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Effects of attentional filtering demands on preparatory ERPs elicited in a spatial cueing task

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ABSTRACT

Objective: We used ERP measures to investigate how attentional filtering requirements affect preparatory attentional control and spatially selective visual processing.

Methods: In a spatial cueing experiment, attentional filtering demands were manipulated by presenting task-relevant visual stimuli either in isolation (target-only task) or together with irrelevant adjacent distractors (target-plus-distractors task). ERPs were recorded in response to informative spatial precues, and in response to subsequent visual stimuli at attended and unattended locations.

Results: The preparatory ADAN component elicited during the cue-target interval was larger and more sustained in the target-plus-distractors task, reflecting the demand of stronger attentional filtering. By contrast, two other preparatory lateralised components (EDAN and LDAP) were unaffected by the attentional filtering demand. Similar enhancements of P1 and N1 components in response to the lateral imperative visual stimuli were observed at cued versus uncued locations, regardless of filtering demand, whereas later attentional-related negativities beyond 200 ms post-stimulus were larger the target-plus-distractor task.

Conclusions: Our results implicate that the ADAN component is linked to preparatory top-down control processes involved in the attentional filtering of irrelevant distractors; such filtering also affects later attention-related negativities recorded after the onset of the imperative stimulus.

Significance: ERPs can reveal effects of expected attentional filtering of irrelevant distractors on preparatory attentional control processes and spatially selective visual processing.

1. Introduction

In the past 25 years, brain mechanisms underlying visual-spatial attention have been increasingly studied with event-related brain potential (ERP) measures. Numerous studies have demonstrated that sensory-specific P1 and N1 components at posterior electrodes are enhanced in response to visual stimuli at attended versus unattended locations (e.g., Eason, 1981; Mangun and Hillyard, 1991; Eimer, 1994). These attentional modulations of early visual ERP components are thought to reflect location-specific sensory gating mechanisms that bias visual processing in favour of stimuli at the current focus of spatial attention. Attentional effects on early visual processing are thought to be controlled by top-down signals from higher-order areas that may specify currently task-relevant locations in advance of stimulation (e.g., Mangun, 1995; Driver et al., 2004). These attentional control processes that mediate endogenous shifts of spatial attention have also been studied with ERP measures. In numerous experiments, ERP components sensitive to the direction of cued attentional shifts were measured by comparing ERP waveforms triggered in the interval between symbolic spatial cues that directed attention to the left versus right side and subsequent target stimuli (e.g., Eimer et al., 2002; Harter et al., 1989; Hopf and Mangun, 2000; Nobre et al., 2000; Yamaguchi et al., 1994). These experiments have uncovered a series of lateralised ERP components during the cue-target interval. An early negative deflection at posterior electrodes contralateral to the direction of the induced attentional shift ('Early Directing Attention Negativity', EDAN) was followed by an enhanced negativity at frontal electrodes contralateral to the direction of attention ('Anterior Directing Attention Negativity', ADAN), and then by a contralateral positivity at posterior electrodes ('Late Directing Attention Positivity', LDAP).

These successive lateralised ERP components elicited during the cue-target interval of spatial cueing tasks have been thought to reflect the activation of cortical processes involved in the con-

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trol of visual-spatial attention. The EDAN was initially interpreted as a marker for activation of occipito-parietal brain areas involved in the decoding of symbolic cues and the subsequent initiation of attentional shifts (e.g., Harter et al., 1989; Hopf and Mangun, 2000). However, more recent results (Van Velzen and Eimer, 2003) show that the EDAN is linked to the visual processing of asymmetric (e.g., arrow) cue stimuli, rather than truly to attentional control processes involved in directing attention. The ADAN is assumed to be generated in lateral premotor cortex and/or the frontal eye fields (e.g., Praamstra et al., 2005; Van der Lubbe et al., 2006), and is thought to be associated with the anterior part of the dorsal frontoparietal attentional control network (Corbetta and Shulman, 2002). The LDAP has been proposed to originate from the lateral occipital cortex (Praamstra et al., 2005). It has previously been linked to spatially specific activation of visual areas in anticipation of task-relevant visual events at attended locations (Harter et al., 1989), or to a higher-order neuronal representation of the attended region of visual space (Hopf and Mangun, 2000).

ADAN and LDAP components are not only elicited during cued shifts of visual attention, but also when visual or auditory cues direct attention towards the location of task-relevant auditory or tactile events (e.g., Eimer et al., 2002, 2003b; Seiss et al., 2007), suggesting that these components might reflect supramodal attentional control processes. Moreover, ADAN and LDAP components are not only found during covert shifts of attention, but also during cued covert preparation of spatial motor acts (e.g., Eimer et al., 2005, 2006; Eimer and Van Velzen, 2006; Gherri et al., 2007; Praamstra et al., 2005) which is in line with the central claim of the premotor theories of spatial attention (e.g., Rizzolatti et al., 1994) that response programming and spatial attention are mediated by shared sensorimotor control structures (e.g., Eimer et al., 2005).

While such aspects of lateralised preparatory ERP components during cued anticipatory shifts of spatial attention have been well studied, here we focus on a new aspect that has received relatively little consideration in ERP studies of spatial attention to date, despite emerging as an important topic in recent psychophysical and neuroimaging studies. This topic concerns those cognitive-control mechanisms that may be involved in filtering out visual distractors and in preparing to do so (e.g., see Awh et al., 2003; Ruff and Driver, 2006; Serences et al., 2004). In most previous typical ERP studies of preparatory lateralised components linked to spatial attention, such as the ADAN and LDAP, lateral targets have appeared on one side in isolation, after a delay following the precue. But in the real world, task-relevant targets may only rarely appear in complete isolation, instead they typically appear in much more cluttered scenes, where they are surrounded by distractors. Recent psychophysical and fMRI studies have begun to study how the brain may prepare to filter out distractors surrounding an upcoming target at a known location (e.g., Awh et al., 2003; Ruff and Driver, 2006; Serences et al., 2004). But to our knowledge, this issue has not previously been studied with the well-developed ERP methods.

If preparatory components related to the direction of spatial attention, such as the ADAN and LDAP, merely reflect which hemifield is currently task-relevant, then presumably they should arise equivalently whether or not surrounding distractors next to the target are anticipated. If instead these ERP markers of preparatory attentional control processes reflect selection of a target from among possible distractors, then presumably they might become larger, and/or more sustained, in cued attention tasks that involve selection of a target from distracting clutter. To our knowledge, only one study investigated possible links between task difficulty and the preparatory lateralised ERP components triggered during cued attentional shifts to date (Hopf and Mangun, 2000), but it did not manipulate distracting clutter per se.

Here, we used ERP methods to directly address the issue of selecting targets in the presence or absence of surrounding distractor clutter. Our critical new manipulation was the level of distractor clutter that could be anticipated. Two task conditions were compared that differed only with respect to the presence or absence of distractors that could accompany lateral task-relevant visual events. In both tasks, a central symbolic cue directed attention to the left or right side, and a diamond-shaped imperative stimulus was then presented 1000 ms after cue onset, along the horizontal meridian on the cued or uncued side (see Fig. 1). Participants had to make a discrimination determined by stimulus shape (diamond shape with a vertical cut on one of its sides versus on both of its sides). Their task was to respond to diamonds with two cuts when they were presented at the cued side only (any event on the other side could simply be ignored). As described thus far, the presentation of a single target item after a delay following a symbolic spatial cue is similar to all prior ERP studies of preparatory attention-related components, such as the ADAN and LDAP (see Fig. 1, top panel). The novel twist here was than in another version of the same task, it could be anticipated that the lateral target would appear closely flanked by surrounding distractors that needed to be filtered out (see Fig 1, bottom panel). In this case, two distractor diamonds (always with only one vertical cut) were presented in close spatial proximity to the imperative target, vertically aligned with it in the same hemifield.

If attentional control processes triggered during covert shifts of attention are modulated by anticipated attentional filtering demands imposed by the expected presence (or absence) of cluttering irrelevant distractors, then lateralised ERP components such

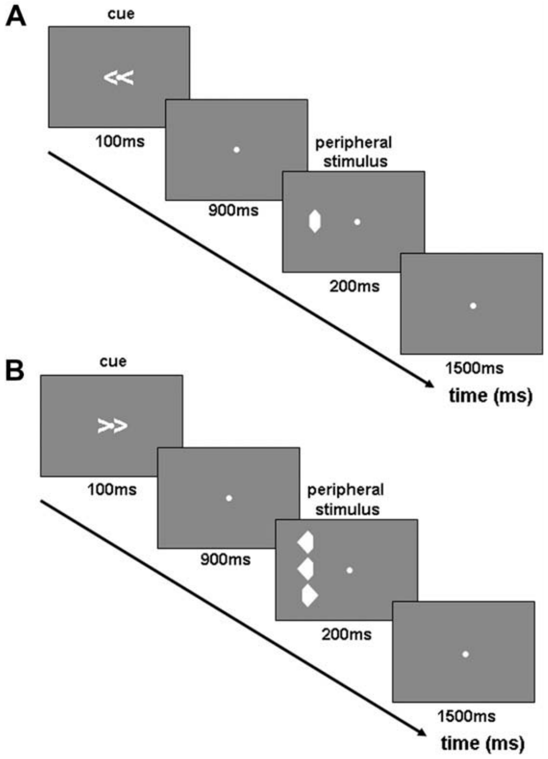

Fig. 1. Trial structure. A central cue (<<, >>) was displayed for 100 ms and followed after an empty interval of 900 ms by a lateral stimulus (diamond with one or two vertical cuts) presented for 200 ms. Participants had to detect and verbally respond only to double-cut diamonds on the cued side. (A) Target-only task; example trial where a double-cut target stimulus is presented on the cued left side. (B) Target-plus-distractors task; example trial where a single-cut nontarget (therefore requiring no verbal response) is presented together with two flanking task-irrelevant distractors on the uncued side, i.e. the left hemifield in this example.

as the ADAN and LDAP should differ between the two tasks. More precisely, we expected one or both of these components to be more pronounced and/or more sustained in the target-plus-distractor task, as this task requires more attentional filtering. Alternatively, if they just reflected which hemifield is currently task-relevant, they should be unaffected, as that aspect of the design (i.e. trial-by-trial cuing of which side to judge) remained the same regardless of the presence or absence of cluttering distractors. We also measured and compared the EDAN component in both tasks. If this component was primarily associated with the spatially selective visual processing of asymmetrical arrow cues, rather than with control processes active during covert attentional shifts, as suggested by our previous results (Van Velzen and Eimer, 2003), it should not be affected by differences in task demands.

In addition to measuring the critical anticipatory ERP components during the cue-target interval, for completeness we also analysed ERPs in response to subsequently presented visual nontarget stimuli (single-cut diamonds) at cued versus uncued locations. In line with many earlier studies (e.g., Eimer, 1994; Hopf and Mangun, 2000; Mangun and Hillyard, 1991), we expected to observe the usual effects of visual-spatial attention at posterior electrodes for visual ERPs (enhanced P1 and N1 amplitudes for stimuli at cued as compared to uncued locations, and a sustained enhanced negativity for items on the cued side at post-stimulus latencies beyond 200 ms), for both task conditions. The question was whether these attentional modulations of visual ERPs would be more pronounced in the target-plus-distractor task relative to the target-only task. Differences in the effects of spatial attention between the two tasks would demonstrate that the manipulation of attentional filtering demands affects visual processing at early sensory-specific stages (as reflected by P1 and N1 components), and/or at later post-perceptual stages (as reflected by the longer-latency sustained attentional negativity). Nevertheless, our more critical new question (see above) was how the preparatory ERP components, in the cue-target interval, would differ for the target-only task versus the target-plus-distractors task.

2. Methods

2.1. Participants

Twenty-one paid volunteers participated. Four were excluded due to poor eye gaze control in the cue-target interval (see below), and one other due to a low signal-to-noise ratio in EEG. Thus sixteen participants (7 females), aged 18–36 years (mean age: 25.3 years), remained. All but one were right handed, and all reported normal or corrected vision.

2.2. Stimuli, apparatus, and procedure

Participants were tested in a dimly lit room, and fixated a white dot (0.2° × 0.2°) displayed continuously at the centre of a grey computer screen located 57 cm in front of them. On each trial, a central visual cue ('<<' or '>>'; 1.2° × 1.0°) was displayed for 100 ms. This cue was followed after an empty interval of 900 ms by a lateral stimulus. In the target-only conditions, this was a diamond with either cuts on both its left and right side (size: 0.8° × 1.4°) or a diamond with just one cut, either on its left or right side (size: 1.1° × 1.4°). These single stimuli were presented for 200 ms on left or right side of the screen, horizontally aligned with the central fixation dot; at an eccentricity of 6.8° from the screen centre (see Fig. 1A). The intertrial interval was 1500 ms.

In the target-plus-distractors version of the task (see Fig. 1B), two additional nontargets (each a diamonds with one cut) were presented immediately above and below the target (vertical centre-to-centre distance from the target: 1.9°). In both tasks, participants were instructed to direct their attention to the side indicated by the cue, and to respond vocally to any double-cut targets presented on the cued side by saying 'yes'. No vocal responses were required to any stimulus appearing on the uncued side (which was equally likely), nor to any single-cut target or distractor. Response onset latencies were recorded by voice key. Vocal rather than manual responses were used in order to avoid any lateralisation associated with unimanual response preparation during the cue-target interval. Even though the control of verbal responses is also lateralised, this lateralisaton will remain constant across all task conditions. The total number of trials for each task was 384, with short breaks every five minutes. In both tasks, single- and double-cut target stimuli were equiprobable, and were equally likely to appear at cued or uncued locations on the left or right side. Thus, only 25% of all trials contained a double-cut target on the cued side and therefore required a vocal response. Any additional flanking distractors always had a single-cut. Both task conditions were presented in a blocked design and the order in which these conditions were delivered was counterbalanced across participants.

2.3. EEG recording and data analysis

The BrainVision Recorder (Brain Products, Munich, Germany) software package (BrainVision Analyzer) was used for EEG recording and analysis. EEG was DC-recorded from 25 Ag-AgCl electrodes relative to a left earlobe reference (all impedances below 5 kΩ; 250 sampling rate; 40 Hz upper cut-off frequency). EEG was digitally re-referenced to the average of the left and right earlobe. Trials with eyeblinks (Fpz exceeding ±80 μV relative to baseline), horizontal eye movements (HEOG exceeding ±30 μV relative to baseline), or other artefacts (a voltage exceeding ±80 μV at any electrode location relative to baseline) were excluded from further analyses. Averaged HEOG waveforms to cues directing attention to the left versus right side were scored for any systematic deviations of eye position, indicating residual eye movements towards the cued location. HEOG deviations exceeding ±4 μV led to the disqualification of four participants. In the grand-averaged HEOG waveforms obtained for the remaining participants, mean residual deviations observed across the 900 ms interval after cue onset in response to left versus right cues were below 0.3 μV in either task condition, and remained below 0.7 μV for any sampling point during this interval.

Separate analyses were conducted for ERP waveforms obtained in the cue-target interval and for ERPs in response to lateral visual stimuli. For the former analysis, EEG was epoched into 1000 ms periods from −100 to 900 ms relative to cue onset, relative to a 100 ms pre-cue baseline, and was averaged for left and right arrow cues, separately for both tasks. Lateralised potentials sensitive to the direction of a cued attentional shift were measured by comparing ERPs recorded at electrodes ipsi- and contralateral to the cued side, as in many previous studies of the ADAN and LDAP component. For completeness, the early directing attention negativity (EDAN) was also quantified on the basis of mean amplitude values at lateral posterior sites (P3/4, P7/8, PO7/8) during a 250–350 ms post-cue interval. The anterior directing attention negativity (ADAN) was measured at lateral anterior sites (F3/4, FC5/6, F7/8) during the 300–500 and 550–900 ms post-cue intervals. The late directing attention positivity (LDAP) was quantified at lateral posterior electrode sites PO7/8 during the 550–900 ms post-cue interval. Mean amplitudes were analysed by repeated measures ANOVAs with the factors of lateralisation (electrode ipsilateral versus contralateral to the cued side), electrode site, and task (target-only versus target-plus-distractors task).

ERPs in response to subsequent lateral visual stimuli were averaged for EEG epochs between −100 and 400 ms relative to the onset of these stimuli (100 ms pre-stimulus baseline). Only ERPs for trials with only single-cut diamonds were analysed, to avoid any contamination by response-related activity. Mean amplitudes were computed at lateral posterior electrodes P3, P4, P7, P8, PO7, and PO8 for two time windows centred on the visual P1 and N1 components (100–140 and 160–200 ms after target onset, respectively), as well as for one longer-latency time window (250–400 ms after target onset). These were analysed by repeated measures ANOVAs for the factors cue validity (valid versus invalid), task (target-only versus target-plus-distractors task), hemisphere (left versus right), and electrode site (P3/4 versus P7/8 versus PO7/8). For all ANOVAs, within-subject effects were corrected for non-sphericity using the Huynh–Feldt correction. Significant effects were further analysed using post hoc tests (t-tests for paired samples). Here, the critical α-level was adjusted according to the Bonferroni correction.

Reaction times and error rates (missed responses to cued double-cut targets; false alarms for single-cut diamonds or uncued double-cut targets) were analysed by means of planned one-tailed t-tests comparing the target-only versus target-plus-distractor tasks.

3. Results

3.1. Behavioural performance

As expected, reaction times were slower in the target-plus-distractor task compared to the target-only task (707 ± 23 ms versus 665 ± 23 ms, respectively; $t(15) = 2.1$, $p = .03$). There was no difference between the two tasks in the percentage of missed responses to targets at cued locations (1.8% versus 2.3% in the target-only versus target-plus-distractor tasks, respectively, $t(15) < 1$), nor in false alarm rates to response-irrelevant stimuli (1.1% versus 0.9% for these two tasks, $t(15) < 1$).

3.2. Lateralised ERP components in the preparatory cue-target interval

Fig. 2 displays grand averaged ERPs waveforms in response to cues directing attention to the left or right side, as observed during the 900 ms interval after cue onset at lateral anterior electrodes (Fig. 2, top panel) and at lateral posterior electrode electrodes PO7/8 and P7/8 (Fig. 2, bottom panel), ipsi- or contralateral to the cued side. ERPs obtained during the target-only task are shown on the left side, and ERPs recorded during the target-plus-distractors task on the right side. Fig. 3 further illustrates the lateralized ERP components obtained during cued attentional shifts in these two tasks as difference waveforms, computed by subtracting ERPs at electrode sites ipsilateral to the side of an attentional shift from contralateral ERPs. In these difference waves, enhanced contralateral negativities are reflected by negative amplitude values (upward deflections), and enhanced contralateral positivities by positive amplitudes (downward deflections). As can be seen from Figs. 2 and 3, all three ERP components previously observed during cued shifts of spatial attention (EDAN, ADAN, and LDAP) were present. The posterior EDAN and LDAP components appear similar in terms of amplitudes and latencies in both the conventional target-only task, and the new target-plus-distractors task. In contrast, the ADAN component was affected by our manipulation of attentional filtering demands, appearing larger in amplitude and longer in duration for the target-plus-distractor task as compared to the target-only task.

These observations were confirmed by statistical analyses. The presence of the EDAN component at lateral posterior electrodes was substantiated by a significant main effect of lateralisation ($F(1, 15) = 6.6$; $p = .02$) in the 250–350 ms interval after cue onset. There was also an interaction between lateralisation and electrode ($F(2, 30) = 4.2$, $p = .03$), and the Bonferroni-corrected follow-up analyses conducted separately for individual posterior electrode pairs revealed that the EDAN was significant at electrode pairs P7/8 ($t(15) = 3.2$, $p = .006$) and P3/4 ($t(15) = 2.7$, $p = .017$), but not at PO7/8 ($t(15) = 1.7$). But more importantly, there was no interaction between the factors lateralisation and task ($F < 1$), demonstrating that the EDAN was unaffected by differences in attentional filtering demands between tasks (as would be expected if the EDAN does indeed just reflect a visual response to the arrow cue, see Van Velzen and Eimer, 2003).

At lateral anterior electrode sites, a main effect of lateralisation in the 300–500 ms post-cue interval ($F(1, 15) = 65.8$, $p < .001$) reflected the early phase of the ADAN component (which we label as ADAN(e) in Figs. 2 and 3). Although this component was numerically larger in the target-plus-distractor task, the lateralisation × task interaction only approached statistical significance ($F(1, 15) = 3.1$, $p = .10$). During the later 550–900 post-cue analysis window, a main effect of lateralisation remained present at lateral anterior electrodes ($F(1, 15) = 13.7$, $p = .002$), reflecting the later phase of the ADAN component (labelled ADAN(l) in Figs. 2 and 3). Most importantly, while the ADAN(l) was present in the target-plus-distractors task, it was strongly attenuated in the target-only task (see Figs. 2 and 3). This differential effect of attentional filtering demands on the ADAN(l) was substantiated by a significant interaction between lateralisation and task ($F(1, 15) = 12.5$, $p = .003$). Follow-up analyses conducted separately for both tasks across all three anterior electrode pairs revealed that the ADAN(l) was reliably present in the target-plus-distractors task ($F(1, 15) = 28.2$, $p < .001$), but not in the target-only task ($F < 1$). In the target-plus-distractor task, there was an interaction between lateralisation and electrode site ($F(2, 30) = 3.5$, $p = .04$), and follow-up analyses revealed that the ADAN(l) was significant for electrode pairs F7/8 ($t(15) = 6.4$, $p < .001$) and FC5/6 ($t(15) = 3.5$, $p = .004$), while it did not reach the Bonferroni-corrected significance level for electrode pair F3/4 ($t(15) = 2.6$, $p = .02$). An interaction between lateralisation and electrode site ($F(2, 30) = 5.9$, $p = .007$) was also present in the target-only task. While the ADAN(l) was entirely absent at FC5/6 and F3/4 (both $t < 1$), a small but significant ADAN(l) was elicited at electrode pair F7/8 ($t(15) = 3.0$, $p = .009$), although it was attenuated relative to the target-plus-distractor task (see Figs. 2 and 3).

Another ERP component sensitive to the side of a cued attentional shift (LDAP) was elicited during the later phase of the cue-target interval obtained at lateral posterior electrodes PO7/8 (see Figs. 2 and 3, bottom panels). The presence of the LDAP was substantiated by a significant lateralisation effect observed during the 550–900 ms post-cue time interval at PO7/8 ($F(1, 15) = 13.5$, $p = .002$). But importantly, and in contrast to the ADAN component, LDAP amplitudes were entirely unaffected by our task manipulation (lateralisation by task interaction: $F = 1.1$).

3.2. Visual ERP components in response to lateral visual nontarget stimuli

The main focus of this study was on preparatory ERP components in the cue-target interval (see above), especially since anticipated distractors had not yet appeared at this point, so that the difference in attentional filtering demands for our two tasks was completely unconfounded from any differences in display appearance across the two tasks. Nevertheless, for completeness we also analysed ERPs in response to the lateral stimuli, as a function of whether these appeared on the cued versus uncued side (a factor which is orthogonal to display appearance, i.e. to the presence or absence of cluttering distractors).

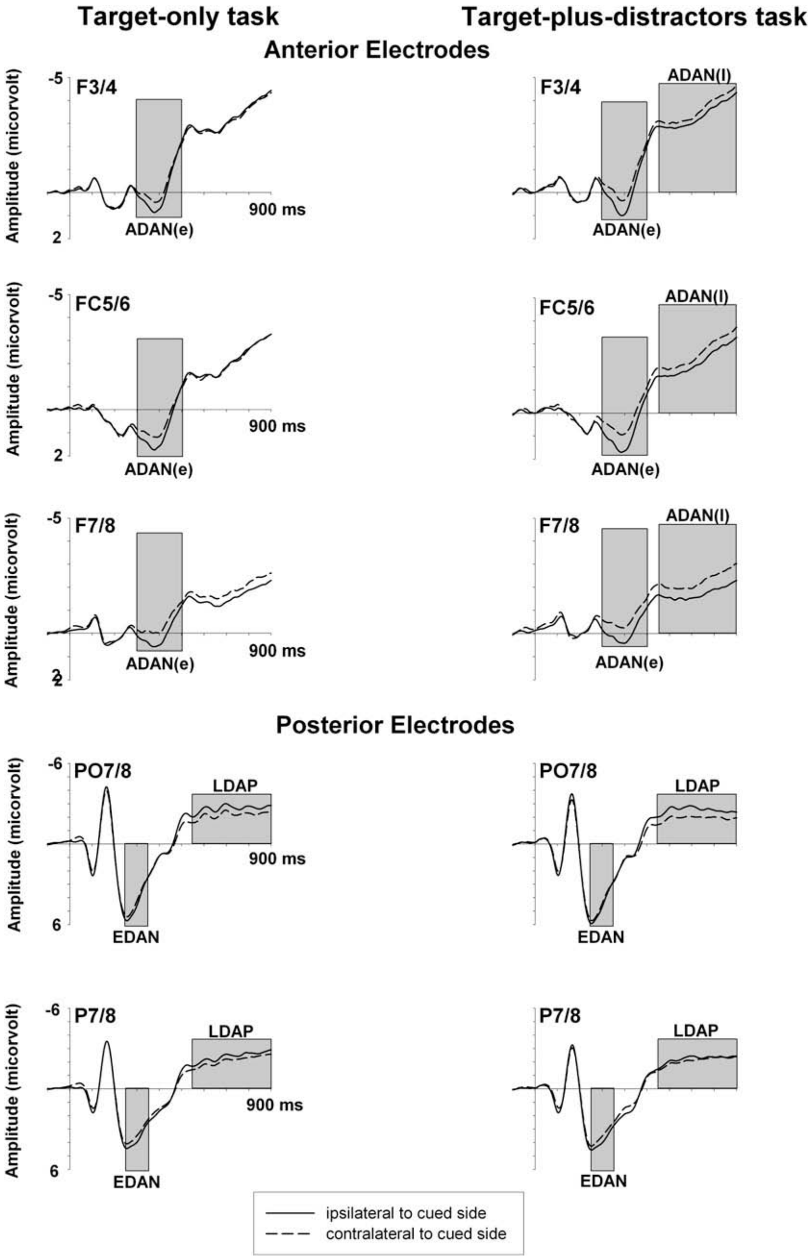

Fig. 2. Grand-averaged ERPs elicited at lateral anterior and posterior electrodes ipsilateral and contralateral to the cued side in the 900 ms interval following cue onset, for either task. ADAN(e), Early Anterior Directing Attention Negativity; ADAN(l), Late Anterior Directing Attention Negativity; EDAN, Early Directing Attention Positivity; LDAP, Late Directing Attention Positivity.

Fig. 4 shows ERPs elicited at lateral posterior electrode pairs, in response to cued or uncued visual nontarget (single-cut) stimuli, separately for the target-only and target-plus-distractors tasks, collapsed across hemispheres. As expected, visual P1 and N1 components were enhanced for stimuli at cued as compared to uncued locations, and these amplitude modulations were elicited in a similar fashion for both tasks. In contrast, the sustained attentional negativity triggered beyond 200 ms post-stimulus was more pronounced for the target-plus-distractor task than the target-only task.

These observations were confirmed by statistical analyses. Significant main effects of cue validity were obtained for P1 mean amplitudes ($F(1, 15) = 13.7$, $p < .002$) as well as for N1 mean amplitudes ($F(1, 15) = 9.6$, $p = .01$) at lateral posterior electrodes, confirming that P1 and N1 components were enhanced for visual stimuli at attended relative to unattended locations, as expected. An interaction between cue validity and electrode site was obtained for P1 amplitudes ($F(2, 30) = 6.6$, $p = .01$), with follow-up analyses revealing that attentional P1 modulations were reliable at PO7/8 ($t(15) = 4.8$, $p < .001$), but failed to reach Bonferroni-corrected significance levels for electrodes P7/8 ($t(15) = 2.6$, $p = .024$) and P3/4 ($t(15) = 1.6$, $p = .12$). There was also a main effect of task on N1 amplitude ($F(1, 15) = 14.1$, $p < .002$), as this component was larger in the target-plus-distractor task (see Fig. 4), where three lateral visual items were presented simultaneously, unlike the target-only task where only one lateral stimulus was shown. However, there was no indication of any cue validity × task interaction for either P1 or N1 amplitudes (both $F < 1$), indicating that attentional amplitude modulations of visual P1 and N1 components at posterior sites were comparable between the two tasks

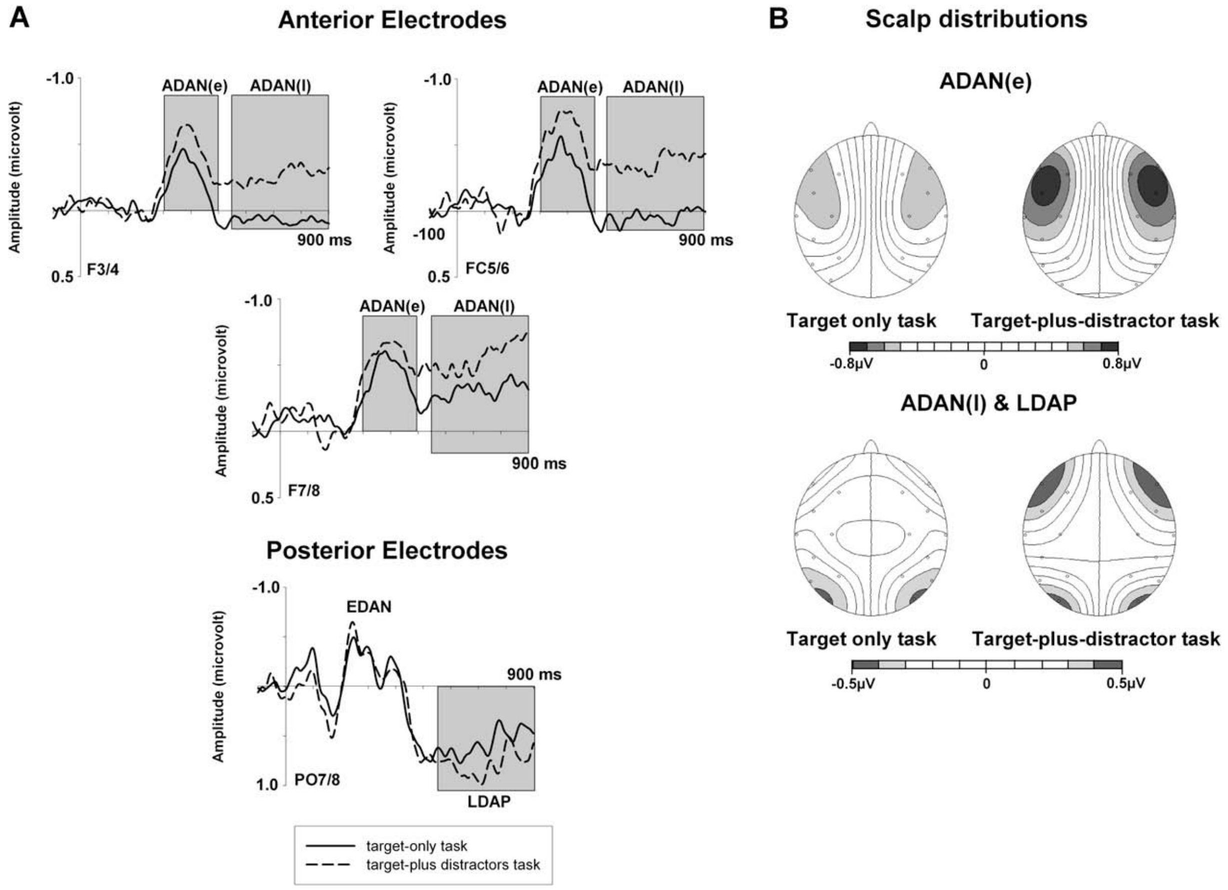

Fig. 3. (A) Grand-averaged difference waveforms in the 900 ms interval following cue onset at F3/4, FC5/6, F7/8, and at PO7/8 and P7/8, obtained by subtracting ERPs ipsilateral to the cued side from contralateral ERPs, for either the target-only task (solid lines) or the target-plus-distractors task (dashed lines). (B) Topographical maps representing differences between brain activity over hemispheres ipsi- and contralateral to the direction indicated by the cue. Maps (top view) are shown for a 20 ms time window centred around the ADAN(e) peak amplitudes (top row), and for the 550–900 ms post-cue time window (bottom row) where the ADAN(l) and LDAP were triggered. These maps were constructed by spherical spline interpolation (Perrin et al., 1989) after mirroring the difference amplitudes to obtain symmetrical but inverse amplitude values for both hemispheres. For the ADAN(e) (top row), amplitudes range between −0.8 and 0.8 µV. For the ADAN(l) and LDAP time window (bottom row), amplitudes range between −0.5 and 0.5 µV. For all topographies, contour lines represent changes of 0.1 µV.

and therefore not modulated by differences in attentional filtering demands.

During the longer-latency analysis window (250–400 ms post-stimulus), a main effect of cue validity was observed at lateral posterior electrodes ($F(1, 15) = 38.9$, $p < .001$), reflecting the enhanced negativity for visual stimuli presented on the cued relative to the uncued side (Fig. 4). An interaction between cue validity and electrode site ($F(2, 30) = 21.1$, $p < .001$) was due to this sustained attentional negativity being largest at P3/4, and smallest at PO7/8 (see Fig. 4). However, follow-up analyses confirmed that sustained attentional negativities were reliably present at all posterior electrode pairs (all $t(15) \geqslant 4.7$, all $p < .001$). In contrast to the results obtained for P1 and N1 amplitudes, a cue validity × task interaction was observed for this longer-latency analysis window ($F(1, 15) = 12.3$, $p = .003$), with larger sustained attentional negativity in the target-plus-distractors task. Follow-up analyses conducted separately for each task confirmed that some attentional negativity was present for both tasks ($t(15) = 8.9$, $p < .001$, for target-plus-distractor; $t(15) = 6.6$, $p < .001$ for target-only).

4. Discussion

We manipulated attentional filtering demands during spatial selective attention, by presenting imperative lateral stimuli either in isolation, or together with two closely flanking distractor items, in a situation where an arrow precue signalled which side was task-relevant for the current trial, and where the presence or absence of distracting clutter could be anticipated (task manipulation). We measured lateralised ERP components triggered during the cue-target interval (and also visual ERPs to subsequent lateral stimuli) to assess the effects of our task manipulation (distractors present or absent) on preparatory attentional control processes. In line with previous ERP studies (c.f. Eimer et al., 2002; Harter et al., 1989; Hopf and Mangun, 2000; Nobre et al., 2000; Yamaguchi et al., 1994), a series of lateralised ERP components (EDAN, ADAN, and LDAP) were observed during the cue-target interval. The EDAN triggered between 250 and 350 ms after cue onset at lateral posterior electrodes did not differ between the target-only and target-plus-distractors tasks. This is unsurprising, since this component has previously been shown to reflect a spatially selective visual response to asymmetric arrow cues (Van Velzen and Eimer, 2003), rather than being directly linked to attentional control mechanisms.

In contrast to the EDAN, the subsequent preparatory ADAN component was significantly affected by our manipulation of attentional filtering demands, via the two different tasks. During its early phase in the 300–500 ms post-cue interval, ADAN amplitudes were numerically but not significantly larger for the target-plus-distractors task. However, during the 550–900 ms post-cue interval, a reliable interaction between lateralisation and task

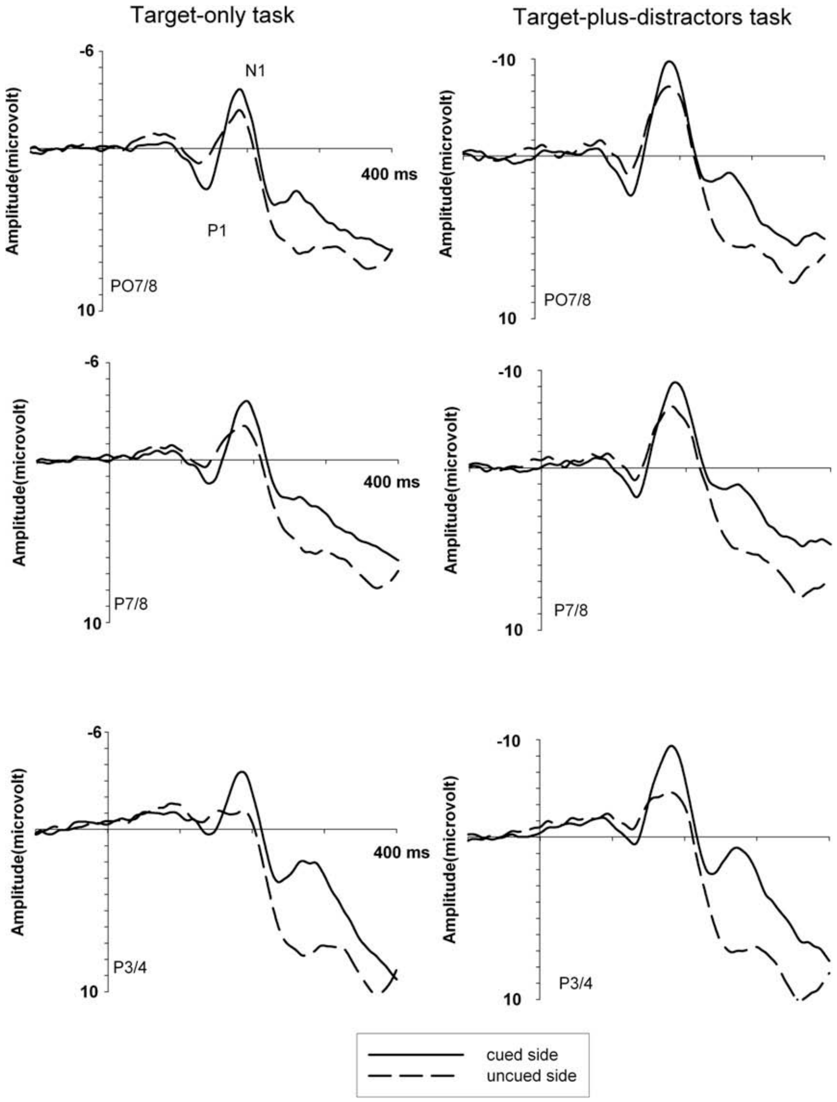

Fig. 4. Grand-averaged ERPs recorded at lateral posterior electrodes in the 400 ms interval following the onset of lateral visual single-cut stimuli presented on the cued or uncued side. Waveforms are collapsed across left-hemisphere and right-hemisphere electrodes, and are shown separately for the two tasks.

was for obtained for the late phase of the ADAN, which was much more pronounced in the target-plus-distractors task. In fact, the late ADAN was entirely absent at F3/4 and FC5/6 in the target-only task (see Figs. 2 and 3). This pattern of results demonstrates for the first time that a lateralised ERP component elicited during covert spatial orienting can be sensitive to the filtering demands of an upcoming attentional selection task. The critical difference between the two tasks employed in the present experiment was the necessity to filter out potentially interfering distractor items in one task but not the other. The presence of a larger and more prolonged ADAN in the target-plus-distractors task suggests that the attentional control processes reflected by this component are involved in such filtering operations. The ADAN may be linked to top-down control processes that act to adjust the size of the attentional focus (rather than merely its hemifield) in line with current task demands, with a more narrow focus in the target-plus-distractor task, as required in order to exclude flanking irrelevant distractor items from attentional processing.

The current finding, that the ADAN was affected by our task manipulation, contrasts markedly with previous results by Hopf and Mangun (2000) who did not obtain systematic effects of task difficulty on lateralised ERP component elicited during attentional orienting. This discrepancy may be due to differences between attentional selection requirements in these two studies. In the Hopf and Mangun (2000) study, participants had to compare visual symbols that were either highly similar or clearly different. Although these two conditions differed in terms of their demands on perceptual discrimination, both symbols were always task-relevant, and no additional task-irrelevant distractors were ever presented, which means that no attentional filtering of distractors was required in either task. In contrast, the two tasks used in the present experiment were designed to explicitly manipulate the demands on attentional filtering. The fact that the ADAN was found to be affected by our task manipulation in the present experiment, but not in the Hopf and Mangun (2000) study, suggests that the neural processes associated with this component may be involved in the top-down control of attentional filtering, per se, but they may not be directly linked to adjustments of attentional selectivity related to the anticipated perceptual difficulty of an upcoming selection task.

In contrast to the ADAN, the posterior LDAP component observed during the later phase of the cue-target interval did not differ systematically between the target-only and target-plus-distractor tasks. Previous studies have suggested that the LDAP primarily reflects attentional control processes that specify the locus of attended sensory events within visually defined coordinates of external space. In line with this hypothesis, the LDAP is absent during attentional shifts in congenitally blind people, as well as during attentional shifts in blindfolded sighted participants (Van Velzen et al., 2006). The LDAP is also larger during attentional shifts towards more peripheral visual locations (Eimer et al., 2004), but is unaffected by variations of body posture when visual target location is held constant (Eimer et al., 2003a). The current finding of no difference in the LDAP component between our tasks may arise because the visual target locations were the same across these tasks; all that differed was whether distractors at neighbouring locations were expected. It should be noted that the absence of task effects on LDAP amplitudes at lateral posterior electrodes does not necessarily provide conclusive evidence that there were no differences in the underlying neural processes. Because ADAN(l) and LDAP components were triggered within the same time window, and have opposite polarity, their amplitudes might have been affected by volume conduction of the underlying source currents from anterior to posterior brain regions, or vice versa. In the target-plus-distractors task where a strong ADAN(l) was present, volume conduction may have reduced posterior LDAP amplitudes recorded on the scalp surface. However, since the LDAP outcome was null for any task differences here, we place more emphasis on the significant task effects for the ADAN component in our study.

Turning to ERPs for the subsequent lateral stimuli, these showed the expected modulations of P1 and N1 amplitudes for stimuli on the cued versus uncued side (cf. Eimer, 1994; Hopf and Mangun, 2000; Mangun and Hillyard, 1991) in a similar manner across our two tasks. By contrast, the sustained negativity triggered at lateral posterior electrodes at post-stimulus latencies beyond 200 ms was affected by task, being more pronounced in the target-plus-distractors task (see Fig. 4). This attentional negativity is indicative of in-depth processing of attended information at later post-perceptual processing stages, and its enhancement may reflect the additional attentional filtering requirements associated with irrelevant distractors. The absence of any differences between tasks for attentional modulations of sensory-specific early visual P1 and N1 components, and the presence of such differences for longer-latency attentional ERP effects suggests that attentional filter settings primarily affect processing stages beyond the early sensory-perceptual analysis of visual information. It remains possible that differences in attentional filtering demands associated with the presence or absence of distractor stimuli in target displays may affect earlier ERP components under different task conditions. For example, the task employed in the present experiment involved a target–nontarget discrimination at attended locations, and responses were only required on a minority of trials where targets were presented on the cued side. It would therefore be interesting to investigate in future studies whether the necessity to filter out distractors is associated with enhanced attentional modulations of P1 and N1 components in tasks that require the discrimination between different target stimuli, and the selection and execution of a response that is determined by target identity on every trial.

In summary, the present experiment found new evidence that differences in attentional filtering demands affect the ADAN component, which is an established ERP marker of preparatory covert attentional shifts. The observation that the ADAN was larger and more sustained when potential target items had to be filtered out from flanking irrelevant distractors, than when target stimuli were presented in isolation, provides evidence that the ADAN is linked to top-down control processes involved in the attentional filtering of irrelevant information. It also shows that the brain can anticipate the filtering demands of upcoming distractors, converging in this respect with other recent evidence from psychophysical or fMRI studies (e.g., Awh et al, 2003; Ruff and Driver, 2006; Serences et al., 2004), but now reaching this conclusion via ERP evidence. The finding that attentional filtering demands affected visual ERPs only at post-stimulus latencies of 200 ms and beyond, but not earlier sensory-specific components, suggests that these top-down control processes primarily modulate visual processing at later post-perceptual stages.

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