

The N2pc component and its links to attention shifts and spatially selective visual processing

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Abstract

The N2pc component has recently become a popular tool in attention research. To investigate whether this component exclusively reflects attentional target selection or also prior stages in attentional processing (covert orienting, target-unspecific spatial attention), a spatial cuing procedure was combined with a visual search task. In some blocks, informative cues indicated the side of upcoming singleton targets that were present on most trials among uniform distractors. In other blocks, cues were spatially uninformative, and no preparatory shifts of attention were possible. The N2pc in response to targets was unaffected by this manipulation, showing that this component is not associated with attention shifts. Following informative cues, an attenuated N2pc was elicited by uniform nontarget arrays, suggesting that the N2pc may also reflect spatially specific processing of stimulus features at task-relevant locations prior to target selection.

Descriptors: Spatial attention, Attentional orienting, Visual search, Event-related potentials

Over the past 30 years, the brain mechanisms underlying visual-spatial attention have been studied intensively with event-related brain potential (ERP) measures. Different ERP components have been found to be modulated during spatially selective visual processing, and these components have been linked to different underlying subprocesses of spatial attention. The first type of attention-sensitive ERP effect was uncovered in early ERP studies where participants were instructed to direct their attention to a specific location on the left or right side and keep it focused for an entire experimental block in order to detect target stimuli at that location (cf. Eason, 1981). Visual stimuli presented within the current focus of spatial attention triggered enhanced sensory-specific visual P1 and N1 components at posterior electrodes. Analogous P1 and N1 amplitude modulations were also observed when attention was manipulated in a trial-by-trial fashion by spatial precues that were presented at the start of each trial (cf. Eimer, 1994; Mangun & Hillyard, 1991). Because these P1/N1 enhancements for stimuli at attended locations were present irrespective of whether these stimuli were targets or nontargets (e.g., Mangun & Hillyard, 1987), they are interpreted as reflecting location-specific sensory gating mechanisms in early visual processing that precede the subsequent selection of targets over

nontargets. They are assumed to be triggered by top-down signals from higher order attentional control areas that bias the excitability of visual cortical areas in favor of any sensory input that originates from currently task-relevant locations (cf. Mangun, 1995).

Other attention-sensitive ERP modulations found in more recent studies during cued shifts of spatial attention were interpreted as electrophysiological markers of top-down attentional control processes. In these studies, ERP components sensitive to the direction of cued attentional shifts were quantified by comparing ERP waveforms triggered in the interval between a spatial cue and a subsequent target stimulus for cues that directed attention to the left versus right side (e.g., Harter, Miller, Price, LaLonde, & Keyes, 1989; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000; Yamaguchi, Tsuchiya, & Kobayashi, 1994). An enhanced negativity at anterior recording sites contralateral to the cued side of an attentional shift (anterior directing attention negativity, ADAN) was followed by a contralateral posterior positivity (late directing attention positivity, LDAP). These lateralized ERP components are assumed to reflect successive phases in the control of visual-spatial attention, such as the initiation of a lateral attention shift and the preparatory activation of visual brain areas. The fact that they are elicited not only during shifts of visual attention but also when participants direct their attention to the location of expected auditory or tactile events (e.g., Eimer, Van Velzen, & Driver, 2002) suggests that they might reflect the activation of modality-unspecific attentional control mechanisms (see Eimer et al., 2002, for more details).

A third type of attention-sensitive ERP effect has been observed in experiments investigating the spatial selection of target

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stimuli in visual search displays. The N2pc component is typically elicited at poststimulus latencies of 200–350 ms at posterior electrodes contralateral to the side of a visual search target that is presented among nontarget items. This component is assumed to reflect the spatially selective processing of task-relevant visual target stimuli in multistimulus displays and/or the attentional suppression of surrounding nontargets (cf. Eimer, 1996; Luck & Hillyard, 1994; Woodman & Luck, 1999, 2003). For visual search displays that contain a perceptually unique singleton item among uniform distractors, an N2pc is triggered when singletons possess task-relevant features (Luck & Hillyard, 1994; but see Hickey, McDonald, & Theeuwes, 2006, for recent evidence that the N2pc is also elicited in the course of exogenous attentional capture by salient, but task-irrelevant visual stimuli). Brain source analyses based on MEG recordings have localized the neural generators responsible for the N2pc in extrastriate visual areas, with a possible contribution of posterior parietal cortex to the early part of this component (e.g., Hopf et al., 2000).

Because the N2pc is becoming an increasingly popular tool in the investigation of attentional processing (cf. Brisson & Jolicœur, 2007; Dell'Acqua, Pesciarelli, Jolicœur, Eimer, & Peressotti, 2007; Dell'Acqua, Sessa, Jolicœur, & Robitaille, 2007; Eimer & Kiss, 2007; Eimer & Mazza, 2005; Hickey et al., 2006; Kiss et al., 2007; Mazza, Turatto, Umiltà, & Eimer, 2007; Robitaille & Jolicœur, 2006; Woodman & Luck, 1999, 2003), it is important to understand more precisely what type of attentional selection mechanisms are reflected by this component. The current interpretation of the N2pc as an electrophysiological marker of the selective attentional processing of targets versus distractors in a multistimulus search array clearly distinguishes this component from components such as the ADAN and LDAP, which are linked to shifts of attention toward expected target locations and also from attentional P1/N1 modulations, which are assumed to reflect sensory gating mechanisms in early visual processing that take place prior to the selection of specific target stimuli. The aim of the present study was to test the assumption that the N2pc is uniquely linked to the selective processing of candidate target stimuli and not to other attentional processes such as the covert orienting of attention or location-specific modulations of visual processing that are unrelated to the presence of a target. More specifically, we investigated whether the N2pc in response to singleton target stimuli in a visual search array is affected by prior cued attention shifts and whether this component can also be observed in response to perceptually uniform search arrays that do not contain any candidate target stimuli.

The possibility that the N2pc might be linked to shifts of spatial attention and in that sense be analogous to preparatory components such as the ADAN and LDAP has not yet been systematically investigated. The reason for this is that, in almost all studies investigating attentional target selection with the N2pc, participants had no advance information about the location of these targets (but see Praamstra, 2006). This contrasts with the procedures used in studies that investigated lateralized preparatory ERP components (ADAN, LDAP), and attentional P1/N1 modulations, where to-be-attended locations were always specified in advance. In these experiments, ERP effects of spatial attention were interpreted in terms of covert attentional orienting and subsequent sensory gating processes that are contingent on advance spatial information. In contrast, in a typical visual search task where the N2pc is observed (e.g., Luck & Hillyard, 1994), targets appear with equal probability and unpredictably at different locations in the visual field. Because it is not possible to direct

attention in advance to specific locations, any attention shift toward the target will necessarily occur after the onset of the search array and could therefore be partly or even primarily responsible for the emergence of the N2pc. Although the N2pc is usually interpreted as an indicator of the spatially selective attentional processing of target versus distractor items in visual search, it might thus also reflect covert shifts of attention to target locations.

Another important question that has not yet been investigated is whether the presence of a potential target stimulus in a visual display is always a necessary condition for the N2pc to emerge. Because previous N2pc studies have quantified this component in response to visual search arrays that contained at least one item with task-relevant or otherwise perceptually unique features, it remains unknown whether this component might also be observed during the spatially specific processing of visual search arrays without any candidate target items, analogous to P1/N1 modulations that are triggered for attended visual stimuli irrespective of their status as targets or nontargets.

The present study was designed to investigate both questions and combined a spatial cuing procedure with a visual search task. On every trial, a centrally presented spatial precue was followed after a 700-ms blank interval by a circular visual search array. On two thirds of all trials, this search array contained a singleton target stimulus (a diamond) among 11 nontargets (squares; see Figure 1). Participants had to decide whether these target diamonds were cut on the left or right side (Bravo & Nakayama, 1992). Targets could appear at the 8, 9, or 10 o'clock position on the left side or at the 2, 3, or 4 o'clock position on the right side. On one third of all trials, a perceptually homogeneous array of 12 nontarget squares was presented instead, and no response was required on these target-absent trials. In one half of the experiment, precues were fully predictive with respect to the side where a target (if present) would appear. After a left cue, target stimuli would always be presented at one of the three possible locations on the left side and never on the right side, and vice versa for right cues. In this informative cue condition, participants were instructed to covertly shift their attention to the cued side during the cue–target interval and prior to the presentation of the visual search array. In the other half of the experiment, cues were spatially nonpredictive, as targets could appear with equal probability at any of the six possible locations on the left and right sides. In this uninformative cue condition, participants were

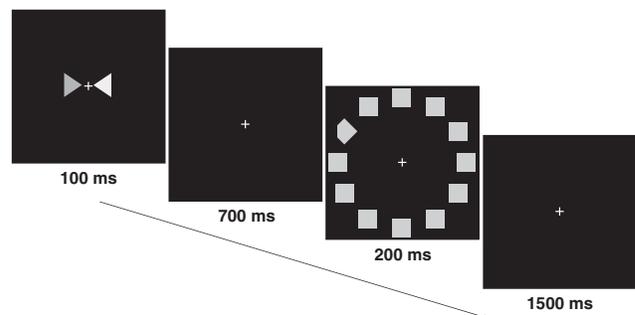


Figure 1. Illustration of the stimulus sequence presented on individual trials. A symmetric cue array consisting of one red and one blue triangle was followed after an empty interval of 700 ms by a circular search array. Search arrays contained a diamond target among distractors (squares) on two thirds of all trials. [Correction added after online publication date 26 October 2007: Figure 1 altered to show the target diamond with a cut rather than as a full diamond in the 200-ms display.]

expected to maintain a diffuse or central focus of attention until the search array was presented.

To investigate whether the N2pc at least in part reflects covert shifts of attention toward a target stimulus in a visual search array, this component was quantified in response to target-present arrays, separately for the informative and uninformative cue condition. With spatially uninformative cues, a clear N2pc was expected in response to targets, as this condition was analogous in terms of the absence of advance spatial information to previous visual search studies where the N2pc was found. The critical question was whether an N2pc of similar amplitude and latency would also be observed in the informative cue condition, where an attention shift toward the side of the target had already taken place during the cue–target interval. If the N2pc primarily reflected shifts of attention toward the target, this component should be strongly attenuated or even entirely absent when search arrays were preceded by informative spatial cues, as such shifts should have been completed prior to the presentation of the search array. In contrast, if the N2pc reflected attentional processes that are unrelated to spatial orienting, it should be elicited in a similar fashion in both task conditions, regardless of cue informativeness. To ascertain that participants did indeed shift their attention to the side signaled by spatially predictive cues, we also measured ERPs elicited during the cue–target interval in order to confirm that lateralized ERP components indicative of covert attentional shifts (ADAN, LDAP) were triggered in response to informative cues but not for the uninformative cue condition.

On one third of all trials, perceptually homogeneous target-absent search arrays consisting of 12 identical squares were presented instead of arrays with a diamond target. These arrays were included to address the question of whether the presence of a stimulus with a target-defining or perceptually unique feature is a necessary condition for the N2pc to emerge or whether this component might also be elicited in the absence of such candidate targets, provided that specific locations within this search array were previously indicated as potentially task relevant. We therefore measured ERPs to homogeneous nontarget arrays in the informative cue condition as a function of whether cues had previously indicated the left or right side of the search array as likely to contain the target. If the N2pc was strictly dependent on the presence of a targetlike stimulus, as implied by the assumption that this component reflects the attentional selection of targets among competing nontarget items, it should be entirely absent for these nontarget trials. In contrast, if the N2pc reflected, at least in part, the spatially selective processing of a search array that is triggered even when no candidate target event is present, it should be observed, although possibly in an attenuated fashion, in response to target-absent arrays that were preceded by informative cues.

Method

Participants

Seventeen neurologically unimpaired people participated in this study. Four participants had to be excluded because of excessive eye movements in the cue–target interval, and 1 other participant was excluded due to poor target detection performance. Thus, data from 12 participants (4 male, 8 female, aged 21–36 years, mean age 28 years) were included in the analyses. All participants were right-handed and had normal or corrected-to-normal

vision. The experiment was performed in compliance with relevant institutional guidelines and was approved by the ethics committee of the School of Psychology, Birkbeck College.

Stimuli and Procedure

Participants were seated in a dimly lit sound-attenuated cabin, viewing a computer monitor at a viewing distance of 70 cm. A central gray fixation cross (subtending $0.4^\circ \times 0.4^\circ$ of visual angle) was visible on screen throughout the experiment. Each trial started with a 100-ms presentation of a spatial precue (see Figure 1). After an interstimulus interval of 700 ms, a circular visual search array was presented, which remained on screen for 200 ms. The intertrial interval was 1500 ms. Spatial precues consisted of two adjacent triangles, presented centrally to the left and right of the fixation cross (size of each triangle: $1.9^\circ \times 2.5^\circ$; size of the whole cue array: $3.5^\circ \times 2.5^\circ$). One triangle was red, the other blue, and they always pointed in opposite directions (“> <” or “< >”). Each search display contained 12 items positioned along a virtual circle at a distance of 4.5° visual angle from the fixation cross. All items in the search display were light gray (RGB values: 204, 204, 204) and subtended a visual angle of $1.0^\circ \times 1.0^\circ$. Distractors were squares and targets were diamonds. On one third of all trials, the search display contained only distractors. On the remaining two thirds of all trials, a target diamond was presented together with 11 distractor squares. These targets appeared with equal probability and in random order at the 8, 9 or 10 o’clock position on the left side of the search display or at the 2, 3, or 4 o’clock position on the right side but never at any other position. Each target diamond had a corner cut off on the left or right side. All stimuli were presented against a uniform black background.

The experiment consisted of 16 blocks with 72 trials per block. In eight successive blocks (informative cue condition), one of the two cue triangles (red or blue) indicated the side of the display where the target would appear on target-present trials. For 6 participants, red cue triangles were relevant, whereas for the other 6 participants, blue triangles were relevant. In 48 trials, target diamonds were presented with equal probability at one of the three possible locations on the cued side but never on the uncued side. Target diamonds were equally likely to have a cut on the left or right side. In the remaining 24 trials per block, a homogeneous nontarget array consisting of 12 squares was presented. Participants were instructed to direct their attention to the side indicated by the cue in order to detect the target diamond when present while maintaining central fixation. They were told to indicate as fast and accurately as possible whether the target diamond had a cut on the left or right side by pressing one of two response keys with the left or right hand and to refrain from responding on nontarget trials.

In the other eight successive blocks (uninformative cue condition), cues contained no information about the location of an upcoming target, which could be presented with equal probability at any of the six possible locations on the left or right side. Participants were informed that cues were nonpredictive, and that no preparatory shifts of attention were therefore possible. In all other respects, this condition was identical to the informative cue condition. The order in which informative and uninformative cue conditions were delivered was counterbalanced between participants.

EEG Data Acquisition and 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, PO7, PO8, and Oz (according to the extended International 10–20 system). Horizontal EOG was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 5 k Ω , and the impedances of the earlobe electrodes were kept as equal as possible. Amplifier bandpass was 0.1–40 Hz, and digitization rate was 200 Hz. Trials with saccades (HEOG exceeding $\pm 30 \mu\text{V}$), eyeblinks (Fpz $\pm 60 \mu\text{V}$), or movement artifacts ($\pm 80 \mu\text{V}$ at all other electrodes) were excluded from further analyses. Averaged HEOG waveforms were scored for systematic deviations of eye position during the cue–target interval in the informative cue condition, indicative of residual small eye movements toward the cued side that were not detected by the automatized eye movement detection and rejection procedures. Four participants were excluded from further analysis due to residual HEOG deflections during the cue–target interval exceeding $\pm 2 \mu\text{V}$.

Two sets of statistical analyses were conducted for the ERP data. First, lateralized ERP components indicative of covert attention shifts during the cue–target interval (ADAN, LDAP) were investigated on the basis of ERPs triggered in response to central spatial precues that were measured relative to a 100-ms precue baseline. For the informative cue condition, separate averages were computed for trials where cues signaled a leftward or rightward attention shift. The same procedure was also adopted for the uninformative cue condition, where cues provided no spatial information. Here, cues were classified as “left” or “right” on the basis of what they signaled for the same participant in informative cue blocks. This was done in order to ascertain that there were no systematic transfer effects of cue-induced attentional shifts from informative to uninformative cue blocks, which was of particular relevance for participants who had completed the informative prior to the uninformative cue condition. Based on previous observations about the latencies and scalp maxima of ADAN and LDAP components (e.g., Eimer et al., 2002; Praamstra, Boutsen, & Humphreys, 2005), the ADAN was quantified on the basis of ERP mean amplitudes obtained between 350 and 650 ms after cue onset at lateral frontocentral electrodes FC5/6, and the LDAP was measured during the 650–800-ms postcue interval at lateral posterior electrodes PO7/PO8. ERP mean amplitudes were analyzed with repeated measures ANOVAs for the factors cue type (informative vs. uninformative), hemisphere (recording electrode on the left vs. right side), and cue-induced laterality (cued side contralateral vs. ipsilateral to recording electrode). Follow-up analyses were then conducted separately for the informative and uninformative cue conditions.

The second set of analyses focused on ERPs triggered in response to visual search arrays elicited at lateral occipital electrodes PO7/PO8. ERP mean amplitudes were computed relative to a 100-ms prestimulus baseline for the 200–300-ms poststimulus time window (where the N2pc was expected to be maximal), separately for target-present and target-absent trials, and for the informative and uninformative cue condition. Mean amplitudes were also computed for two longer latency time intervals (350–500 ms and 500–1000 ms poststimulus) that were included to measure the sustained posterior contralateral negativity (SPCN) previously observed in tasks where lateralized target stimuli had to be maintained in visual working memory (e.g., Jolicœur, Sessa, Dell’Acqua, & Robitaille, 2006a, 2006b; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004). This component was expected to be elicited in the present study after the N2pc during the in-depth processing of target stimuli re-

quired to discriminate the side of its cut. For target-present trials, repeated measures ANOVAs were conducted on ERP mean amplitude values for the factors cue type (informative vs. uninformative), target side (left vs. right), and contralaterality (electrode ipsilateral or contralateral to the target side). Analogous analyses were also conducted for target-absent trials in the uninformative cue condition to investigate the possibility that the spatially selective attentional processing of perceptually homogeneous nontarget arrays was reflected by lateralized occipital ERP activity in the N2pc and SPCN time range. In these analyses, the factor cue type was omitted, and contralaterality was now defined relative to the side cued as likely to contain a target stimulus.

Behavioral performance on target-present trials (reaction time, error rate) was analyzed with repeated measures ANOVAs for the factors cue type (informative vs. uninformative), target side (left vs. right), and stimulus–response compatibility (target and response on the same side vs. opposite sides).

Results

Behavioral Performance

Reaction times (RTs) to targets were faster with informative cues (573 ms) than with uninformative cues (601 ms), and this was reflected by a main effect of cue type, $F(1,11) = 10.7$, $p < .007$. RTs tended to be faster when target and response locations were spatially compatible relative to spatially incompatible trials (573 vs. 601 ms), resulting in an almost significant main effect of stimulus–response compatibility, $F(1,11) = 4.4$, $p < .06$. Accuracy on target-present trials did not differ significantly between the informative and uninformative cue condition (96.2% and 95.8%, respectively), $F(1,11) = 1.5$, $p = .242$, but was higher on spatially compatible relative to incompatible trials (98.0% vs. 94.0%); main effect of stimulus–response compatibility: $F(1,11) = 8.8$, $p < .013$. False alarms on target-absent trials occurred on less than 2.5% of these trials.

Lateralized ERP Components Elicited in the Cue–Target Interval

Figure 2 (left and middle panels) shows ERPs triggered in response to spatially informative and uninformative cues during the 800-ms cue–target interval at lateral frontocentral electrodes FC5/FC6 (top) and lateral occipital electrodes PO7/PO8 (bottom) for cues signaling a covert shift of spatial attention toward the left side (solid lines) or right side (dashed lines) in the informative cue condition. For uninformative cues (middle panel), these waveforms were computed on the basis of how cues were assigned to the direction of spatial attention for each participant during the informative cue condition. For informative cues, an enhanced negativity contralateral to the direction of a cued attentional shift (ADAN) appears to be present between 350 and 650 ms after cue onset at FC5/6. In addition, an enhanced positivity contralateral to the direction of an attentional shift (LDAP) appears to be elicited during the final 200 ms of the cue–target interval at PO7/8. These lateralized components can also be seen in the difference waveforms shown in Figure 2 (right panel, solid lines). Difference waves were generated by subtracting ERPs recorded in response to right cues from ERPs to left cues, and then subtracting the resulting difference waves for right-hemisphere electrodes from the difference waves for homologous electrodes over the left hemisphere. In the resulting double subtraction waveforms, a negativity contralateral to the side of a cued attentional shift is reflected by positive amplitude

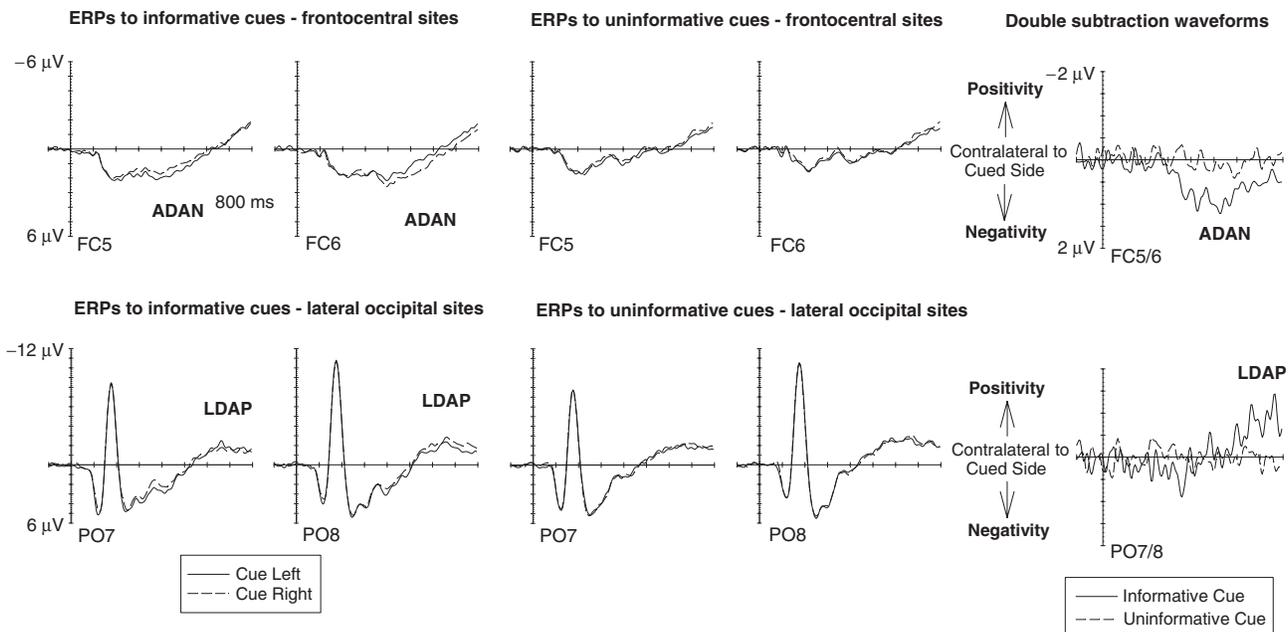


Figure 2. Left and middle panels: Grand-averaged ERPs elicited in the cue–target interval in response to spatially informative cues (left) and uninformative cues (middle) over the left and right hemisphere at frontocentral (FC5/6, top) and lateral posterior (PO7/8, bottom) electrode pairs. Waveforms show the 800-ms interval following the onset of a color cue that signaled a leftward (solid lines) or rightward (dashed lines) attention shift. For the uninformative cue condition, where cues were spatially nonpredictive, waveforms were computed on the basis of the mapping of cue color to direction of attention that was relevant in the informative cue condition. Please note the different voltage scales for frontocentral and posterior electrodes. Right panel: Difference waveforms obtained at FC5/6 (top) and PO7/8 (bottom) in the cue–target interval in response to spatially informative cues (solid lines) and uninformative cues (dashed lines). Enhanced negativities contralateral to the cued side are reflected by positive values (downward deflections), and enhanced contralateral positivities are reflected by negative values (upward deflections). ADAN: anterior directing attention negativity; LDAP: late directing attention positivity.

values (downward-going deflections), and a contralateral positivity is indicated by negative values (upward-going deflections). Analogous difference waveforms are also shown for uninformative cues (Figure 2, right panel, dashed lines), based on the assignments of cues to attention shifts that were relevant during the informative cue condition. Although ADAN and LDAP are clearly visible with informative cues, no systematic lateralized activity appears to be elicited in the uninformative cue condition.

In the 350–650-ms postcue interval, a main effect of cue-induced laterality at FC5/6, $F(1,11) = 16.1$, $p < .002$, was accompanied by a Cue Type \times Cue-Induced Laterality interaction, $F(1,11) = 11.2$, $p < .007$. Follow-up analyses conducted separately for the informative and uninformative cue conditions revealed a highly significant effect of cue-induced laterality in response to spatially informative cues, $F(1,11) = 18.9$, $p < .001$, and no interaction between cue-induced laterality and hemisphere, $F < 1$. This confirms that the ADAN component was reliably present when cues specified the side of an upcoming target within a visual search array. In contrast, there was no evidence for any ADAN in response to spatially uninformative cues, $F < 1$, demonstrating that there was no transfer of any cue-triggered attention shifts from blocks where cues were informative to blocks where the same cues could not be used to anticipate the side of upcoming target stimuli.

In the 650–800-ms postcue interval, the two-way interaction (Cue Type \times Cue-Induced Laterality) was almost significant at PO7/8, $F(1,11) = 4.3$, $p < .063$, suggesting a strong tendency for the LDAP to be present with informative cues, but absent in the uninformative cue condition (see also Figure 2). Follow-up an-

alyses conducted separately for the informative and uninformative cue conditions confirmed that the LDAP was absent with uninformative cues (cue-induced laterality: $F < 1$), but only revealed a trend toward the presence of the LDAP in the informative cue condition that fell short of statistical significance, cue-induced laterality: $F(1,11) = 3.8$; $p < .077$. No interaction between cue-induced laterality and hemisphere was present in the informative cue condition, $F < 1$.

Lateralized Posterior ERP Activity in Response to Visual Search Arrays

Figure 3 (top panels) shows ERPs in response to search arrays containing a target diamond on the left or right side at lateral posterior electrodes PO7/8 contralateral and ipsilateral to the side of the target, shown separately for the informative cue condition (left side) and uninformative cue condition (right side). As can be seen clearly, an N2pc component was elicited in both conditions and was followed in both conditions by an SPCN. The N2pc appears very similar in terms of its latency and amplitude for both cue conditions, thus suggesting that this component was largely unaffected by previous preparatory shifts of spatial attention. This can also be seen in the difference waveforms shown in Figure 4 (top panel; target-present trials: solid and dashed lines), which were computed by subtracting ERPs at PO7/8 ipsilateral to the side of a target from ERPs at contralateral electrodes. The N2pc emerged at about 180 ms poststimulus, returned to baseline at around 300 ms after search display onset, and was then followed by the SPCN, which emerged at about 350 ms poststimulus and remained present throughout the

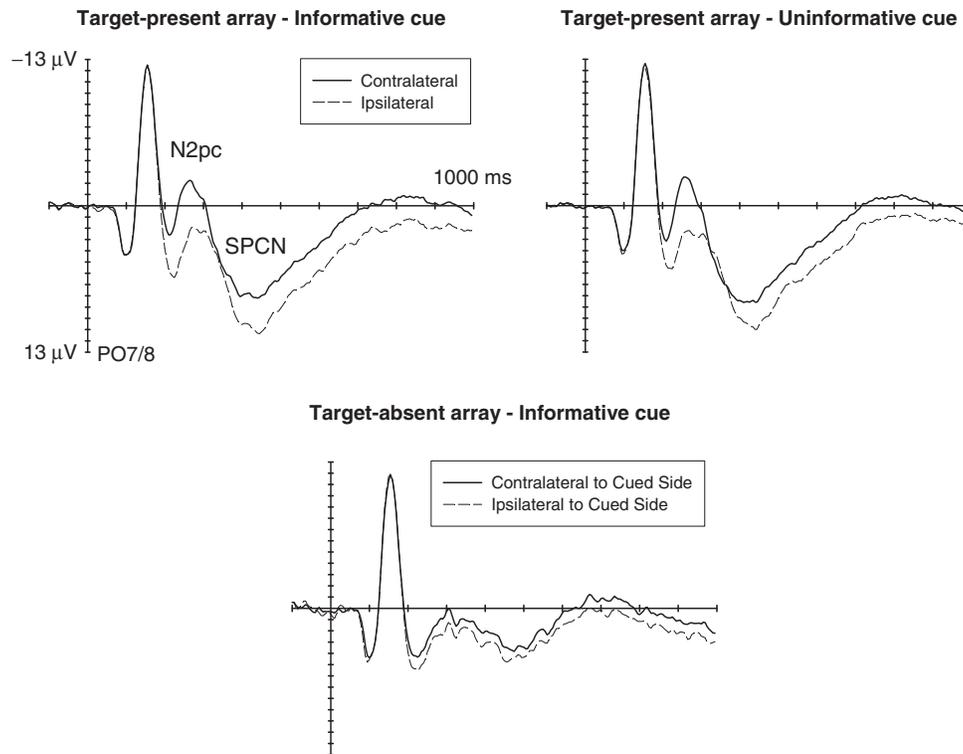


Figure 3. Grand-averaged visual ERPs elicited in the 1000-ms interval after the onset of a visual search array at lateral posterior electrodes PO7/8. Top: ERPs in response to target-present arrays at electrodes contralateral (solid lines) and ipsilateral (dashed lines) to the side of the target for the informative cue condition (left) and uninformative cue condition (right). Contralateral ERPs were computed by averaging ERPs obtained in response to left targets at PO8 and to right targets at PO7; ipsilateral ERPs represent averages of ERPs to left targets at PO7 and right targets at PO8. Bottom: ERPs in response to target-absent arrays in the informative cue condition at electrodes contralateral (solid lines) and ipsilateral (dashed lines) to the side of a cued attentional shift.

1000-ms analysis interval. Importantly, N2pc amplitudes and latencies were similar in the informative and uninformative cue conditions. The subsequent SPCN was also present for both cue conditions but appeared slightly attenuated when cues were spatially uninformative.

These informal observations were substantiated by statistical analyses of ERPs to target-present arrays. A highly significant main effect of contralaterality was obtained for the 200–300-ms time window, $F(1,11) = 39.8$, $p < .001$, demonstrating the presence of the N2pc. Importantly, there was no indication of any Cue Type \times Contralaterality interaction, $F < 1$, thus confirming that the N2pc was essentially unaffected by whether or not preparatory shifts of spatial attention had occurred during the preceding cue–target interval. The presence of an SPCN was reflected by significant main effects of contralaterality during the 350–500-ms and 500–1000-ms intervals, $F(1,11) = 14.9$ and 83.1 , $p < .003$ and $.001$, respectively. Interactions of cue type and contralaterality in both time windows, $F(1,11) = 7.5$ and 6.6 , $p < .02$ and $.03$, for the 350–500-ms and 500–1000-ms intervals, indicated that the SPCN was larger in the informative cue condition (see Figure 4, top panel). However, subsequent analyses conducted separately for both conditions confirmed the presence of a reliable SPCN with informative and uninformative cues in both time windows, all $F(1,11) > 9.2$, all $p < .02$.

Figure 3 (bottom panel) shows ERPs elicited at PO7/8 in the informative cue condition in response to target-absent search arrays consisting of a homogeneous set of squares, displayed separately for electrodes contralateral and ipsilateral to the di-

rection of a cued attentional shift. A sustained enhanced negativity contralateral to the cued (attended) side of the visual search array appeared to be present, with an onset latency comparable to the onset of the N2pc in response to target-present search arrays. This is further illustrated by the difference waveform shown in Figure 4 (gray solid line), which was computed by subtracting target-absent ERPs at PO7/8 ipsilateral to the cued side from contralateral ERPs. A contralateral negativity started at almost exactly the same time as the N2pc to target-present arrays and appeared to remain present in a sustained fashion throughout the 1000-ms analysis interval. This was confirmed by statistical analyses, which revealed main effects of contralaterality for ERPs to nontarget arrays in the informative cue condition during the initial 200–300-ms poststimulus window, $F(1,11) = 15.2$, $p < .002$, as well as for the 350–500- and 500–1000-ms time intervals, $F(1,11) = 8.8$ and 25.1 , $p < .02$ and $.001$, respectively.

Figure 4 (bottom) shows the scalp distributions of the lateralized posterior ERP negativities obtained in the informative cue condition in response to target-present and target-absent arrays during the three successive analysis windows. Although the number of electrodes used in the present study is insufficient to draw any conclusions about subtle topographic differences, these maps suggest that the lateralized effects observed during the N2pc and SPCN latency range did not differ systematically between target-present and target-absent trials in terms of their overall lateral posterior focus. However, the amplitudes of these lateralized effects were clearly different, with substantially larger

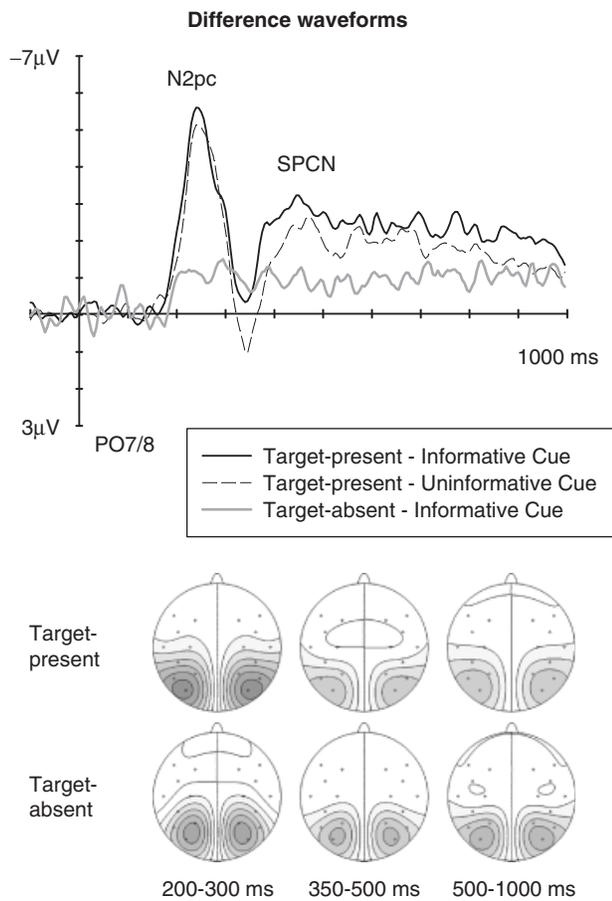


Figure 4. Difference waveforms obtained by subtracting ERPs at lateral posterior electrodes PO7/8 ipsilateral to the side of a target (for target-present trials) or ipsilateral to the side of a cued attention shift (for target-absent trials), from ERPs at contralateral electrodes. Waveforms are shown separately for target-present trials in the informative cue condition (black solid lines), target-present trials in the uninformative cue condition (dashed lines), and for target-absent trials in the informative cue condition (gray solid lines). The bottom panel shows topographical maps of the difference waveforms obtained in the informative cue condition for target-present and target-absent trials. These maps were constructed by spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989) after mirroring the difference waveforms representing the contralaterally enhanced negativity to obtain symmetrical voltages for both hemispheres. Each isocontour line represents a change of 0.6 μ V for the target-present maps and 0.2 μ V for the target-absent maps.

contralateral negativities observed in response to search arrays that contained a target (Figure 4, top panel, black vs. gray solid lines). To directly compare the amplitude of contralateral posterior negativities between target-present and target-absent arrays in the informative cue condition, additional analyses were conducted that included both types of trials, with target presence (present vs. absent) as an additional factor. In the 200–300-ms poststimulus time window, main effects of contralaterality, $F(1,11) = 31.5$, $p < .001$, and target presence, $F(1,11) = 19.4$, $p < .001$, were accompanied by a significant Target Presence \times Contralaterality interaction, $F(1,11) = 39.6$, $p < .001$, confirming that although reliably present, the contralaterally enhanced negativity in response to target-absent arrays was smaller than the N2pc triggered in response to target-present arrays. Similar results were obtained for the 350–500- and 500–1000-ms time

windows, where significant Target Presence \times Contralaterality interactions, $F(1,11) = 9.4$ and 47.3, $p < .02$ and $.001$, respectively, demonstrated that contralateral negativities in target-absent trials were smaller than in target-present trials.

Discussion

The aim of this study was to investigate which attentional processes are reflected by the N2pc component that has now become popular as a tool to study attentional selectivity in visual search and related tasks (cf. Eimer & Mazza, 2005; Hickey et al., 2006; Kiss et al., 2007; Robitaille & Jolicoeur, 2006; Woodman & Luck, 1999, 2003). Here, we studied two specific issues. First, we investigated whether the N2pc is linked to preparatory shifts of spatial attention or exclusively reflects processes of attentional selectivity that take place after attentional orienting. Second, we addressed the question of whether or not the presence of a candidate target stimulus in a visual search array is a necessary condition for the N2pc to emerge or whether this component is also triggered during the spatially selective processing of perceptually uniform nontarget arrays.

To investigate whether the N2pc reflects, at least partially, covert shifts of spatial attention toward the location of a target stimulus in a visual search array, we measured this component in response to visual search arrays that contained a shape singleton target (diamond) among uniform distractors (squares) and were preceded by precues that were either informative or uninformative with respect to the side of upcoming target stimulus. In the informative cue condition, where precues validly indicated the side where a target, when present, would appear, participants were instructed to use this information to covertly shift their attention to the cued side during the cue–target interval. Reaction times to targets were faster with informative than with uninformative cues, suggesting that preparatory attentional shifts were in fact triggered by informative cues. This was further confirmed by the observation that a lateralized ERP component (ADAN) known to be elicited during cued shifts of spatial attention at frontocentral sites (e.g., Eimer et al., 2002; Hopf & Mangun, 2000; Nobre et al., 2000) was reliably present in response to informative cues, but not when the same cues were spatially nonpredictive. There was also some evidence that a second lateralized ERP component indicative of attentional orienting (LDAP) was triggered in response to informative cues, although this lateralized effect only approached statistical significance. The LDAP is assumed to reflect the control of attention in visually mediated external space (Van Velzen, Forster, Eardley, & Eimer, 2006), and has previously been shown to be attenuated when cued target locations are close to central fixation (Eimer, Forster, Fieger, & Harbich, 2004). The fact that target locations were less peripheral (4.5°) in the present study than in many other experiments where the LDAP was observed may be partly responsible for the fact that this component did not reach statistical significance.

Given that participants directed their attention toward the side indicated by informative cues and the fact that the cue–target interval (700 ms) was long enough to ensure that attention shifts were completed prior to the presentation of the search array, the critical question was how these attention shifts would affect the N2pc component. In the uninformative cue condition, where participants had no advance information about target location, a clear N2pc was elicited between 200 and 300 ms poststimulus

(see Figures 3 and 4), analogous to previous visual search studies where target location was not known in advance (e.g., Hickey et al., 2006; Luck & Hillyard, 1994; Mazza et al., 2007; Woodman & Luck, 1999). In the informative cue condition, the N2pc component was not only clearly present, but was very similar to the N2pc observed with uninformative cues (see Figures 3 and 4). The presence of an N2pc under conditions where attention was previously cued to a specific location is compatible with recent findings by Praamstra (2006), who investigated how advance spatial information affected lateralized ERPs to bilateral stimulus arrays consisting of one target and one nontarget. Although links between the N2pc and attentional orienting were not the primary focus of this experiment, a reliable N2pc was found when target location was known in advance, although its amplitude was reduced relative to a condition where target location was uncertain. The present finding that the N2pc to shape singleton targets in a visual search array was entirely unaffected by cue informativeness, and thus by prior shifts of spatial attention, suggests that this component is essentially unrelated to such attention shifts and that the N2pc is instead linked to processes that occur after such shifts have been completed.

One could argue that the absence of any N2pc differences between trials with informative and uninformative cues might be related to the fact that the shape targets used in the present study were highly salient singleton stimuli that were presented in the left or right visual hemifield. These pop-out targets might have attracted spatial attention in a purely bottom-up fashion, thereby eliminating any differential effects of informative versus uninformative cues. However, if attentional target selection in the present experiment was driven exclusively by the bottom-up salience of shape targets and not at all by cued endogenous attention shifts, no behavioral spatial cuing effects should have been observed. In fact, RTs were found to be reliably faster when targets were preceded by informative cues as compared to uninformative cue trials, suggesting that endogenous attention did have systematic effects on target detection and discrimination processes. Furthermore, any exogenous effects of laterally presented shape singletons on ERP waveforms should have given rise to lateralized modulations of components that precede the N2pc, such as the P1. However, no such early P1 modulations were observed (see Figure 3). The important question of whether the pattern of N2pc results obtained in the present study in response to pop-out targets can also be observed in visual search tasks where the detection of targets among distractors is more difficult (e.g., when targets are defined by feature conjunctions) needs to be investigated in future experiments.

An additional question addressed in the present study was whether the presence of a candidate target stimulus is a necessary condition for the N2pc to appear. For this purpose, ERPs to perceptually uniform target-absent arrays in the informative cue condition were analysed as a function of whether the cue had previously indicated that a target, when present, would appear on the left or right side. A small but highly consistent posterior negativity was indeed found contralateral to the cued side for target-absent trials (see Figure 3, bottom, and Figure 4, gray solid line). Interestingly, this effect started at approximately the same time as the N2pc to target-present trials, although its amplitude was strongly attenuated relative to the target-induced N2pc. It remained present in a sustained fashion throughout the 1000-ms analysis interval investigated here.

It is possible that the early phase of the contralateral posterior negativity triggered on target-absent trials represents an atten-

uated N2pc. Although the number of electrodes used in the present study is insufficient to warrant any firm conclusions about possible topographical variations, the maps shown in Figure 4 (bottom panel) suggest that there were no obvious differences between target-present and target-absent trials in the lateral posterior scalp distribution of lateralized ERP effects during the N2pc time window (200–300 ms poststimulus). In addition, the fact that a contralateral negativity on target-absent trials emerged at almost exactly the same time as the N2pc on target-present trials also suggests that these effects might reflect similar processes for both types of trials. For example, the early phase of the contralateral negativity that is elicited on both target-present and target-absent trials might represent an N2pc-like component triggered during the initial spatially selective processing of stimulus features at potentially task-relevant locations that occurs prior to target selection. The point in time where the difference waveforms for target-present and -absent trials begin to diverge (at about 200 ms poststimulus in the present experiment; see Figure 4) could thus mark the time when selective attentional processing starts to be driven by the presence of a target. In this context, it is interesting to note that Hopf et al. (2000) have described two distinct sources for the N2pc as observed on the basis of MEG recordings—an early parietal source active between 180 and 200 ms after stimulus onset and a later occipitotemporal source with a latency of 220–240 ms. It is possible, although speculative at this moment, that the early target-unspecific phase of the N2pc observed in the present study might be due to parietal activity, whereas the later target-specific N2pc was triggered by the activation of ventral extrastriate areas.

The presence of a small but reliable N2pc for perceptually homogeneous target-absent arrays in the present study may appear inconsistent with previous observations by Luck and Hillyard (1994, Exp. 4). These authors found that the N2pc observed in response to pop-out targets was strongly attenuated or even eliminated in a “global condition” where all unilaterally presented items within a search array were identical, and spatially selective processing was therefore not required. The critical difference between this experiment and our current study concerns the predictability of homogeneous versus pop-out displays. In the Luck and Hillyard (1994) experiment, homogeneous and pop-out arrays were delivered in separate blocks, so that participants knew in advance that no target–nontarget discriminations would be required in “global” blocks. In contrast, target-present and target-absent arrays were presented in random order and were therefore entirely unpredictable in the present study, which should result in a much stronger tendency to selectively process cued and thus potentially task-relevant locations on both types of trials.

Because the singleton shape targets used in the present study were highly salient and could therefore be detected rapidly (see above), it is not surprising that the difference between target-present and target-absent trials started early and soon after the N2pc first emerged, with N2pc amplitudes subsequently much larger on target-present trials (see Figure 4). The possibility that N2pc-like effects observed during visual search might reflect successive dissociable stages of attentional selectivity (i.e., an initial spatially specific processing of potentially task-relevant stimulus features that is followed by attentional target selection) can be investigated in future studies that combine spatial cuing procedures with visual search for targets defined by feature conjunctions. When target detection is more difficult, spatially selective feature processing and the subsequent selection of targets

should be more clearly separated in time, and N2pc amplitude differences between target-present and target-absent trials therefore emerge substantially later.

In addition to the N2pc, a sustained posterior contralateral negativity was also observed in the present study. This component emerged at about 350 ms poststimulus and remained present throughout the 1000-ms analysis interval investigated here. An SPCN has previously been observed when lateralized target stimuli had to be maintained in visual working memory for in-depth processing (e.g., Mazza et al., 2007; McCollough et al., 2007; Robitaille & Jolicoeur, 2006; Vogel & Machizawa, 2004). Although both N2pc and SPCN reflect enhanced contralateral negativities over posterior cortical areas, McCollough et al. have recently found evidence for systematic scalp topography differences between these two components, with the N2pc distributed more ventrally and laterally relative to the SPCN. In the present study, where search arrays were presented for only 200 ms, participants had to rely on working memory representations when discriminating the side of the cut for target diamonds on target-present trials. On these trials, a reliable SPCN was observed in the informative as well as in the uninformative cue conditions. The fact that SPCN amplitude was significantly larger when search arrays were preceded by informative cues suggests that prior spatial orienting may have had a modulatory effect on the efficiency of working memory processes indicated by this component. Interestingly, an

SPCN-like effect was also observed on target-absent trials (see Figure 4), which may reflect working memory activity related to the search for a target and/or processes involved in the confirmation of its absence. The observation that the sustained contralateral activity on target-absent trials was substantially attenuated relative to the SPCN found for target-present trials is likely due to the fact that nontarget search arrays were perceptually uniform and should therefore have been rapidly rejected as task-irrelevant on most trials. It should be noted that sustained posterior negativities have been observed in previous studies that investigated ERP correlates of attention directed to nonspatial features such as color or shape (e.g., Hillyard & Anllo-Vento, 1998). However, and in marked contrast to the effects described here, such attentional modulations are generally nonlateralized.

In summary, the present study has demonstrated that the N2pc triggered in response to pop-out visual search targets does not reflect processes involved in covert shifts of spatial attention, but is instead linked to spatially selective attentional mechanisms that occur after such shifts are completed. The fact that this component was also elicited, albeit in an attenuated fashion, for perceptually uniform nontarget arrays suggests that it may not only be indicative of attentional target selection, but also, at least to some degree, it may reflect the spatially specific processing of potentially task-relevant features that takes place prior to the selection of candidate target events.

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