Electrophysiological Indices of Target and Distractor Processing in Visual Search

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Abstract

■ Attentional selection of a target presented among distractors can be indexed with an event-related potential (ERP) component known as the N2pc. Theoretical interpretation of the N2pc has suggested that it reflects a fundamental mechanism of attention that shelters the cortical representation of targets by suppressing neural activity stemming from distractors. Results from fields other than human electrophysiology, however, suggest that attention does not act solely through distractor suppression; rather, it modulates the processing of both target and distractors. We conducted four ERP experiments designed to investigate whether the N2pc reflects multiple attentional mechanisms. Our goal was to reconcile ostensibly conflicting outcomes obtained in electrophysiological studies of attention with those obtained using other methodologies. Participants viewed visual search arrays containing one target and one distractor. In Experiments 1 through 3, the distractor was isoluminant with the background, and therefore, did not elicit early lateralized ERP activity. This work revealed a novel contralateral ERP component that appears to reflect direct suppression of the cortical representation of the distractor. We accordingly name this component the distractor positivity (P_D). In Experiment 4, an ERP component associated with target processing was additionally isolated. We refer to this component as the target negativity (N_T). We believe that the N2pc reflects the summation of the P_D and N_T, and that these discrete components may have been confounded in earlier electrophysiological studies. Overall, this study demonstrates that attention acts on both target and distractor representations, and that this can be indexed in the visual ERP. ■

INTRODUCTION

In everyday experience, we are confronted with a wide range of visual stimuli from which to select objects of interest. In laboratory studies, an experimental paradigm known as *visual search* has been used extensively to investigate the factors that govern this attentional selectivity. In a typical visual search experiment, observers are presented with displays containing a number of items and are asked to respond based on target characteristics. In recent years, noninvasive electrophysiological techniques have been used to supplement conventional behavioral techniques in visual search investigations.

In human electrophysiological studies of visual search, the general approach has been to compute event-related potentials (ERPs) that are time-locked to the onset of search displays. ERP components related to visual selection can be identified in the resulting waveforms by looking for modulation as a function of factors such as the location of the target or type of distractors. With this approach, investigators have identified a specific component of the visual ERP that appears to reflect the allocation of attention to items in the search display (Luck, Girelli, McDermott, & Ford, 1997; Eimer, 1996;

Luck & Hillyard, 1994a, 1994b). Commonly referred to as the *N2pc*, this component is a negative ERP difference beginning ~175 msec poststimulus at electrode sites contralateral to the target relative to electrode sites ipsilateral to the target. The label stems from the latency of the component, which is in the range of the visual N2, and its scalp topography, which is posterior and contralateral to an attended stimulus.

Early investigation linked the N2pc to the suppression of distractor stimuli (Luck & Hillyard, 1994a, 1994b). One study in particular (Luck & Hillyard, 1994b) provided several key pieces of evidence for this hypothesis. It showed that targets that elicited the N2pc in the presence of distractors failed to elicit the N2pc under at least three conditions: (a) when distractors were absent (Experiment 3); (b) when distractors provided essential information about the presence or absence of the target, and thus, could not be suppressed (Experiment 2); and (c) when distractors shared task-relevant features with the target (Experiment 4). Subsequent research identified a close correspondence between the characteristics of the scalp-recorded N2pc and the suppressive effect of attention observed within the monkey visual cortex (Luck, Chelazzi, Hillyard, & Desimone, 1997; Chelazzi, Miller, Duncan, & Desimone, 1993; Moran & Desimone, 1985). Both the suppression of monkey cortical activity and the N2pc are, in evidence, approximately 175 msec

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after the onset of a search array and are more pro-nounced for difficult discrimination tasks than for simple detection tasks and when distractors are near the target rather than far away (Luck, Girelli, et al., 1997).

The apparent relationship between the N2pc and distractor-suppression led Luck, Girelli, et al. (1997) to propose a theory of visual attention in which distractor-suppression plays a central role. This theory, known as *ambiguity resolution theory*, proposes that ambiguities in the representation of object features can arise when the binding of features to individual stimuli is required (as occurs in the discrimination of fine details but not in the detection of simple features) and multiple objects are present such that they share neural receptive fields. According to this account, attention acts to resolve this ambiguity through the suppression of information stem-ming from unattended stimuli. The action of this sup-pressive mechanism is said to be indexed by the N2pc.

Empirical studies from fields other than human elec-trophysiology, however, suggest that attentional selec-tion involves mechanisms in addition to distractor suppression. For example, single-unit studies in animals have shown that neural activity associated with a stim-ulus is enhanced when attention is deployed to the stimulus location. The types of enhancement identi-fied in this work have ranged from raw increases in baseline rates of neural firing (Treue & Maunsell, 1999; Roelfsema, Lamme, & Spekreijse, 1998; Motter, 1993; Spitzer, Desimone, & Moran, 1988) to more complicated mechanisms such as the modulation of single-neuron re-sponse selectivity to target characteristics (Spitzer et al., 1988; although see McAdams & Maunsell, 1999).

It is, in fact, unclear whether distractor suppression itself is a unitary phenomenon. Research with the N2pc has suggested that distractor suppression may act through the inhibition of input to neurons responsible for representing the target (Luck, Girelli, et al., 1997). It has been proposed that this type of suppression is instantiated as a spatially circumscribed ring that sur-rounds the focus of attention (Hopf et al., 2006; Slotnick, Hopfinger, Klein, & Sutter, 2001; Mounts, 2000). Other studies, however, have shown that target selection can result in the direct suppression of neural activity trig-gered by distractor stimuli, even when targets and distractors are spatially separate (Ruff & Driver, 2006; Cepeda, Cave, Bichot, & Kim, 1998). This suggests that more than one suppressive mechanism may be involved in attentional selection.

The idea that spatial attention is instantiated through the action of multiple mechanisms raises the possibility that lateralized ERP activity associated with attentional selection—the N2pc—may reflect more than one of these mechanisms. In fact, some ERP results have linked the N2pc to target processing rather than distractor suppression, consistent with the hypothesis that this component indexes processes tied to the target as well as processes tied to the distractors. For example, the

N2pc has been observed contralateral to a single later-alized stereoscopic stimulus in the absence of conven-tional distractors (Shedden & Nordgaard, 2001), and contralateral to a target when that target is the only stimulus presented in one visual hemifield with all distractors presented to the opposite hemifield (Eimer, 1996). This latter finding is important because it con-flicts with the notion that the N2pc reflects direct suppression of the representation of distractor stimuli, as neural activity responsible for directly inhibiting dis-tractors should presumably be observed contralateral to the distractors themselves.

The present study was premised on the idea that selection in visual search is unlikely to rely on a single attentional mechanism, and that some of the mecha-nisms responsible for selection are likely to act on target representations while others are likely to act on distrac-tor representations. To isolate the electrophysiological signatures of target and distractor processing in visual search, we recorded ERPs to visual search displays that had three key characteristics. First, they contained only two stimuli, one target and one distractor. Second, each stimulus was presented on the vertical meridian on some trials so that lateralized ERP activity could be attributed to the other, lateralized stimulus (Woodman & Luck, 2003; see also Hickey, McDonald, & Theeuwes, 2006). Third, the brightness of one stimulus was matched with that of the background in order to minimize lateralized sensory ERP activity in critical ex-perimental conditions.

EXPERIMENT 1

Methods

Participants

Twelve healthy students of Simon Fraser University gave informed consent before beginning the experiment. All participants reported normal or corrected-to-normal vi-sion and normal color vision and received course credit for their participation. Ten of 12 participants (4 men; mean $\pm$ *SD* age = 18.8 $\pm$ 1.4 years) were right-handed.

Procedure

Before beginning the experiment, each participant was required to complete a modified method-of-limits pro-cedure designed to psychophysically match the bright-ness of two colors. This involved adjusting the luminance of a square gray patch presented on the computer screen so that it matched the brightness of a concurrently presented square red patch. Participants could increase the luminance of the gray patch by pressing the left button of a standard computer mouse, decrease it with the right button, and accept it as equal-ly bright to the red by pressing the middle mouse

button. Four matches were made. In two instances, the initial luminance of the gray patch was ∼2.5 cd/m² greater than that of the red, and participants were instructed to decrease the luminance of the gray patch until its brightness matched that of the red patch. In the remaining instances, the initial luminance of the gray patch was ∼2.5 cd/m² less than that of the red, and participants were instructed to increase the luminance of the gray patch until its brightness matched that of the red. The numeric values associated with the shade of gray arrived at in each of these matches were mean averaged to define the background luminance used in the experiment.

The experiment itself consisted of 20 blocks of 60 trials, for a total of 1200 trials per participant. All stimuli were presented on a CRT monitor located 60 cm from the observer's eyes. Trials began with the presentation of a fixation point for 1350–1650 msec followed by the presentation of the search array. The array contained two stimuli, a green square that could be rotated 45° to have a diamond form (0.6° × 0.6°) and a horizontal red line that could be either long (1.2° × 0.15°) or short (0.8° × 0.15°). Although the shade of green used to define the shape stimulus was substantially more luminous than the background (42.41 cd/m²), the shade of red used to define the line stimulus (3.92 cd/m²) was the color of the standard used in the brightness-matching procedure described above, and was thus perceived as having the same brightness as the background.

Individual stimuli could be presented to one of six screen locations. These locations were equidistant from a central fixation point and from each other (5°). Two positions were on the vertical meridian (i.e., directly above or below fixation). The remaining four positions were located at 60°, 120°, 240°, and 300° off vertical. There were therefore two lateralized positions located above the horizontal meridian and two lateralized positions located below the horizontal meridian. The stimuli remained on the screen until either a participant's response was detected or 750 msec passed, following either of which a new trial began.

Stimulus locations were varied pseudorandomly from trial to trial such that in one third of trials the shape stimulus was presented on the vertical meridian; in another third, the line stimulus was presented on the vertical meridian; and in the remaining third, the shape stimulus was presented in one hemifield with the line stimulus presented in the opposite hemifield (see Figure 1 for examples of search arrays).

In each trial, the form of the shape stimulus and length of the line stimulus were chosen randomly. Participants indicated the form of the shape stimulus (square or diamond) with the right hand via a standard computer mouse. Half the participants pressed the left mouse button with their index finger when the target was a diamond and the right mouse button with their middle finger when it was a square, with the remaining half of participants using the opposite response map. Participants were instructed to respond as quickly as possible while maintaining an average accuracy of 90% or better and accuracy feedback was given following each block of trials.

Recording and Analysis

Electroencephalogram (EEG) was recorded from 63 tin electrodes, 62 of which were mounted in an elastic cap (Electro-Cap International, Eaton, OH). Electrode positions were a subset of the International 10–10 system sites. Horizontal electrooculogram (HEOG) was recorded bipolarly from electrodes 1 cm lateral to the external canthi. All other electrodes were referenced during recording to the right mastoid and later digitally
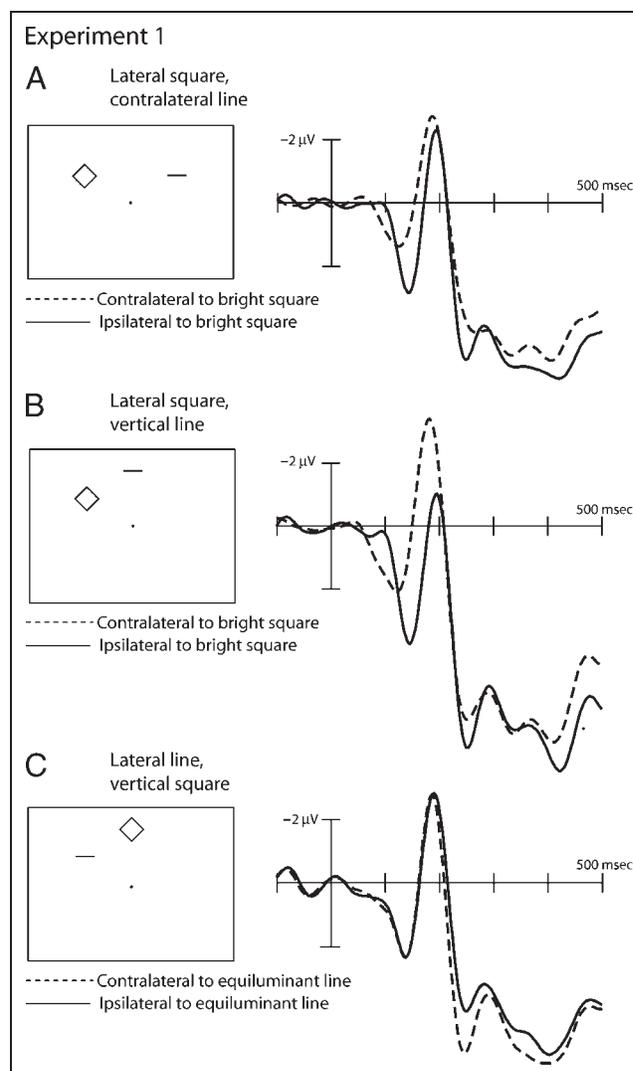
Figure 1. Grand-averaged ERPs elicited in Experiment 1. As with all ERPs presented in this article, these ERPs were recorded at posterior lateral electrode sites PO7 and PO8. Note that negative is plotted upward, and that stimulus onset occurred at 0 msec and is indexed by the *y*-axis.

re-referenced to the algebraic average of the signals recorded at the left and right mastoids. The EEG was amplified with a gain of 20,000 and a band pass of 0.1–100 Hz, digitized at 500 Hz, stored on a microcomputer, and averaged off-line. Electrode impedances were kept below 10 kΩ.

An automated artifact-rejection procedure was applied to the EEG in order to remove trials containing blinks, eye movements, or amplifier-blocking artifacts. Electrode site Fp1 was used in the detection of blinks and vertical eye movements and HEOG was used in the detection of horizontal eye movements. All trials containing artifacts in a 1000-msec epoch beginning 200 msec before stimulus onset were removed from further analysis, as were all trials in which participants made incorrect responses.

The waveforms presented in the figures were recorded at electrode sites PO7 and PO8 and were digitally low-pass filtered in order to remove high-frequency noise produced by muscle activity and external electrical sources. Filtering was conducted using an idealized filter kernel constructed in the frequency domain such that it had a length of 255 data points and half-amplitude attenuation at 20 Hz. Statistical analysis was conducted prior to digital filtering. ERP baselines for both statistical and display purposes were computed with respect to a 100-msec prestimulus period.

Results

Behavioral Results

The mean ($\pm SD$) average of gray shades arrived at by the 12 participants in the color-matching procedure had a luminance of 2.45 ± 2.09 cd/m^2, reasonably close to the 3.92 cd/m^2 measured luminance of the red line stimulus. The interparticipant mean correct reaction time (RT) was 555 msec and mean error rate was 3.1%.

Electrophysiological Results

Figure 1 shows ERPs observed at the lateral occipital electrode sites PO7 and PO8 for the three stimulus configurations possible in Experiment 1: lateral line with contralateral square (Figure 1A), central line with lateral square (Figure 1B), and lateral line with central square (Figure 1C). The waveforms consist of a series of positive and negative peaks oscillating at approximately 10 Hz, including P1 (120 msec), N1 (180 msec), P2 (250 msec), and N2 (280 msec) components. When the bright green stimulus was presented at a lateral location, the contralateral and ipsilateral waveforms diverged soon after stimulus presentation (Figure 1A and B). This is likely a product of imbalances in sensory energy resulting from the lateral presentation of the bright square stimulus with no corresponding stimulus in the contralateral hemifield. When luminance was balanced across the visual field (Figure 1C), the first evidence of divergence between the ipsilateral and contralateral waveforms became apparent at approximately 200 msec, at which point the contralateral waveform became more positive than the ipsilateral. This amplitude difference had a mean magnitude of 1.37 μV in the 220–260 msec post-stimulus interval and was statistically assessed in a repeated measures analysis of variance (RANOVA) with within-participant factors for distractor side (left vs. right) and electrode laterality (ipsilateral vs. contralateral). This test revealed a main effect of electrode laterality [$F(1, 11) = 6.483, p = .027$], which indicates that there was a significant difference between ipsilateral and contralateral waveforms. No other effects were significant ($Fs < 1$).

An additional RANOVA was conducted in order to examine the effect of stimulus elevation on the divergence between ipsilateral and contralateral waveforms in Figure 1C. This test had factors for target elevation (upper hemifield vs. lower hemifield) and distractor elevation (upper hemifield vs. lower hemifield), and was conducted on the mean amplitude of the contralateral-minus-ipsilateral difference waveforms in the 200–260 msec latency interval. A main effect of distractor elevation was observed, with a larger difference between ipsilateral and contralateral waveforms elicited when the distractor was in the upper hemifield (1.67 μV) than when it was in the lower hemifield (0.87 μV) [$F(1, 11) = 5.145, p = .044$]. Target elevation had no effect on the magnitude of the positivity seen at the 200–260 msec latency range (Figure 1C; $F < 1$), and there was no interaction of target elevation and distractor elevation [$F(1, 11) = 2.346, p = .154$].

Discussion

The principal finding in Experiment 1 is illustrated in Figure 1C. When the display contained a lateralized distractor and a vertical target, the ERP waveforms over the posterior scalp were more positive contralateral to the distractor than ipsilateral to the distractor. This positivity was maximal in the latency range of the N2pc (∼200–300 msec). The polarity and timing of this posterior positivity are notable when contrasted with the posterior negativity found in the same latency range contralateral to attended targets in conventional visual search experiments (i.e., the N2pc; Luck & Hillyard, 1994b). It is unlikely that the positivity was related to target processing because central targets typically do not elicit lateralized ERP components (Woodman & Luck, 2003).

These results invite the hypothesis that the posterior contralateral positivity reflects processing of the distractor rather than processing of the target. This hypothesis is supported by the finding that the amplitude of the positivity was modulated by distractor elevation but was independent of target elevation. In light of these results,

we refer to this new ERP component as the distractor positivity (P_D).

Before the P_D can be regarded unequivocally as an index of distractor suppression, an alternative account based on residual sensory processing must be considered. In making the distractor isoluminant with the background, our goal was to minimize lateralized sensory ERP activity in the critical display illustrated in Figure 1C. Because the display was not entirely balanced in terms of sensory energy, it is possible that the P_D may have arisen from some lateralized residual sensory process. Experiment 1 provides some evidence against this sensory interpretation in that no differences between the contralateral and ipsilateral waveforms were observed in the period preceding the P_D. Imbalances in sensory energy typically affect cortical activity in the range of the P1 and N1 components, as can be seen in Figure 1A and B. The absence of any P1 or N1 laterality in Figure 1C suggests that any residual hemispheric imbalance in Experiment 1 was minimal, if present at all. This does not, however, constitute conclusive evidence. In order to directly test the possibility that the P_D is a product of imbalanced sensory activity, and thus, unrelated to attention, we conducted an additional experiment.

In Experiment 2, participants were presented with the same sparse visual search arrays as in Experiment 1, but were required simply to detect the presence of the target stimulus rather than discriminate its form. Detection is less attentionally demanding than discrimination (Lavie, 2005), and possibly takes place preattentively (Luck, Girelli, et al., 1997; Treisman & Gelade, 1980). If the P_D reflects attentional processing, it should be reduced or absent when the task requires fewer attentional resources. Alternatively, if the P_D reflects sensory activity, the results of Experiment 2 should parallel those of Experiment 1.

EXPERIMENT 2

Methods

Participants

Twelve healthy students of Simon Fraser University gave informed consent before beginning the experiment. None of the participants had taken part in Experiment 1. All participants reported normal or corrected-to-normal vision and normal color vision and received course credit for their participation. Data from two participants were discarded due to excessive eye movement artifacts in the EEG. One of the remaining participants (5 men; mean ± SD age = 20.3 ± 3.0 years) was left-handed.

Procedure

As in Experiment 1, participants completed a luminance matching procedure before beginning Experiment 2.

This procedure was identical to that in Experiment 1 with the following exception. In Experiment 1, matches began with the gray patch differing from the standard by ∼2.5 cd/m^2; in Experiment 2 this initial difference was ∼0.5 cd/m^2.

In Experiment 1, participants were required to discriminate the form of the target. In Experiment 2, participants were required simply to respond with the index finger of the right hand when the target was present. When the target was absent, as occurred in one third of total trials, no response was required. The addition of no-target conditions resulted in the proportional reduction of trials in target-present conditions such that participants in Experiment 2 took part in as many total trials as participants in Experiment 1. All other experimental characteristics were as in Experiment 1.

Recording and Analysis

EEG recording and analysis procedures were as in Experiment 1.

Results

Behavioral Results

The mean (±SD) average of gray shades arrived at in the color-matching procedure had a luminance of 8.6 ± 0.50 cd/m^2, somewhat brighter than the 3.92 cd/m^2 measured luminance of the red line stimulus. Interparticipant mean correct RT was 383 msec to displays containing both target and distractor and 382 msec to displays containing only the target. Mean error rate was 0.1%.

Electrophysiological Results

Figure 2 shows the ipsilateral and contralateral ERPs observed at the lateral occipital electrode sites PO7 and PO8 in the critical condition of Experiment 2, in which the isoluminant line was presented at a lateral location while the superluminant square was presented on the
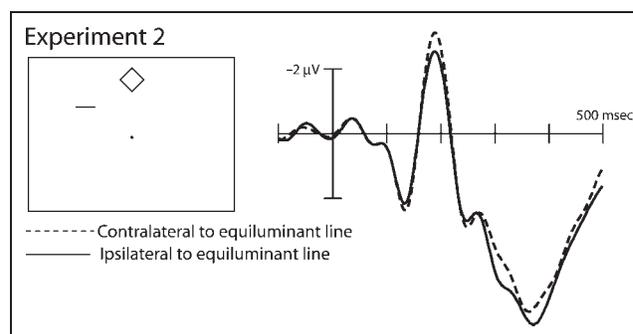
Figure 2. Grand-averaged ERP elicited in Experiment 2 when participants detected the presence of the square stimulus.

vertical meridian. A clear divergence of the ipsilateral and contralateral waveforms is in evidence in the latency of the P1 (~120–140 msec poststimulus) and N1 (~150–210 msec poststimulus) components. These differences likely reflect imbalances of sensory energy across the hemispheres.

At the latency range of the N2pc and the P_D (220–260 msec), only minimal divergence between the ipsilateral and contralateral waveforms is visible. This difference has a mean magnitude of 0.17 μV in the 220–260 msec poststimulus latency interval. In a statistical analysis, a RANOVA with factors for distractor side (left vs. right) and electrode laterality (ipsilateral vs. contralateral) based on mean amplitude in the 220–260 msec poststimulus latency interval revealed no significant effects [Distractor side: $F < 1$; Electrode laterality: $F(1, 9) = 1.644$, $p = .232$; Distractor side × Electrode laterality: $F(1, 9) = 2.100, p = .181$].

Visual and numerical comparison of the results of Experiment 1 (see Figure 1C) and Experiment 2 (see Figure 2) suggests that the distractor stimulus elicited a P_D in Experiment 1 but not in Experiment 2. This possibility was assessed with a between-group t test based on the 220–260 msec ipsilateral-minus-contralateral amplitude difference observed in the critical condition in each of the two experiments. This test revealed a significant difference in P_D amplitude between experiments [mean magnitude of difference: 1.38 μV; $t(20) = 4.15$, $p < .0001$]. As this test was based on unequal group sizes ($n = 12$ in Experiment 1, $n = 10$ in Experiment 2), between-group differences in variance may have caused this test to render an inaccurate p value. This possibility was assessed using the Brown and Forsythe (1974) test of homogeneity of variance [$F(1, 20) = 2.77, p = .11$]. Results from this test, along with the very low p value observed in the t test, suggest that the change in P_D amplitude between Experiments 1 and 2 is reliable.

Discussion

The results of Experiment 2 are consistent with the idea that the P_D reflects attentional activity as distinct from sensory activity. The critical comparison in this respect is between the evidence for the P_D obtained in Experiments 1 and 2. We reasoned that, to the extent that the P_D reflects sensory processes, it should be equally in evidence in both experiments. In fact, by changing the experimental task from discrimination to detection, and thus, reducing attentional demands, the P_D was effectively eliminated in Experiment 2.

This is not to say that sensory effects were absent in Experiment 2. As can be seen in Figure 2, the presence of a lateral, isoluminant distractor caused the ipsilateral and contralateral waveforms to diverge in the latency range of the P1 and N1 components. It is likely that this

represents a lateralized sensory effect that emerged despite the brightness-equalization procedure that participants performed prior to the experiment proper. This sensory effect may have occurred in Experiment 2 but not in Experiment 1 (Figure 1C) because the raw luminance difference between the distractor and the background was larger in Experiment 2 (4.68 cd/m^2 vs. 1.47 cd/m^2). Alternatively, the less demanding detection task in Experiment 2 may have allowed for the deployment of more processing resources to the distractor, resulting in increased cortical activity indexed by the P1 and N1. This is consistent with previous results suggesting that distractors exert greater influence when the experimental task is easy (Lavie, 2005).

Experiments 1 and 2 have provided evidence that ignoring a distractor stimulus elicits an ERP component, the P_D, which differs in polarity from the N2pc and cannot be explained as a product of imbalances in sensory energy. These results are consistent with the idea that the P_D indexes neural activity involved in suppression of distractor stimuli.

As noted in the Introduction, distractor suppression may occur in at least two ways. It may be that suppression acts through direct inhibition of the cortical representation of a suppressed item. Because of the contralateral nature of the visual system, electrophysiological activity associated with the action of this mechanism would presumably be apparent in the hemisphere contralateral to the distractor. Alternatively, it may be that distractor suppression acts indirectly, modulating distractor-related input into neurons responsible for representing the target. This type of distractor suppression could possibly occur in—or close to—the cortex responsible for processing the target. Electrophysiological activity associated with this form of suppression would presumably be apparent in the hemisphere contralateral to the target.

Identification of the polarity of the P_D thus becomes an important step in identifying the cognitive mechanism reflected by this component. There are two possibilities. The P_D may be a positivity elicited in the hemisphere contralateral to the distractor, as has been tacitly assumed in the pages above. This would suggest that the component reflects a suppressive mechanism that acts on the neural representation of the distractor itself. Alternatively, the component may be a negativity elicited in the hemisphere ipsilateral to the distractor. Such a result would be theoretically rather confusing, but possibly interpretable as evidence of a suppressive mechanism acting to shelter the neural representation of the target. In order to discriminate between these possibilities we conducted a third experiment.

In Experiment 3, participants were once again presented with the sparse visual search arrays employed in Experiment 1. Although in Experiment 1 the displays always contained one lateralized stimulus (in order to increase signal-to-noise ratios in relevant conditions),

Experiment 3 also included displays in which both the target and the distractor were presented on the vertical meridian. The ERP elicited by this nonlateralized display was employed as a baseline to which the lateralized-distractor ERPs could be compared. If the P_D reflects an ipsilateral negativity, the waveform elicited *ipsilateral* to an ignored stimulus should be more *negative* than the waveform elicited by the nonlateralized display. In contrast, if the P_D reflects a contralateral positivity, the waveform elicited *contralateral* to the ignored stimulus should be more *positive* than that elicited by the non-lateralized display.

EXPERIMENT 3

Methods

Participants

Ten healthy female students of Simon Fraser University gave informed consent before beginning the experiment. None of the participants had taken part in Experiment 1 or 2. All participants reported normal or corrected-to-normal vision and normal color vision and received course credit for their participation. Data from one participant were discarded due to excessive eye movement artifacts in the EEG, and data from one other participant were discarded due to inaccuracy in the isoluminance-matching procedure that preceded experimental participation. All eight remaining participants (mean ± *SD* age = 22.6 ± 8.1 years) were right-handed.

Procedure

The procedure of Experiment 3 was identical to that of Experiment 1, with the addition of a display configuration in which both the target and distractor stimuli were presented on the vertical meridian. The addition of the both-vertical condition resulted in the proportional reduction of trials in the other conditions such that participants in Experiment 3 took part in as many total trials as participants in Experiment 1.

Recording and Analysis

EEG recording and analysis procedures were as in Experiment 1.

Results

Behavioral Results

The mean (±*SD*) average of gray shades arrived at in the color-matching procedure had a luminance of 8.3 ± 0.90 cd/m^2, somewhat brighter than the 3.92 cd/m^2 measured luminance of the red line stimulus. The interparticipant mean correct RT was 564 msec and mean error rate was 4.4%.

Electrophysiological Results

Figure 3 presents the three ERP waveforms recorded at lateral occipital electrode sites PO7 and PO8 in Experiment 3. One of these was elicited contralateral to the ignored distractor when the target was on the vertical meridian. The second was elicited ipsilateral to the ignored distractor when the target was on the vertical meridian. The third is an average of the signals elicited at lateral electrode sites PO7 and PO8 when the target and the distractor were both presented on the vertical meridian.

The ipsilateral and contralateral ERPs presented in Figure 3 were elicited under circumstances identical to those of Experiment 1. The results are accordingly similar. A P_D became apparent in the 200–260 msec poststimulus interval. This component had a mean magnitude of 1.23 μV and was statistically assessed in a RANOVA with within-participant factors for distractor side and electrode laterality. This test revealed a main effect of electrode laterality [$F(1, 7) = 17.20, p = .004$], which indicates that there was a significant difference between ipsilateral and contralateral waveforms. No other effects were significant ($Fs < 1$).

The third ERP presented in Figure 3 (dotted line), elicited when both stimuli were presented on the vertical meridian of the display, appears to match the ERP elicited ipsilateral to an ignored distractor (Figure 3, segmented line). These two waveforms were not statistically distinguishable from one another through the 200–260 msec poststimulus interval [mean magnitude of difference: 0.19 μV; $t(7) = 0.399; p = .702$]. In contrast, the ERP elicited contralateral to the ignored distractor (Figure 3, segmented line) differs significantly over this latency period from the ERP elicited when both stimuli were on the vertical meridian (Figure 3, dotted line) [mean magnitude of difference: 0.94 μV; $t(7) = 2.578; p = .037$].
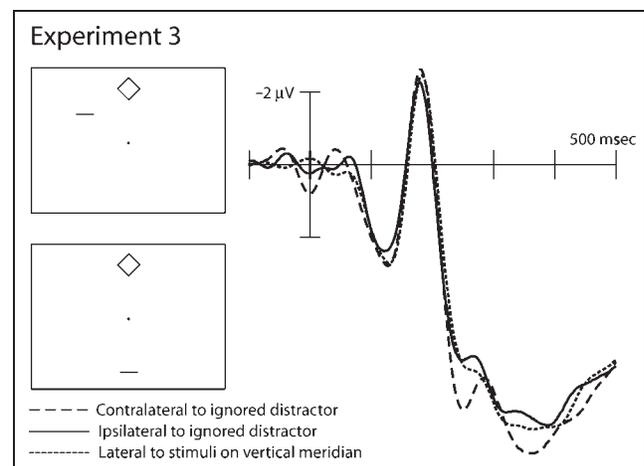
Figure 3. Grand-averaged ERPs elicited in Experiment 3 when participants discriminated the orientation of the square stimulus.

Discussion

Experiment 3 shows that the waveform elicited contralateral to an ignored distractor is, in fact, more positive than that elicited by a nonlateralized display, and thus, demonstrates that the P_D is a positive ERP component elicited contralateral to the location of an ignored distractor. These results are consistent with the idea that the P_D reflects a suppressive mechanism that acts on the cortical representation of distractor stimuli.

The experiments reported to this point have been aimed at isolating neural activity tied to distractor processing. What was not addressed was the issue of the corresponding neural activity related to target processing. The electrophysiological activity related to target processing has been the object of earlier investigations that led to the identification of the N2pc (e.g., Eimer, 1996; Luck & Hillyard, 1994a). Those studies employed stimuli displays that were designed to balance sensory energy across the visual hemifields, allowing for lateralized ERP effects to be unambiguously attributed to attention rather than sensory activity. This was done by presenting a salient nontarget item in the hemifield contralateral to the target, such that each visual hemifield contained an equal number of salient and nonsalient visual stimuli. Results from the present experiments, however, suggest a potential drawback to this strategy. Because the N2pc is defined as the difference between signals recorded over the ipsilateral and contralateral hemispheres, the N2pc elicited in response to balanced displays may consist in part of activity related to processing of the salient distractor elicited in the visual cortex ipsilateral to the target—in other words, the P_D. Thus, the N2pc may not be an index of a single attentional process, but rather reflect neural activity triggered by more than one attentional mechanism.

Experiment 4 was designed to isolate the ERP components related to target processing from those related to distractor processing, and vice-versa. Once again, participants in Experiment 4 were presented with the sparse search arrays used in Experiment 1. However, in contrast to Experiment 1, participants were instructed to attend to the square stimulus in one half the experiment and to the line in the other half. Through the use of this procedure, the lateralized ERP activity triggered by the lateralized line—whether target or distractor—could be unambiguously associated with the processing of that stimulus.

EXPERIMENT 4

Methods

Participants

Fifteen healthy students of Simon Fraser University gave informed consent before beginning Experiment 4. None of the participants had taken part in Experiment 1, 2, or 3. All participants reported normal or corrected-to-normal vision and normal color vision and received course credit for their participation. Data from two participants were discarded due to excessive eye movement artifacts in the EEG, and data from one participant were discarded due to inaccuracy in the isoluminance-matching procedure that preceded experimental participation. All of the remaining 12 participants (5 men; mean ± SD age = 22.8 ± 3.1 years) were right handed.

Procedure

In Experiment 4, participants attended to the isoluminant line stimulus for half of all blocks and to the bright shape stimulus for the remainder of the experiment. Order of conditions was counterbalanced across participants. In the *attend-square* condition, participants were required to indicate whether the bright green stimulus was a square or a diamond (as in Experiments 1 and 3). In the *attend-line* condition, the response was based on the length of the isoluminant red line; half the participants pressed the left mouse button when the line was long and the right when the line was short, with the remainder using the opposite map. All participants responded with their right hand. All other details were as in Experiment 1.

Recording and Analysis

EEG recording and analysis procedures were as in Experiment 1.

Results

Behavioral Results

The mean ($\pm SD$) average of gray shades arrived at by the 12 participants in Experiment 4 had a luminance of 3.84 ± 0.18 cd/m^2, closely matching the 3.92 cd/m^2 luminance of the red standard stimulus.

Table 1 presents the RT and error data obtained in each of the experimental conditions. The mean correct RT was 585 msec for the attend-line condition and 558 msec for the attend-square condition. This 27-msec difference was found to be significant in a RANOVA with a within-participant factor for condition (attend-line vs. attend-square) and a between-participant factor for condition order (attend-line first vs. attend-square first) [Condition: $F(1, 10) = 9.36$, $p = .012$; Condition order: $F < 1$; Condition × Condition order: $F(1, 10) = 1.90$, $p = .198$]. A similar analysis of errors found that mean error rate in the attend-line condition (5.4%) was significantly greater than that observed in the attend-square condition (2.8%) [Condition: $F(1, 10) = 12.20$, $p = .006$,

Table 1. Experiment 4: Mean Correct Response Times (msec) and Error Rates (%) by Condition

Experimental Condition	Mean RT (SD)	Error Rate (SD)
(a) Attend-shape	558 (73)	2.8 (2.1)
A: Lateral target, contralateral distractor	562 (75)	3.1 (2.4)
B: Lateral target, vertical distractor	551 (72)	2.6 (2.3)
C: Vertical target, lateral distractor	561 (73)	2.3 (2.0)
(b) Attend-line	585 (74)	5.4 (2.9)
A: Lateral target, contralateral distractor	582 (73)	5.3 (3.1)
B: Lateral target, vertical distractor	587 (78)	4.8 (2.8)
C: Vertical target, lateral distractor	586 (73)	6.1 (4.5)

Condition order: $F(1, 10) = 1.76$, $p = .214$, Condition × Condition order: $F < 1$].

Electrophysiological Results

Figures 4 and 5 present the ERPs obtained in each of the three stimulus configurations in the attend-square (Figure 4A–C) and attend-line conditions (Figure 5A–C). As in Experiment 1, lateralized ERP differences were observed in the latency of the posterior P1 and N1 components when displays contained a lateralized bright green square, regardless of whether this stimulus was the target or the distractor (Figure 4A and B; Figure 5A and B). These differences were not apparent when the square was presented on the vertical meridian of the search display (Figures 4C and 5C). It seems likely that these effects arise from differences in lateralized sensory processes triggered by differences in stimulus luminance.

To isolate activity associated with target and distractor processing, we examined ERP waveforms elicited by displays containing a lateralized isoluminant line and a central square (Figures 4C and 5C). As in Experiment 1, when participants were instructed to attend to the central square and ignore the lateral line, the P_D was recorded at posterior electrode locations contralateral to the line (Figure 4C). The P_D began at ∼230 msec, returned to baseline at ∼280 msec, and had a mean amplitude of 0.99 μV through this time period. In contrast, when participants were instructed to attend to the lateral line and ignore the central square, the same visual search display elicited a large negative component over posterior electrode locations contralateral to the attended line (Figure 5C). This negative component began at ∼175 msec, returned to baseline at ∼325 msec, and had a mean amplitude of 1.48 μV through this time period. This component appears to be very similar to the N2pc: It is negative in polarity, occurs in the latency range of the N2pc, and is elicited contralateral to an attended target. However, the negativity

Experiment 4 - Attend to square

A Lateral square contralateral line

−2 μV

500 msec

Contralateral to bright square
Ipsilateral to bright square

B Lateral square, vertical line

−2 μV

500 msec

Contralateral to bright square
Ipsilateral to bright square

C Lateral line, vertical square

−2 μV

500 msec

Contralateral to equiluminant line
Ipsilateral to equiluminant line

Figure 4. Grand-averaged ERPs elicited in Experiment 4 when participants discriminated the orientation of the square stimulus.
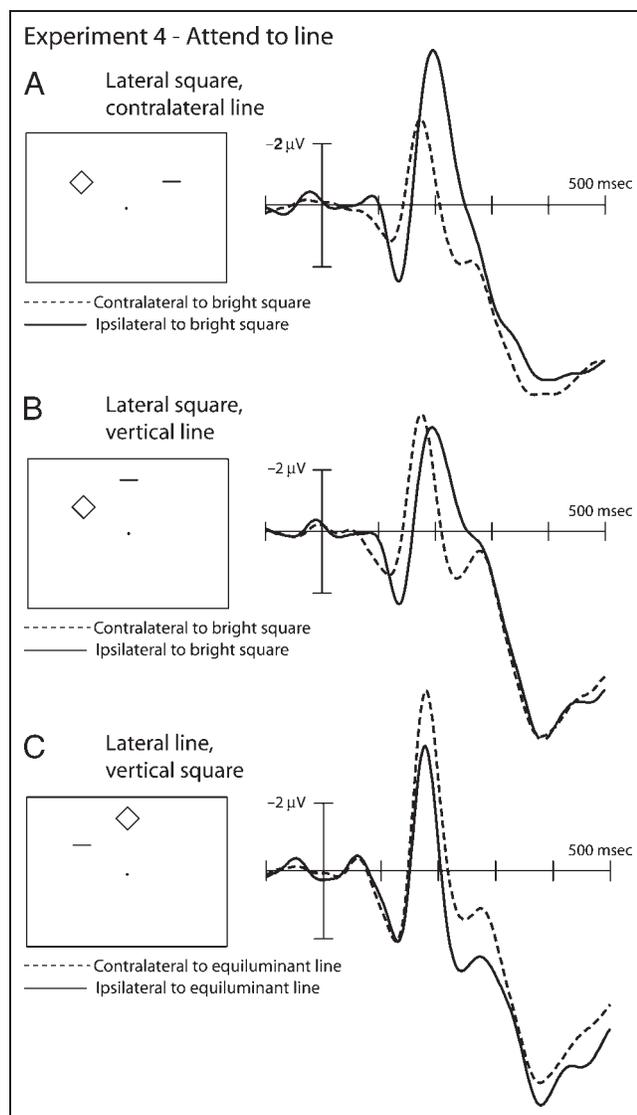
Figure 5. Grand-averaged ERPs elicited in Experiment 4 when participants discriminated the length of the line stimulus.

obtained in the present experiment arose from a display that was not balanced across the visual hemifields. This means that the negativity might reflect a combination of sensory and attentional factors. The more important consideration for the present purposes, however, is that this negativity is related exclusively to target processing. In contrast, the N2pc elicited by balanced displays, although unaffected by sensory processes, reflects attentional activity that may stem from processing of both the target and the salient distractor. For these reasons, we distinguish the negativity illustrated in Figure 5C from the N2pc and refer to it as the *target negativity*, or N_T.

In order to assess the N_T and P_D statistically, RANOVAs were performed on the mean amplitude of the ERPs as measured across a 175–325 msec poststimulus interval in the attend-line condition and across a 230–280 msec

poststimulus interval in the attend-square condition (corresponding to latencies of the observed contralateral negativity and positivity, respectively). An initial RANOVA had within-participant factors for condition (attend-line vs. attend-square), stimulus side (left visual hemifield vs. right visual hemifield), and electrode laterality (ipsilateral vs. contralateral), and a between-participant factor for condition order (attend-line first vs. attend-square first). The Condition × Electrode laterality interaction was significant [$F(1, 10) = 25.74$, $p < .001$], reflecting the fact that a posterior contralateral *positivity* was observed in the attend-square condition (Figure 4C) and a posterior contralateral *negativity* was observed in the attend-line condition (Figure 5C). No other effect approached significance ($Fs < 1$).

Two further RANOVAs were conducted to test the P_D and N_T in isolation. These tests had within-participant factors for stimulus side (left visual hemifield vs. right visual hemifield) and electrode laterality (ipsilateral vs. contralateral) and a between-participant factors for condition order (attend-line first vs. attend-square first). Significant main effects of electrode laterality were observed for both the N_T [$F(1, 10) = 16.14$, $p = .002$] and the P_D [$F(1, 10) = 9.93$, $p = .010$], attesting to the reliability of both components. Only one other effect reached significance in these analyses, a Stimulus side × Electrode laterality × Condition order interaction in analysis of the P_D [$F(1, 10) = 5.23$, $p = .045$; all other $Fs < 1$]. This interaction may reflect a change in neural mechanisms employed in order to ignore a stimulus when that stimulus has previously been a target.

As in Experiment 1, additional RANOVAs were conducted in order to examine the influence of stimulus elevation on component amplitudes. These tests had within-participant factors for target elevation (upper hemifield vs. lower hemifield) and distractor elevation (upper hemifield vs. lower hemifield), and were conducted on mean P_D or N_T amplitude computed over the 200–260 msec poststimulus interval (see Figures 4C and 5C). A main effect of target elevation was found in the N_T, with this component larger when the target line was presented in the lower hemifield (-2.21 μV) than when it was presented in the upper hemifield (-1.23 μV) [$F(1, 11) = 7.822$, $p = .017$]. Distractor elevation and the interaction of target elevation with distractor elevation had no significant effect on the N_T ($Fs < 1$). In the analysis of the P_D, a main effect of distractor elevation approached significance, with this component larger when the distractor line was presented in the upper hemifield (1.31 μV) than when it was presented in the lower hemifield (0.48 μV) [$F(1, 11) = 2.868$, $p = .119$]. This analysis was significant in Experiment 1, suggesting that the trend observed in Experiment 4 reflects a reliable effect. Target elevation ($F < 1$) and the interaction of target elevation and distractor elevation [$F(1, 11) = 1.532$, $p = .242$] had no significant effect on the P_D.
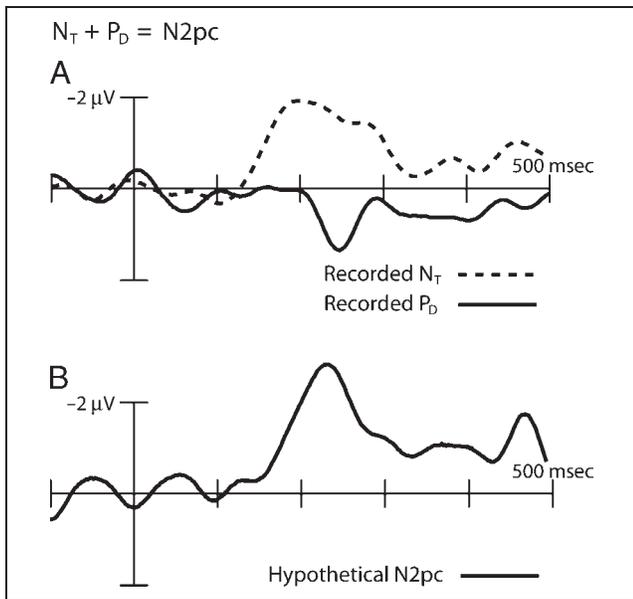
Figure 6. (A) Contralateral-minus-ipsilateral difference waves based on the data presented in Figures 4C and 5C. The lateral N_T and P_D are denoted. (B) The absolute algebraic sum of the N_T and P_D.

Figure 6A presents the contralateral-minus-ipsilateral difference waves based on the ERPs presented in Figures 4C and 5C. These difference waves show that the N_T peaked before the P_D (250 msec vs. 289 msec, respectively). This latency difference was statistically significant in a RANOVA with a within-participant factor for condition (attend-line vs. attend-square) and a between-participant factor for condition order (attend-line first vs. attend-square first) [Condition: $F(1, 10) = 5.110$, $p = .045$; Condition order: $F < 1$; Condition × Condition Order: $F(1, 10) = 1.048$, $p = .328$].

Spherical-spline-interpolated scalp maps of both the P_D and N_T components are presented in Figure 7. These half-head scalp maps were created from the contralateral–ipsilateral difference waves by mirroring the data across the midline and artificially setting the values on the midline to zero. Figure 7A and B presents the mean voltage topography across a 250–280 msec interval, whereas Figure 7C and D presents interpolations of t-statistic values associated with the difference between contralateral and ipsilateral waveforms in the same latency interval. The topographical t-statistic maps in Figure 7C and D were thresholded such that only spline gradients corresponding to a p value of less than approximately .05 are displayed. The t statistic, however, was employed as a descriptive measure that represents the combination of effect size and variability; the maps are not intended to provide inferential statistical content.

Both components were distributed over the posterior scalp. Voltage and t-statistic maps show that the N_T was focused more ventrally than the P_D (Figure 7). To assess the reliability of this topographical difference, a RANOVA

was conducted based on mean P_D and N_T amplitude recorded from a subset of electrodes, with factors for component (N_T vs. P_D), laterality (medial vs. lateral), and posteriority (anterior vs. mid vs. posterior). The electrode locations used in this analysis are identified in Figure 7C and D, with medial electrodes denoted by circles and lateral electrodes by squares. The effects of interest were the Condition × Laterality interaction, which was significant [$F(2, 22) = 13.64$, $p < .001$], and the Condition × Posteriority interaction, which was marginally significant [$F(2, 22) = 3.18$, $p = .061$]. These results provide some support for the idea that the P_D and N_T differ in terms of topography.

Discussion

As in the previous experiments, the critical stimulus configuration in Experiment 4 consisted of a bright green square on the vertical meridian and a red line at a lateral location. When the bright square was attended and the lateral line was *ignored*, the experimental procedure was identical to the corresponding conditions in Experiments 1 and 3. Consistent with these previous experiments, a contralateral *positivity*—the P_D—was observed through the 230–280 msec poststimulus interval (Figure 4C). In contrast, when the bright square was ignored and the line was *attended*, a contralateral *negativity*—the N_T—was obtained through the same latency interval (Figure 5C).

We noted above that although the N_T bears distinct similarities to the N2pc, there are trenchant reasons why the two components should be distinguished from one another. To our minds, the most important of these is that the N2pc reported in previous studies may have reflected the summation of the N_T and P_D components. This is plausible because the N2pc is generally identified through the comparison of ipsilateral and contralateral waveforms elicited by the presentation of a balanced search display (e.g., Woodman & Luck, 1999, 2003; Luck & Ford, 1998; Eimer, 1996; Luck & Hillyard, 1994a, 1994b). Balanced displays contain a salient target in one hemifield, a salient nontarget in the contralateral hemifield, and a number of low-salience distractors equally distributed across the visual field. The cortical activity elicited by balanced displays may therefore include not only a negative component—the N_T—in the hemisphere contralateral to the target, but also a positive component—the P_D—in the hemisphere contralateral to the salient nontarget. Given that the N2pc is calculated by subtraction of the contralateral from the ipsilateral waveforms, it is possible that the N2pc obtained in earlier studies under balanced-display conditions may have thus consisted of the summation of the N_T and the P_D components. This line of reasoning is based on the plausible assumption that the activity elicited by the nonsalient distractors that are distributed

Figure 7. Spherical-spline-interpolated scalp maps of the N_T and P_D. (A and B) Voltage topography. (C and D) The *t*-statistic topography.
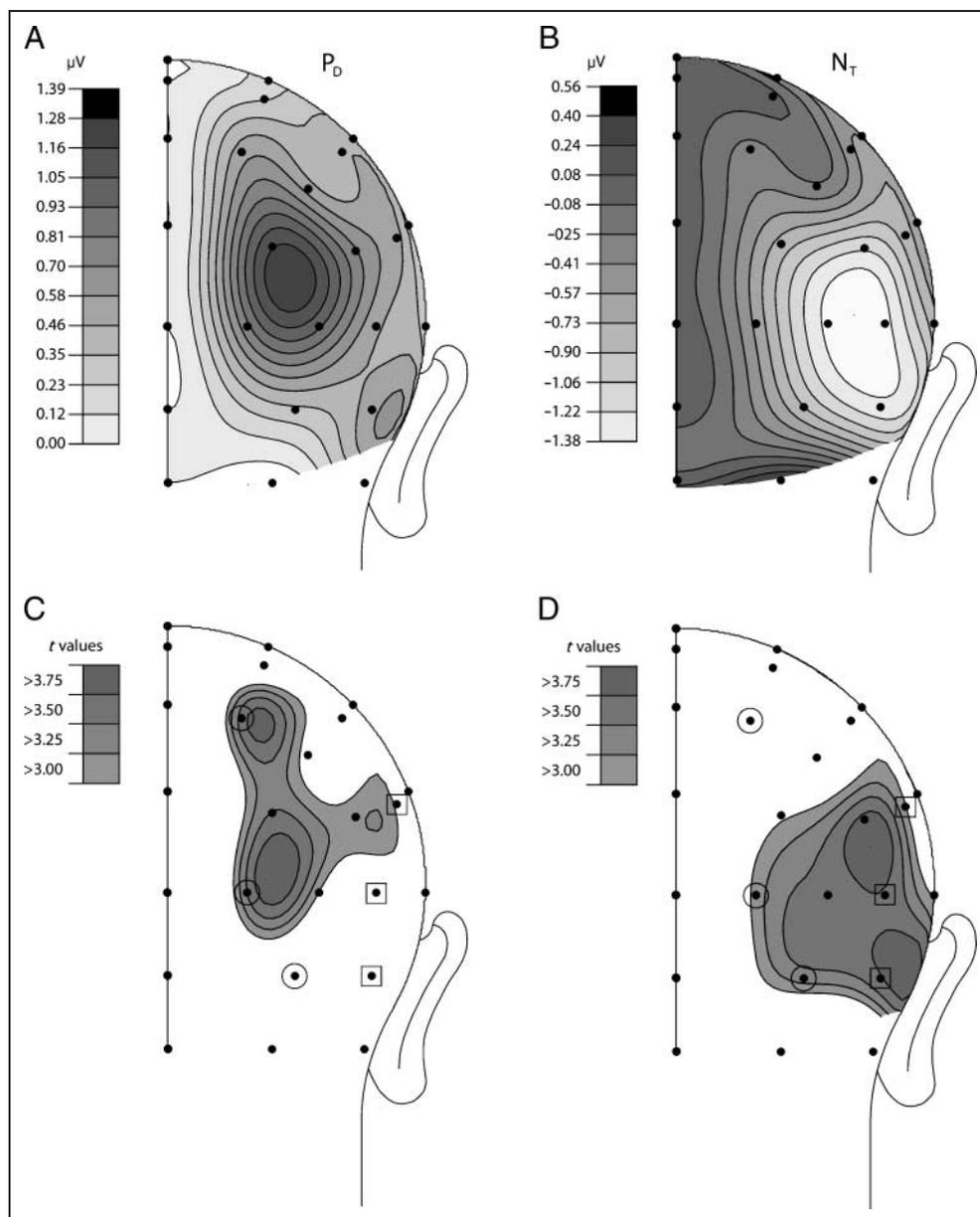
evenly across the visual field would cancel out across the cortical hemispheres.

Hypothetical summation of the P_D and N_T components is illustrated in Figure 6. Figure 6A contains two difference waves labeled P_D and N_T. The P_D waveform was calculated by subtracting the contralateral from the ipsilateral waveform in Figure 4C. Similarly, the N_T waveform was calculated by subtracting the contralateral from the ipsilateral waveform in Figure 5C. The outcome of Experiment 4 suggests that the N_T represents attentional modulation of neural activity related to target processing—whether excitatory or suppressive. By the same token, the P_D represents attentional modulation of neural activity related to distractor processing—presumably suppressive. Figure 6B illustrates the abso-

lute algebraic summation of the P_D and N_T waveforms. The waveform in Figure 6B is thus a hypothetical representation of the N2pc obtained in experiments that employ balanced search displays.

In contrast to the N2pc, which may reflect both target and distractor processing, the N_T can be unequivocally linked to the target stimulus. This component may reflect the suppression of distractor-related input into neurons responsible for target representation, as has been suggested of the N2pc (Luck, Girelli, et al., 1997). As discussed above, this type of distractor suppression could result in electrophysiological activity in the cortical hemisphere contralateral to the target. Alternatively, the present results are consistent with the suggestion that the N_T may represent increased

neural activity associated with enhanced target processing, as reported in the animal literature (Treue & Maunsell, 1999; Roelfsema et al., 1998; Spitzer et al., 1988). At any rate, the temporal pattern of components observed in Experiment 4—first an N_T and later a P_D—is consistent with the idea that selection in visual search may begin with target-related processing and progress through the direct suppression of distractor stimuli. A similar sequence of events has been suggested in the animal literature, with the attention-related enhancement of neural activity preceding distractor processing (Treue, 2001).

Because the P_D and the N_T were elicited in the same experiment by identical displays, Experiment 4 allowed for direct comparison between the two components. In terms of their relationship to display characteristics, both components were found to vary as a function of stimulus location. However, although the P_D was larger when the distractor was in the upper hemifield and was unaffected by the location of the target, the N_T was larger when the target was in the lower hemifield and was unaffected by the location of the distractor.

The N_T and P_D additionally differed in terms of topography. Although the P_D occurred over the dorsomedial cortex (Figure 7A and C), the N_T occurred over the ventrolateral cortex (Figure 7B and D). This pattern of results may reflect the broad division of processing in the visual cortex into dorsal and ventral streams. The dorsal stream has been associated with the processing of spatial information, whereas the ventral stream has been associated with the processing of object identity (Ungerleider & Mishkin, 1982). As such, the dorsal topography seen in Figure 7A and C suggests that the P_D may arise from processing tied to a spatial location, as would be expected if the component reflects a spatially select suppressive mechanism. In contrast, the ventral topography seen in Figure 7B and D suggests that the N_T may arise from neural activity tied more closely to the processing of object features.

The pattern of topographic results observed in Experiment 4 shows interesting similarities to results reported in Hopf et al. (2000). In that study magnetoencephalographic recordings were made while subjects viewed balanced visual search displays and attended to a target stimulus. The magnetic equivalent of the electrical N2pc was found to show two distinct loci of activity, with one smaller, earlier source located in the posterior parietal cortex and one larger, later source located in the extrastriate cortex. Hopf et al. interpreted this pattern as reflecting the action of an attentional mechanism in the parietal cortex that changes visual processing in extrastriate areas. However, the present results raise the possibility that the distinct source loci identified in Hopf et al. may rather reflect the P_D and N_T. The dorsal topography of the P_D is consistent with a parietal generator, whereas the ventral topography of the N_T is

in line with a source in the extrastriate cortex. One caveat must be attached to this possibility; Hopf et al. found that the posterior parietal generator became active prior to the extrastriate generator. In contrast, the present results show a ventral focus—the N_T—that precedes the more dorsal P_D.

GENERAL DISCUSSION

The principal objective of this study was to identify dissociable neural correlates of target and distractor processing in visual search. We conducted four experiments in which ERPs were recorded while participants viewed sparse search arrays containing a square, which was brighter than the background, and a line, which was of equal brightness with the background. These stimuli could be presented at positions located directly above or below fixation, and thus, on the vertical meridian of the display, or at lateral positions in the upper or lower hemifields (see figures for examples). The critical condition was that in which participants were presented with a line at a lateral display position and a square at a position on the vertical meridian. This display allowed for the identification of lateralized ERP components tied to processing of the line, as stimuli presented on the vertical meridian do not elicit lateralized ERP activity (Woodman & Luck, 2003; see also Hickey et al., 2006).

Crucially, the type of ERP component recorded in the critical condition (lateral line, vertical square) depended not on the stimulus configuration—which was invariant—but on the deployment of attention. This critical configuration elicited an ERP negativity—the N_T—contralateral to the line when it was attended but an ERP positivity—the P_D—contralateral to the line when it was ignored.

The P_D and N_T did not differ only in terms of polarity. Although both were focused over the posterior scalp, the P_D occurred over more medial and dorsal areas relative to the N_T which occurred over more lateral and ventral areas. This is consistent with the hypothesis that the P_D and the N_T may reflect processing activity in the dorsal and ventral streams, respectively (Milner & Goodale, 1995; Ungerleider & Mishkin, 1982). In addition to these differences in topography, the components differed in their relationship to the location of stimuli. The P_D appears to be tied to the location of the distractor stimulus, being larger when the distractor was in the upper field and smaller when it was in the lower field. The N_T, in contrast, appears to be tied to the location of the target, being larger when the target was in the lower field and smaller when it was in the upper field. Together, these characteristics suggest that the components reflect two distinct processes involved in visual search, one spatial in nature and involved in the processing of distractor stimuli, the other related to

object features and involved in the processing of target stimuli.

We would like to note that the present results are consistent with what might be expected on the basis of activity at the cellular level. A positive-going effect contralateral to the distractor (P_D) and a negative-going effect contralateral to the target (N_T) are precisely what would be expected given excitatory postsynaptic potentials (PSPs) in the cortex responsible for target representation and inhibitory PSPs in the cortex responsible for distractor representation. We hasten to note that relating ERP polarity to excitatory and inhibitory cellular activity is far from straightforward. However, the ERP is widely thought to reflect the summation of PSPs of pyramidal neurons in the cerebral cortex, with excitatory activity generating depolarization, and thus, negative PSPs and inhibitory activity generating polarization, and thus, positive PSPs (see, for discussion, Luck, 2006; Rugg & Coles, 1995).

The P_D: An Electrophysiological Index of Distractor Suppression

We believe that the P_D indexes direct suppression of the cortical representation of distractor stimuli. This interpretation is based on results showing that the P_D is elicited contralateral to the distractor, that it varies as a function of distractor position, and that it stems from areas of the visual cortex that are spatial in nature.

The idea that distractor representations are directly suppressed is consistent with results from other studies. Behavioral work, for example, has shown that response times to probe stimuli presented at distractor locations are slower than those to probes at blank locations, even when distractors are far removed from the target location (Cepeda et al., 1998). In the human brain, distractor suppression in a sustained attentional task has been associated with changes in cortical activity throughout the visual cortex, from V1 to higher extrastriate areas (Slotnick, Schwarzbach, & Yantis, 2003). This modulation of activity has been observed even in response to a cue indicating the location of a distractor stimulus (Ruff & Driver, 2006). In the monkey brain, distractor-related neural activity in the lateral intraparietal area is reduced when the distractor is ignored and attention is correctly deployed to the target, even when target and distractor are not close to one another (Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006). These and related results have led to the inclusion of a mechanism responsible for the direct suppression of distractor-related activity in many influential theories of attention (e.g., Desimone & Duncan, 1995; LaBerge, 1995).

In summary, extensive evidence of direct distractor suppression has been reported in a number of studies that used a variety of experimental approaches. The present results suggest that the P_D is an electrophysiological index of the type of distractor suppression identified in earlier behavioral, neurophysiological, and imaging research.

The N_T: An Electrophysiological Index of Target Processing

Whereas the P_D appears to index neural activity involved in distractor processing, the N_T appears to index processing that is tied to the target itself. It may be that the neural activity that underlies the N_T is involved in the enhancement of the cortical representation of attended stimuli, as has been observed in electrophysiological studies with animals (Treue & Maunsell, 1999; Roelfsema et al., 1998; Spitzer et al., 1988) and with humans using paradigms other than visual search (Mangun & Hillyard, 1991). Alternatively, the N_T may reflect more complex aspects of target processing, such as the testing of perceptual hypotheses (Shedden & Nordgaard, 2001; Di Lollo, Enns, & Rensink, 2000).

Importantly, however, results tying the N_T to the location of the target are not necessarily inconsistent with a distractor-suppression role for this component. As discussed above, the suppression of distractor information may occur in the cortex that contains a representation of the target. As the N2pc appears to be often constituted of the N_T and P_D components, this last possibility is consistent with the substantial body of literature that has linked the N2pc to distractor suppression (e.g., Luck, Girelli, et al., 1997; Luck & Hillyard, 1994a, 1994b).

Concluding Comments: $P_D + N_T = $ N2pc

In earlier electrophysiological studies of visual search, no distinction was drawn between attentional processing tied to the target and attentional processing tied to the distractors. In those studies, the N2pc was thought to reflect cognitive processes involved in target selection (e.g., Luck & Ford, 1998; Eimer, 1996). We believe that, when balanced displays were employed, the resulting N2pc may not have been a unitary component but may have rather reflected a summation of the N_T and P_D components. In the present work, we have identified the P_D and the N_T as integral independent components, and we have suggested how they may combine to form the conventional N2pc.

In conclusion, the present study was motivated by results from the ERP literature and from other empirical sources that lent themselves to alternative interpretations of target selection in visual search. Here, we resolved this ambiguity by proposing that the electrophysiological correlate of selection in visual search—the N2pc—is an aggregate measure of at least two distinct

processes, one tied to the spatial location of distractor stimuli (P_D), the other to the spatial location of target stimuli (N_T).

Acknowledgments

REFERENCES

Brown, M. B., & Forsythe, A. B. (1974). Robust tests for equality of variance. *Journal of the American Statistical Association, 69,* 364–367.

Cepeda, N. J., Cave, K. R., Bichot, N. P., & Kim, M. S. (1998). Spatial selection via feature-driven inhibition of distractor locations. *Perception & Psychophysics, 60,* 727–746.

Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature, 363,* 345–347.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18,* 193–222.

Di Lollo, V., Enns, J. T., & Rensink, R. A. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *Journal of Experimental Psychology: General, 129,* 481–507.

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology, 99,* 225–234.

Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neuroscience, 18,* 604–613.

Hopf, J. M., Boehler, C. N., Luck, S. J., Tsotsos, J. K., Heinze, H. J., & Schoenfeld, M. A. (2006). Direct neurophysiological evidence for spatial suppression surrounding the focus of attention in vision. *Proceedings of the National Academy of Sciences, U.S.A., 103,* 3532–3540.

Hopf, J.-M., Luck, S. J., Girelli, M., Hagner, T., Mangun, G. R., Scheich, H., et al. (2000). Neural sources of focused attention in visual search. *Cerebral Cortex, 10,* 1233–1241.

Ipata, A. E., Gee, A. L., Gottlieb, J., Bisley, J. W., & Goldberg, M. E. (2006). LIP responses to a popout stimulus are reduced if it is overtly ignored. *Nature Neuroscience, 9,* 1071–1076.

LaBerge, D. (1995). *Attentional processing: The brain's art of mindfulness*. Cambridge: Harvard University Press.

Lavie, N. (2005). Distracted and confused?: Selective attention under load. *Trends in Cognitive Science, 9,* 75–82.

Luck, S. J. (2006). *An introduction to the event-related potential technique*. Cambridge: The MIT Press.

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology, 77,* 24–42.

Luck, S. J., & Ford, M. A. (1998). On the role of selective attention in visual perception. *Proceedings of the National Academy of Sciences, U.S.A., 95,* 825–830.

Luck, S. J., Girelli, M., McDermott, M. T., & Ford, M. A. (1997). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cognitive Psychology, 33,* 64–87.

Luck, S. J., & Hillyard, S. A. (1994a). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology, 31,* 291–308.

Luck, S. J., & Hillyard, S. A. (1994b). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance, 20,* 1000–1014.

Mangun, G. R., & Hillyard, S. A. (1991). Modulations of sensory evoked brain potentials indicate changes in perceptual processing during visual–spatial priming. *Journal of Experimental Psychology: Human Perception and Performance, 17,* 1057–1074.

McAdams, C. J., & Maunsell, J. H. (1999). Effects of attention on the reliability of individual neurons in monkey visual cortex. *Neuron, 23,* 765–773.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford, UK: Oxford University Press.

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science, 229,* 782–784.

Motter, B. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *Journal of Neurophysiology, 3,* 909–919.

Mounts, J. R. (2000). Evidence for suppressive mechanisms in attentional selection: Feature singletons produce inhibitory surrounds. *Perception & Psychophysics, 62,* 969–983.

Roelfsema, P. R., Lamme, V. A., & Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature, 395,* 376–381.

Ruff, C. C., & Driver, J. (2006). Attentional preparation for a lateralized visual distractor: Behavioral and fMRI evidence. *Journal of Cognitive Neuroscience, 18,* 522–538.

Rugg, M. D., & Coles, M. G. (1995). *Electrophysiology of mind*. Oxford, UK: Oxford University Press.

Shedden, J. M., & Nordgaard, C. L. (2001). ERP time course of perceptual and post-perceptual mechanisms of spatial selection. *Cognitive Brain Research, 11,* 59–75.

Slotnick, S. D., Hopfinger, J. B., Klein, S. A., & Sutter, E. E. (2001). Darkness beyond the light: Attentional inhibition surrounding the classic spotlight. *NeuroReport, 13,* 773–778.

Slotnick, S. D., Schwarzbach, J., & Yantis, S. (2003). Attentional inhibition of visual processing in human striate and extrastriate cortex. *Neuroimage, 19,* 1602–1611.

Spitzer, H., Desimone, R., & Moran, J. (1988). Increased attention enhances both behavioral and neuronal performance. *Science, 240,* 338–340.

Treisman, A., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12,* 97–136.

Treue, S. (2001). The neural correlates of attention in primate visual cortex. *Trends in Neurosciences, 24,* 295–300.

Treue, S., & Maunsell, J. H. (1999). Effects of attention on the processing of motion in macaque middle temporal and medial superior temporal visual cortical areas. *Journal of Neuroscience, 19,* 7591–7602.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge: The MIT Press.

Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature, 400,* 867–869.

Woodman, G. F., & Luck, S. J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology: Human Perception and Performance, 29,* 121–138.