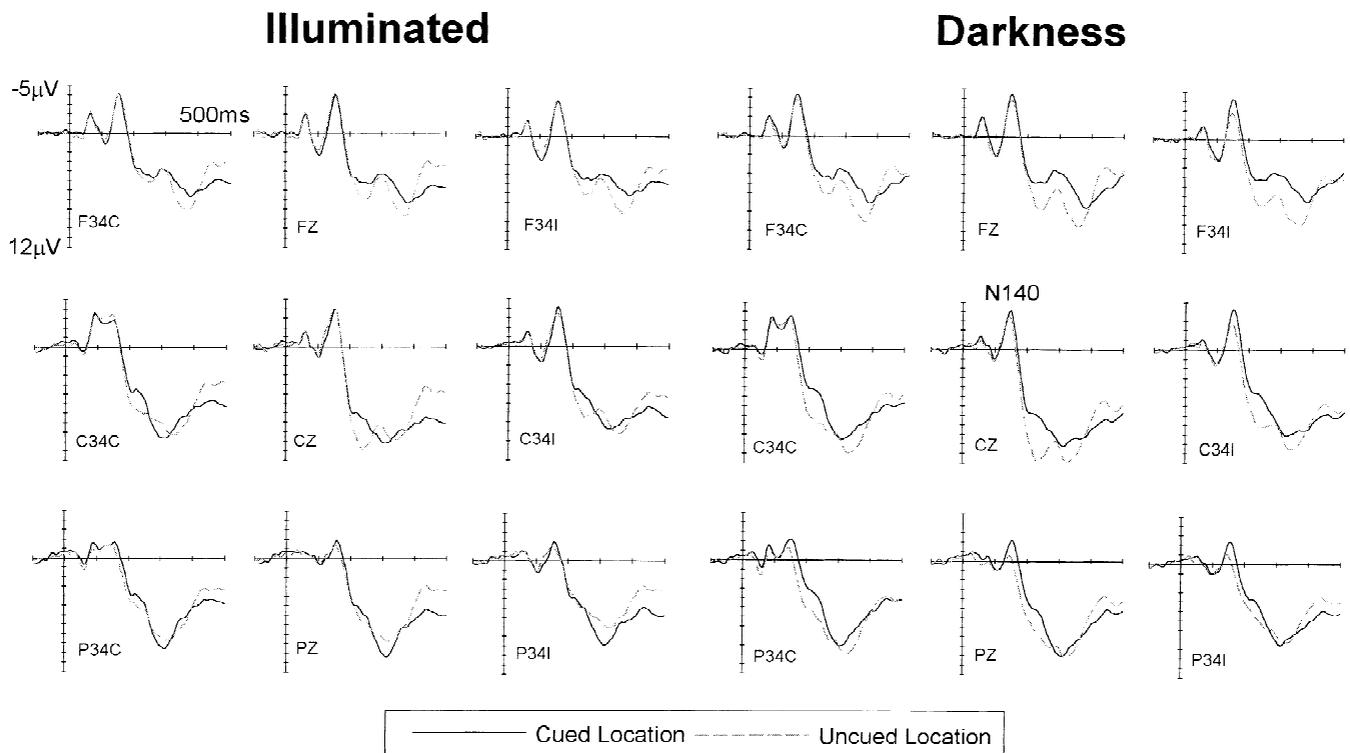


Fig. 7. Grand-averaged somatosensory ERPs elicited at midline electrodes, and at sites contralateral (C) and ipsilateral (I) to the side of stimulus presentation, by tactile non-target stimuli (i.e., with no gaps, requiring no response) at cued locations (solid lines) and uncued locations (dashed lines) in the 500-ms interval following stimulus onset. Left panel: Illuminated condition. Right panel: Darkness condition.

4. Discussion

Crossmodal links in human endogenous spatial attention have now been demonstrated in several behavioural and electrophysiological experiments (e.g., Refs. [7,8,10–12,16,17,30,31]; see also Refs. [4,6,9] for reviews). However, such experiments have typically been conducted in illuminated environments, so that the possible locations of auditory and tactile stimuli (as well as of visual stimuli) were continuously visible. This might have led to shifts of attention towards the currently relevant location arising primarily in the visual domain, even when another modality (e.g., audition or touch) was task-relevant. In a continuously visible environment, the high spatial acuity of vision might allow spatial attention to be anchored most effectively at the relevant location. If so, this would challenge previous interpretations of crossmodal effects as reflecting supramodal attentional control processes (e.g., Refs. [12]). Instead, many of the previously observed crossmodal effects might involve attention being directed primarily within representations of visible space. For instance, the previous finding [8] that directing attention to one hand for a tactile task can spatially affect visual ERPs might reflect *visual* selection of the relevant hand, rather than crossmodal influences from tactile attention upon vision. Likewise, the fact that highly similar ERP correlates of spatial orienting are elicited during anticipatory shifts of covert attention shifts, regardless of whether vision, audition, or

touch is the task-relevant modality [12], might just indicate that such shifts can be guided by ambient visual–spatial information in lit environments, rather than reflecting strictly supramodal attentional control processes.

The present study sought to clarify these issues by manipulating whether the environment was illuminated or in darkness, while measuring (i) ERP correlates of anticipatory shifts of spatial attention to one hand or the other, for a tactile task, and (ii) subsequent effects of covert spatial attention on somatosensory or visual ERPs for stimuli appearing at cued or uncued locations. Participants had to direct attention to the side indicated symbolically by an auditory cue at the beginning of each trial, in order to detect and respond to infrequent tactile oddballs at the cued location. Tactile stimuli at uncued locations were simply to be ignored, and likewise for any task-irrelevant visual stimuli, regardless of their location. In the Illuminated condition, the possible locations of any tactile or visual stimuli were continuously visible throughout, whereas this did not apply when the experimental chamber was in darkness.

ERPs measured in the cue–target interval revealed systematic lateralised modulations sensitive to the direction of an anticipatory attentional shift. Similar to previous investigations of control processes, which had examined only visual-spatial orienting (cf. [15,18,23,28,34,35], an anterior directing attention negativity (ADAN) and an occipital late directing attention positivity (LDAP) were

elicited at electrodes contralateral to the direction of an attentional shift towards the side that was cued for the tactile task.³ Recall that these lateralised effects, associated with anticipatory shifts of covert attention to one side, had also been found in a previous study [12] that examined attentional shifts towards the location of relevant auditory or tactile stimuli. In the present experiment, these effects were again observed during shifts of attention to relevant tactile locations, providing further confirmation that ERP correlates of anticipatory attentional shifts are very similar regardless of which modality is currently task-relevant. It should also be noted that these effects were elicited here in spite of the fact that the direction for spatial orienting was now indicated symbolically by an auditory (rather than visual) precue, suggesting that the control processes involved in covert attention shifts do not depend critically on the cue modality.

Most importantly, the ADAN and LDAP effects were observed here not only in the Illuminated condition, where continuously visible information might have been used to guide the selection of relevant tactile locations, but also in the Darkness condition. This result suggests that the similarity in ERP correlates of covert attentional shifts when attention is directed to relevant locations for different modalities (as found in Ref. [12]) is *not* due merely to such shifts always being directed by continuously visible peripheral information. If this had been so, such ERP correlates should not have been observed during attentional shifts in darkness. The continued presence of ADAN and LDAP effects even in the Darkness condition thus appears more consistent with our proposal that they may reflect supramodal attentional control processes [12,13].

However, one could argue that the irrelevant peripheral visual stimuli in the present experiment may have served as ‘place-holders’ that might allow attention still to be directed visually for the tactile task. The peripheral visual stimuli were indeed located in close proximity to the hand on each side. But they were presented on only half the trials, and were never illuminated during the cue–target interval for which we observed ADAN and LDAP components. Moreover, they were too dim to illuminate the hands or environment in the Darkness condition, and were also sufficiently dim that any after-image (even for dark-adapted subjects) should not endure throughout the inter-trial and then the cue–target intervals. Nevertheless, it must be acknowledged that short-term memory for these visual locations could have played a role in directing attention in the otherwise dark environment, with each of

the trials that contained a peripheral visual event potentially providing a ‘reminder’ about the locations of possible tactile events.⁴

To investigate the possibility that attentional shifts might still be guided by peripheral visual sources of spatial information even in the Darkness condition, we ran a follow-up experiment. Task and procedure were identical to the previous Darkness condition, except that now no peripheral visual stimuli were ever presented (moreover, no Illuminated condition was included in this follow-up experiment). ERPs were recorded from 12 new participants (four female, aged 18–36 years, all right-handed) in the interval between symbolic auditory cue and subsequent peripheral tactile stimulus, separately for leftward and rightward attentional shifts. Fig. 8 (solid lines) shows ERP lateralisations sensitive to the direction of attentional shifts obtained in this follow-up experiment, at lateral frontocentral sites (FC5/6) and lateral occipital electrodes (OL/R). As in Fig. 4, these difference-waveforms were generated by first subtracting ERPs for rightward shifts from ERPs elicited during leftward attentional shifts, and then subtracting the resulting difference-waves at right electrodes from difference-waves at corresponding left electrodes. To enable visual comparisons between ERP correlates of attentional shifts in darkness when no peripheral visual stimuli were ever presented (i.e., in the follow-up study), versus when they could occur (i.e., in the original experiment), Fig. 8 also includes difference-waves obtained in the Darkness condition of the main experiment (dashed lines).

Both the anterior contralateral negativity (ADAN; downward-going deflections in Fig. 8, top), and the posterior contralateral positivity (LDAP; upward-going deflections in Fig. 8, bottom) still appear present in darkness, even when no peripheral visual stimulation ever occurs (i.e., in the follow-up study; solid lines in Fig. 8). This was confirmed by statistical analyses. As in the main experiment, significant hemisphere \times cued direction interactions were present for both analysis windows (i.e., 300–500 and 500–700 ms after cue onset) at lateral anterior sites (both $F(1,11) > 26.5$; both $P < 0.001$), reflecting the presence of the ADAN effect. In addition, a recording site \times hemisphere \times cued direction interaction was observed in the final 200 ms of the cue–target interval at lateral posterior electrodes ($F(2,22) = 5.2$; $P < 0.023$; $\epsilon = 0.788$), again analogous to the results observed on the main experiment. A hemisphere \times cued direction interaction was present at OL/R ($F(1,11) = 7.73$; $P < 0.018$), reflecting the LDAP component (see Fig. 8, bottom).

It should be noted that the LDAP obtained in this follow-up experiment, without any peripheral visual stimulation, appeared numerically smaller than the LDAP measured in the Darkness condition of the main experiment,

³In contrast to previous ERP investigations of attentional control processes in the cue–target interval [15,28,34,35], but in line with previous results from our lab [11,12], no early posterior EDAN component was observed. Given that other studies used asymmetric visual precues, the EDAN might primarily reflect a lateralised visual response triggered by asymmetric visual cues (e.g., arrows), unlike the symbolic auditory cues used here.

⁴We thank two anonymous reviewers for raising these important points.

Double Subtraction Waveforms

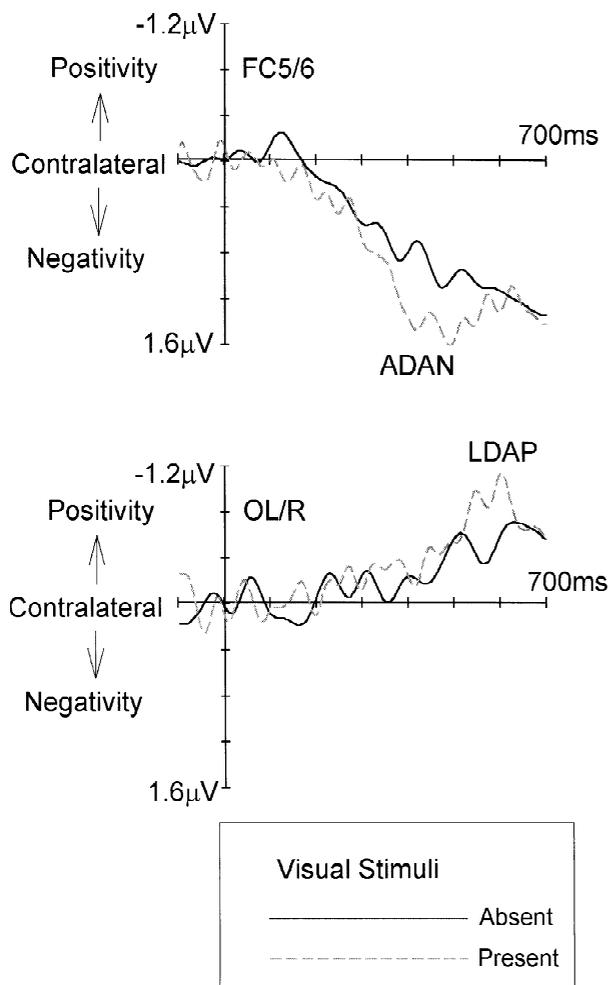


Fig. 8. Difference waveforms obtained at lateral anterior sites FC5/6 (top) and lateral occipital electrodes OL/R (bottom) in the 700-ms interval between cue onset and onset of the subsequent peripheral stimulus, reflecting lateralised ERP modulations sensitive to the direction of attentional shifts. As in Fig. 4, difference waves were computed by subtracting ERPs during rightward attentional shifts from ERPs during leftward shifts, and then subtracting the resulting difference waves at FC6 and OR (right hemisphere) from the corresponding difference waves at FC5 and OL (left hemisphere). Solid lines show lateralisations obtained in a follow-up experiment, which replicated the Darkness condition but now without ever presenting peripheral visual stimuli. Dashed line show the corresponding lateralisations obtained in the Darkness condition of the main experiment, where peripheral visual stimuli could occur.

which was itself numerically (albeit not significantly) smaller than the LDAP obtained for the Illuminated condition of that experiment (see Fig. 4, bottom). This may indicate that the processes underlying the LDAP are not completely unaffected by the availability of visible sources of spatial information. However, the important point remains that both the ADAN and LDAP were still reliably elicited even when no peripheral visual stimulation was present to serve as a visual reference for guiding covert attentional shifts in darkness. This provides additional

support for our proposal that these components involve supramodal attentional control processes.

Of course it could be suggested that, even in darkness, when no peripheral visual stimuli ever occur, the brain might still utilise visual representations of space in the control of attention. However, it should be noted that this possibility is very different from the use of currently *visible* information about the exact position of the currently relevant location when guiding attention. If any ‘visual’ representations are indeed used when directing attention in complete darkness, and in anticipation of a tactile target, describing these as ‘visual’ can at most only be a claim about where such representations may be located in the brain (i.e., perhaps including regions that have traditionally been regarded as unimodal visual cortex). It could not be a claim about an exclusively visual function in relation to attention, if these representations are used equally when directing spatial attention for any other modality, and regardless of whether ambient visuo-spatial information is available or not.

In addition to our principal findings concerning ERP correlates of anticipatory attentional shifts during the cue–target interval, the main experiment also examined any modulations of stimulus-locked ERPs, as a function of which side was attended for the tactile task. We found that processing of the task-irrelevant visual stimuli, when present, was modulated by spatial attention for the tactile task even in the Darkness condition. The presence of attentional modulations of visual N1 components even in an otherwise dark environment demonstrates that these effects do not depend on tactile selection being guided by continuously available ambient visible information about the possible tactile locations during the preparatory cue–target interval.⁵

A final aspect of the results was that the effects of spatial attention on somatosensory ERPs were somewhat more pronounced in the Darkness condition (although significant effects were found for the Illuminated situation also); while attentional effects on visual ERPs tended to be larger in the Illuminated condition (although again reliable effects were found in both conditions). We have recently proposed [12] that effects of spatial attention on phasic stimulus-locked ERPs might be larger in amplitude when the corresponding modality is tonically more active. This could explain the pattern of modulation here, on the reasonable assumption that vision is tonically more active in a lit environment than in total darkness, and vice-versa for touch.

⁵Attentional effects for somatosensory ERPs were somewhat delayed relative to previous ERP studies of crossmodal attention where touch was task-relevant [7,8]. One possible reason for the delay is that the pitch/hand mappings employed here to indicate the cued side were more arbitrary than the arrow/location mappings used previously. This might also account for the observation that no crossmodal attentional effects were found here for the visual P1 component, only for the N1.

In summary, the main contribution of the present study was to examine the ERP correlates of attentional shifts in darkness as well as in the more conventional lit environment, in relation to crossmodal issues. The results showed that ERP components associated with the direction of a cued preparatory attentional shift (specifically, the ADAN and LDAP components) are still found even in darkness; and that directing attention to the cued hand for a tactile task modulates visual as well as somatosensory ERPs even in a dark environment. These findings argue against the possibility that crossmodal interactions in endogenous spatial attention only arise when attention is guided to relevant locations on the basis of continuously visible, ambient information in a well-lit environment. Instead, they are consistent with our proposal that such crossmodal interactions reflect supramodal attentional control processes, and as a consequence can be observed in both lit and dark environments.

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