BRIEF REPORT

Temporal dynamics of lateralized ERP components elicited during endogenous attentional shifts to relevant tactile events

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Abstract

To investigate the temporal dynamics of lateralized event-related brain potential (ERP) components elicited during covert shifts of spatial attention, ERPs were recorded in a task where central visual symbolic cues instructed participants to direct attention to their left or right hand in order to detect infrequent tactile targets presented to that hand, and to ignore tactile stimuli presented to the other hand, as well as all randomly intermingled peripheral visual stimuli. In different blocks, the stimulus onset asynchrony (SOA) between cue and target was 300 ms, 700 ms, or 1,100 ms. Anterior and posterior ERP modulations sensitive to the direction of an attentional shift were time-locked to the attentional cue, rather than to the anticipated arrival of a task-relevant stimulus. These components thus appear to reflect central attentional control rather than the anticipatory preparation of sensory areas. In addition, attentional modulations of ERPs to task-irrelevant visual stimuli were found, providing further evidence for crossmodal links in spatial attention between touch and vision.

Descriptors: Tactile-spatial attention, Attentional orienting, Cross-modal attention, Attentional control, Event-related brain potentials

Numerous event-related brain potentials (ERP) studies have found that sensory-perceptual processes are modulated by the current focus of spatial attention (for a review, see Luck, Woodman, & Vogel, 2000). Some ERP studies have also examined anticipatory attentional shifts, which arise prior to the onset of task-relevant stimuli. Shifts of attention triggered by central visual cues indicating the likely side of a relevant visual event are accompanied by a posterior early directing attention negativity (EDAN) and late directing attention positivity (LDAP), as well as by a frontal contralateral negativity (anterior directing attention negativity, ADAN) contralateral to the direction of an attentional shift (Harter, Miller, Price, LaLonde, & Keyes, 1989; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000). These lateralized ERP components may reflect different stages in the control of spatial orienting. For example, the ADAN has been associated with the initiation of attentional shifts within an anterior attention system (Nobre et al., 2000), whereas the LDAP has been linked to the preparation of sensory processing in anticipation of an upcoming visual stimulus (Harter et al., 1989). Recent findings that these components are elicited not only during shifts of visual attention, but also when attention is directed to the location of relevant auditory or tactile events (Eimer & Van Velzen, 2002; Eimer, Van Velzen, & Driver, 2002) suggest that they might reflect spatial selection processes at a supramodal level (cf. Farah, Wong, Monheit, & Morrow, 1989).

The present experiment investigated the temporal dynamics of these lateralized ERP components in a task where a central visual cue instructed participants to direct attention to their left or right hand in order to detect infrequent tactile targets presented to that hand, and to ignore tactile stimuli presented to the other hand (as well as all randomly intermingled peripheral visual stimuli). In different blocks, the stimulus onset asynchrony (SOA) between cues and subsequent peripheral stimuli was 300 ms, 700 ms, or 1,100 ms. If the ADAN reflects the initiation of an attentional shift triggered by the cue, it should be time-locked to cue onset, and not be affected by the SOA manipulation. If the LDAP is associated with anticipatory preparation, it should be maximal at the expected onset of a target (i.e., extended in time when the target is expected at a later point), and thus be strongly affected by SOA. Another aim of this study was to further investigate crossmodal links in spatial attention from touch to vision (cf. Eimer & Driver, 2000) by studying whether ERPs elicited by irrelevant left or right visual stimuli are affected by attention directed to the location of relevant tactile events.

Methods

Participants
Eighteen paid volunteers participated in the experiment. Two were excluded due to excessive eye blinks and 3 due to insufficient eye fixation control. Thus 12 participants (9 women), aged 19–40 years (mean 25.8 years) remained.

Stimuli and Apparatus
Participants sat in a dimly illuminated experimental chamber, wearing a head-mounted microphone. Two adjacent triangles, presented centrally on a computer screen at a viewing distance of 55 cm (visual angle: $3.5° \times 2.5°$), served as cue stimuli. One triangle was red, the other blue, and they always pointed in opposite directions ("▶ ◀" or "◀ ▶"). A central fixation cross, located between both triangles, was continuously present throughout the experimental blocks. Tactile stimuli were presented using 5-V solenoids, driving a metal rod with a blunt conical tip to the outside of either index finger, making contact whenever a current was passed through the solenoid. Rods and fingertips were occluded to prevent visibility of the rod movements. White noise (62 dB SPL) was continuously present to mask any sounds made by the tactile stimulators. Peripheral visual stimuli were presented by illuminating an ensemble of green LEDs, consisting of six LEDs arranged in a circle plus one central LED element (angular size of single LEDs: 0.65°; circle diameter: 2.4°). Two tactile stimulators and two LED ensembles were placed on a table in close spatial register 25° to the left and right of fixation. Tactile nontarget stimuli consisted of one rod contacting a finger for 200 ms. Tactile target stimuli had a gap, where this contact was interrupted for 10 ms after 95 ms. For visual stimulation, one LED ensemble was illuminated for 200 ms.

Procedure
Twenty-four experimental blocks of 76 trials each were run. Each trial started with a 100-ms presentation of the central cue. Cue–target SOA was 300 ms, 700 ms, or 1,100 ms. Each SOA condition was presented in eight successive blocks, and the order of SOA conditions was balanced across participants. Participants had to respond vocally ("yes") whenever a tactile gap stimulus was detected at the cued location. Relevant locations were cued by the direction of one of the triangles. For half of the participants, blue triangles were relevant, and red triangles were relevant for the other half. Relevant left-pointing and right-pointing triangles were presented with equal probability to the left or right of fixation. In 64 trials, visual or tactile nontargets were presented with equal probability on the left or right side, and were preceded with equal probability by a left or right cue, resulting in eight trials for each combination of cued location, stimulus modality, and stimulus location. The remaining 12 trials contained tactile targets. Eight targets were presented at cued locations, and four at uncued locations.

Recording and Data Analysis
EEG was recorded with Ag-AgCl electrodes and linked-earlobe reference from 23 scalp electrodes. Horizontal EOG was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 5 kO, amplifier bandpass was 0.1–40 Hz, and digitization rate was 200 Hz. Separate averages were computed for the cue–target interval (relative to a 100-ms precue baseline), and in response to peripheral nontarget stimuli (relative to a 100-ms prestimulus baseline). Trials with eye-blinks, horizontal eye movements, or muscle artifacts were excluded. Averaged HEOG waveforms for trials where attention was directed to the left versus right were scored for systematic deviations of eye position. Three participants were disqualified due to residual HEOG deflections exceeding ± 2 μV.

ERP mean amplitudes obtained in the cue–target interval were analyzed with repeated measures ANOVAs, separately for lateral anterior (F7/8, F3/4, FC5/6), lateral central (C3/4, T7/8, CP5/6), and lateral posterior sites (OL/R, P3/4, P7/8), for the factors electrode site, SOA, cue direction, and hemisphere. For brevity, ERP results for peripheral nontarget stimuli are only reported for electrodes over primary visual and somatosensory projection areas contralateral to the side of stimulus presentation (C3/C4 for somatosensory ERPs; OL/OR for visual ERPs). These analyses included the factors SOA, attention (stimulus at cued location vs. uncued location), and stimulus side. Greenhouse–Geisser adjustments to the degrees of freedom were performed when appropriate, and adjusted p values are reported.

Results

Behavioral Performance
Mean vocal reaction times (measured with a voice key) were 690 ms, 660 ms, and 646 ms for long, medium, and short SOAs (main effect of SOA, $F(2,22) = 5.16$, $p < .017$, $\epsilon = .928$. Reaction times were delayed for long relative to medium and short SOAs, both $F(1,11) > 6.4$, both $p < .03$, but did not differ significantly between medium and short SOAs. Participants missed 4.8%, 4.7%, and 2.3% of relevant targets with long, medium, and short SOAs, and these differences were not significant. False alarms occurred on less than 1% of nontarget trials.

ERPs Elicited in the Cue–Target Interval
Figure 1 shows ERPs in response to cues directing attention to the left or right hand, at frontal (top) and occipital (bottom) electrode pairs. These waveforms are time-locked to cue onset, and ERP lateralizations sensitive to the direction of attentional shifts are reflected by deflections of opposite polarity at left and right electrodes (indicated by arrows in Figure 1). Although no early directing attention negativity (EDAN) was elicited in the present study, an anterior negativity contralateral to the direction of an attentional shift (ADAN) and a posterior contralateral positivity (LDAP) were present for all SOA conditions. With short SOAs, these components were elicited *after* target onset, and are thus superimposed on components elicited in response to visual and tactile stimuli (Figure 1, right). The time course of these effects can be seen more clearly in the difference waveforms shown in Figure 2 (see legend for details). The latencies and durations of the ADAN and LDAP relative to cue onset appear similar for all three SOA conditions, suggesting that both components are time-locked to the attentional cue.[1]

In our statistical analyses, which included all lateral electrode pairs (see Methods), ERP lateralizations sensitive to the direction of attentional shifts should be reflected in Hemisphere $\times$ Cued Direction interactions. No such effects were observed within the first 300 ms following cue onset. In the 350–550 ms postcue interval, a Hemisphere $\times$ Cue Direction interaction (reflecting the

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[1]The similarity of ADAN and LDAP effects with short relative to medium and long SOAs indicates that these components were not substantially affected by their overlap with target-related activation in the short SOA condition.
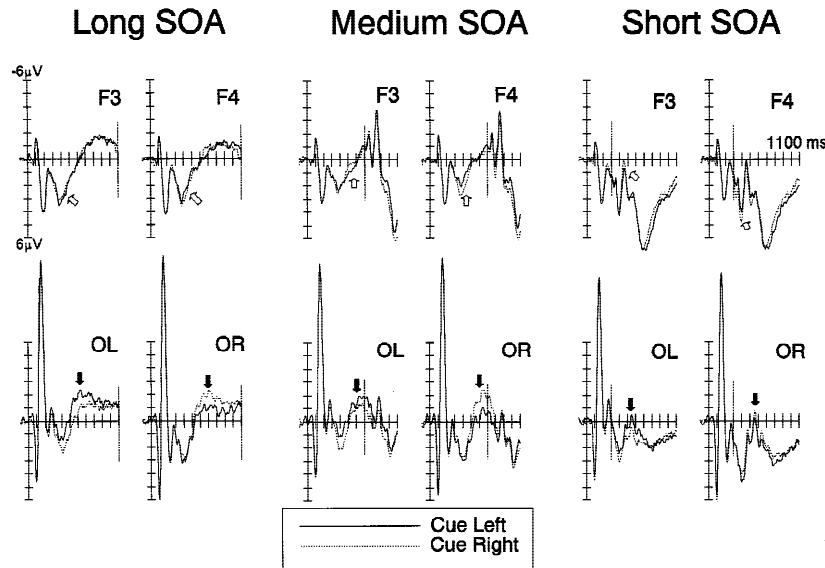
Figure 1. Grand-averaged ERPs elicited lateral anterior electrodes F3/F4 (top) and lateral posterior electrodes OL/OR (bottom) in the 1,100-ms interval following cues directing attention to the left or right side, for long, medium, and short SOAs. Dashed vertical lines indicate the onset of the subsequent peripheral stimulus. ERPs show a frontocentral negativity (anterior directing attention negativity; white arrows) and a posterior positivity (late directing attention positivity; black arrows) contralateral to the direction of the cued attentional shift.

ADAN) was present at lateral anterior electrode pairs, $F(1,11) = 9.84$, $p < .009$, but not at lateral central or posterior sites. Importantly, this anterior effect was not affected by SOA (SOA × Hemisphere × Cue Direction, $F < 1$).
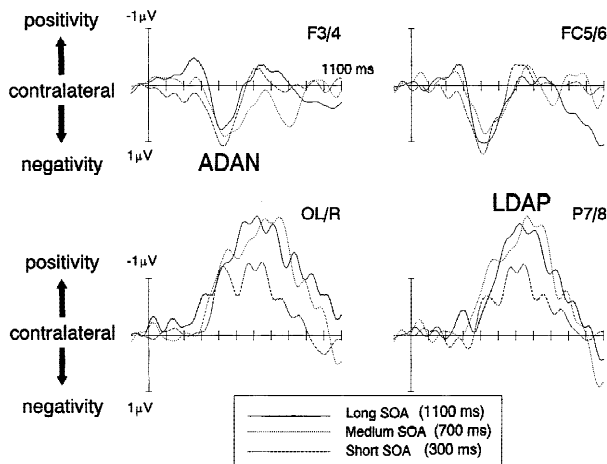

Figure 2. Difference waveforms obtained at lateral anterior (F3/4; FC5/6; top) and posterior (OL/R, P7/8; bottom) electrode pairs in the 1,100-ms interval following cue onset and onset with long, medium, and short SOAs, reflecting lateralized ERP modulations sensitive to the direction of attentional shifts. These difference waves were generated by subtracting ERPs recorded during rightward attentional shifts from ERPs elicited during leftward attentional shifts, and then subtracting the resulting difference waveforms at right electrodes from difference waveforms at corresponding electrodes over the left hemisphere. A net negativity contralateral to the direction of attentional shifts (ADAN) is reflected by positive amplitude values and a net positivity at contralateral sites (LDAP) is reflected by negative values.

The LDAP was analyzed in the 500–700 ms postcue latency range. A Hemisphere × Cue Direction interaction was present at posterior electrode pairs, $F(1,11) = 22.5$, $p < .001$, but not at central or frontal sites. Although a SOA × Hemisphere × Cue Direction interaction was obtained, $F(2,22) = 4.6$, $p < .03$, $\epsilon = .882$, Hemisphere × Cue Direction interactions were present for all three SOA conditions, all $F(1,11) > 13.9$, all $p < .003$. With long SOAs, LDAP amplitude decreased at the end of the cue–target interval (Figure 2, bottom), instead of increasing towards the anticipated onset of task-relevant events, as predicted. In the final 200 ms of this long cue–target interval (900–1100 ms postcue), a Hemisphere × Cue Direction interaction was only found at OL/R, $F(1,11) = 5.0$, $p < .05$. This "late" occipital LDAP was compared to the LDAP obtained in the 500–700-ms post-cue interval. A significant difference was obtained, $t(11) = 3.37$, $p < .008$, demonstrating that LDAP amplitude decreased prior to anticipated target onset in the long SOA condition.

Effects of Spatial Orienting on Somatosensory and Visual ERPs

Figure 3 shows ERPs elicited by cued and uncued nontargets at C3/4 (somatosensory ERPs, top) and OL/R (visual ERPs, bottom) contralateral to the side of stimulus presentation. For somatosensory N140 amplitude (quantified as mean amplitude between 130 and 170 ms poststimulus), an SOA × Attention interaction was obtained, $F(2,22) = 5.7$, $p < .018$, $\epsilon = .770$. Attentional N140 enhancements were obtained for medium SOAs, $F(1,11) = 8.6$, $p < .014$, but not with short or long SOAs. Between 200 and 250 ms poststimulus, an effect of attention, $F(1,11) = 5.5$, $p < .04$, was accompanied by an SOA × Attention interaction, $F(2,22) = 13.0$, $p < .001$, $\epsilon = .966$. Enhanced negativities for tactile stimuli at cued versus uncued locations were present for long and medium SOAs, $F(1,11) = 5.1$ and 20.0, $p < .05$ and $.001$, respectively, but not for short SOAs.
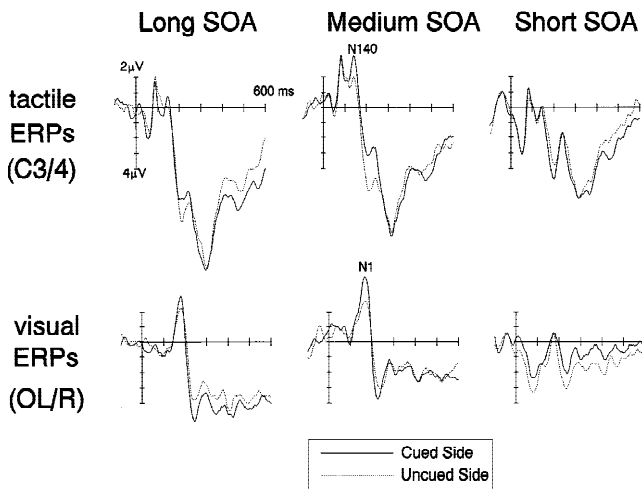
Figure 3. Grand-averaged ERPs elicited contralateral to the side of stimulus presentation in response to tactile nontargets at C3/4 (top) and to visual nontargets at OL/R (bottom) at cued and uncued locations.

Attention did not affect visual P1 amplitudes (90–130 ms). For the visual N1 component (140–180 ms), a crossmodal effect of attention in the tactile task, $F(1,11) = 8.2$, $p < .02$, was accompanied by an almost significant SOA × Attention interaction, $F(2,22) = 3.6$, $p < .06$, $\epsilon = .785$. Enhanced N1 components amplitudes for visual stimuli at cued locations were present with long and medium SOAs, $F(1,11) = 5.7$ and 5.8, respectively, both $p < .04$, reflecting crossmodal links in spatial attention from touch to vision. No N1 enhancements were found with short SOAs.

Discussion

The present study investigated the temporal dynamics of ERP lateralizations sensitive to the direction of endogenous attentional shifts by manipulating the SOA separating central cues and subsequent peripheral tactile or visual stimuli. Participants directed attention to one hand to detect infrequent tactile targets presented to the cued hand, while ignoring tactile stimulation of the uncued hand and all visual stimuli, regardless of their location. With medium and long SOAs, attention directed to the location of relevant tactile events resulted in an enhanced negativity of somatosensory ERPs to tactile stimuli at cued locations as well as in an enhancement of the N140 component in the medium SOA condition. More importantly, attentional modulations of the contralateral occipital visual N1 were also found for these conditions, even though visual stimuli were completely irrelevant. This finding corroborates earlier evidence for crossmodal links in spatial attention between touch and vision (Eimer & Driver, 2000; Eimer & Van Velzen, 2002).

The central finding of the present experiment was that the latencies of ERP components sensitive to the direction of an attentional shift (ADAN, LDAP) were very similar across SOA conditions. This demonstrates for the first time that these components are time-locked to the onset of an attentional cue and not to the anticipated arrival of an upcoming task-relevant stimulus. This supports the hypothesis that the ADAN reflects anterior attentional control signals initiating shifts of attention in response to a cue but appears inconsistent with the view that the LDAP is linked to sustained anticipatory preparation for task-relevant stimuli (Harter et al., 1989). Because SOAs were blocked, and the onset of peripheral stimuli thus fully predictable, anticipatory preparation should have been maximal at the expected stimulus onset. However, LDAP amplitudes were largest between 500 and 700 ms after cue onset for all three SOAs. With long SOAs, the LDAP was maximal 400 ms *before* stimulus onset and decreased towards the end of the cue–target interval (that is, when sustained preparation should have been maximal). With SOAs of 300 ms, this maximal LDAP effect was elicited 200 ms *after* the arrival of a peripheral stimulus, indicating that this short SOA was insufficient for attentional orienting to be completed prior to target onset.[2] Accordingly, no attentional effects on somatosensory and visual ERPs were observed in this condition.[3]

Overall, these results indicate that both the ADAN and the LDAP are unaffected by temporal characteristics of an experimental task, such as the anticipated arrival of task-relevant events relative to a preceding cue. These components appear to reflect transient and time-invariant central attentional control processes triggered by spatial cues, rather than an anticipatory sustained preparation of more peripheral sensory areas. Finally, it should be noted that these components were observed during shifts of attention towards anticipated relevant *tactile* events and that they were similar in terms of their latencies and scalp distributions to effects observed previously for attentional shifts to the location of relevant visual or auditory events (see Eimer et al., 2002, for a direct comparison of LDAP scalp distributions elicited during shifts of attention towards relevant visual, auditory, or tactile events). These observations support the hypothesis that the ADAN and LDAP reflect the operation of a unitary supramodal attentional system (see Eimer & Van Velzen, 2002; Eimer et al., 2002; Farah et al., 1989; for further discussion of supramodal attentional control) that initiates and controls spatial orienting processes for different modalities, regardless of which sensory modality is currently task-relevant.

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[2]The fact that responses to infrequent tactile target stimuli were faster with short as compared to long SOAs (which may seem inconsistent with the hypothesis that attentional orienting was incomplete in the short SOA condition) could result from an unspecific alerting effect of visual cues presented in close temporal succession to subsequent targets.

[3]It is possible that the absence of attentional cueing effects on visual and somatosensory ERP components in the short SOA condition may at least in part be due to an overlap of these components with the ADAN and/or LDAP.

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