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Original Research

VERTICAL ELEVATION AS A KEY FACTOR FOR THE NEURAL DISTINCTION OF TARGET SELECTION AND DISTRACTOR SUPPRESSION IN VISUAL SEARCH

Abstract

Background:

Directing attention to relevant visual objects while ignoring distracting stimuli is crucial for effective perception and goal-directed behavior. Event-related potential (ERP) studies using the additional-singleton paradigm have provided valuable insights into how the human brain processes competing salient stimuli by monitoring N2pc and P_D, two event-related components thought to reflect target selection and distractor suppression, respectively. However, whether these components reflect the activity of a single or distinct neural mechanisms remains controversial. Here, we investigated the neural substrate of N2pc and P_D by manipulating the vertical elevation of target and distractor relative to the visual horizontal meridian using two variants of the additional-singleton paradigm.

Methods:

In Experiment 1, participants searched for a shape singleton and identified the orientation of an embedded tilted bar while ignoring a color singleton. In Experiment 2, the tilted bars were removed and participants performed a shape search while ignoring a color singleton. EEG recordings at posterior sites (PO7/8) measured N2pc and P_D components. Reaction times and ERP amplitudes were analyzed across conditions.

Results:

The results of both Experiments 1 and 2 showed that N2pc and P_D responded in opposite ways to the manipulation of vertical elevation. N2pc was robust for targets in the lower visual hemifield and reversed in polarity (i.e., PNP) for targets in the upper visual hemifield. Conversely, P_D was more pronounced for distractors in the upper visual hemifield and nil for those in the lower visual hemifield. Critically, vertical elevation did not influence psychophysical estimates of search efficiency in either experiment, suggesting that the relationship between these components and their functional significance is less straightforward than previously thought.

Conclusions:

These results provide empirical support for the idea that N2pc and P_D are influenced by the retinotopic organization of the visual cortex in a manner consistent with the neural and functional

dissociation of target selection and distractor suppression in visual search.

Keywords: Additional-singleton, visual search, N2pc, P_D, neural substrate

1. Introduction

Directing attention to visual objects is relatively straightforward when these objects are physically salient. Bright colors, moving lights, and other forms of visual distinctiveness are commonly used to capture the attention of drivers on a motorway, for instance, helping them avoid potentially dangerous situations. However, there are circumstances where attention must be focused on relevant salient objects while preventing distraction by other, equally salient, objects. For instance, drivers need to concentrate on traffic signals while ignoring flashy roadside advertisements.

Over the last three decades, event-related potential (ERP) studies have provided significant insights into how attention is controlled when two salient objects — one that needs to be attended to and another that must be ignored — compete for attention. A frequently used experimental design employed in these studies is the additional-singleton paradigm [1] illustrated in Fig. 1. In this paradigm, two salient visual objects, singletons along some feature dimension, are presented among uniform objects. Participants are instructed to judge an aspect of the target singleton (e.g., 'Is the bar inside the diamond shape tilted left or right?') while ignoring the distractor singleton (e.g., a red circle).

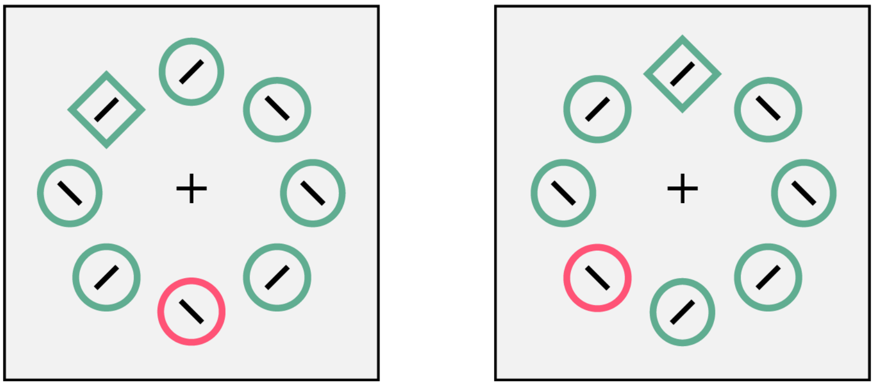

Fig. 1. Examples of search arrays in an additional-singleton paradigm. Target and distractor could appear in any of six positions along the circle (excluding the left and right horizontal midline positions): upper-left, upper-right, lower-left, lower-right, middle-upper, and middle-lower. Left panel: Array in which a shape singleton (i.e., the green diamond) is laterally displayed, and a color singleton (i.e., the

red circle) is displayed along the vertical meridian. Right panel: Array in which a color singleton is laterally displayed, and a shape singleton is displayed along the vertical meridian.

ERP studies have revealed that attentional control in the additional-singleton paradigm can be tracked by monitoring two distinct event-related lateralizations (ERLs), usually recorded at posterior electrode sites between about 100 and 350 milliseconds after the onset of the visual array. When a target is presented laterally relative to the vertical midline, like the green diamond in the left panel of Fig. 1, the ERP recorded at sites contralateral to the visual hemifield containing the target is more negative compared to symmetrical ipsilateral sites. This ERL can be ascribed to the processing of visual elements in the visual hemifield containing a target, for a midline distractor, like the red circle in the left panel of Fig. 1, is represented bilaterally in the visual cortex and is unlikely to cause any ERLs [2–3]. This ERL, typically isolated by subtracting the ipsilateral ERP from the contralateral ERP, is known as N2pc [4–6]. Although N2pc has been initially thought to reflect the suppression of distractors near the target [5], current evidence strongly suggests N2pc reflects attention deployment to the target, whether through covert attention shifts [7], short-term consolidation [8] of task-relevant features of the target [9–11], or the enhancement of activation of the target's cortical representation [2, see 12, for a review].

In contrast, when the distractor is presented laterally with a concomitant midline target, as shown in the right panel of Fig. 1, the ERP recorded at sites contralateral to the visual hemifield containing the distractor is more positive compared to ipsilateral sites. This ERL, isolated by subtracting the ipsilateral ERP from the contralateral ERP, is termed P_D, for distractor positivity [13]. Since its initial discovery, P_D has been recognized as a neural correlate of suppressive processing. Its functional significance, however, varies depending on its temporal occurrence and whether it is observed in isolation or follows the N2pc component.

In ERP studies where P_D was the solely observed ERL, particularly when P_D was observed before about 200 ms (i.e., in an earlier time-window than that typical of N2pc), P_D was interpreted as proactive suppression of the distractor's cortical representation. This suppression facilitates the subsequent or concomitant deployment of attention to the target [14,15 see 16,17, for a review]. Evidence supporting this interpretation includes findings that the amplitude of this early P_D is inversely correlated with the time taken to respond to the target [18,19], suggesting that more efficient proactive suppression of a distractor leads to faster attention allocation to the target [19,20]. Evidence from other studies, however, suggests a distractor can indeed capture attention in advance of being suppressed. This is reflected in an observed distractor-induced N2pc temporally trailed by a P_D, which together indicate a reactive shift of attention away from the distractor [21,22,23, see 24, for a detailed discussion of the ERP pattern predicted by attentional capture]. This reactive shift may involve either disengaging attention from the distractor [25,26, see 27, for a review] or inhibiting the previously attended distractor location, a process analogous to the inhibition of return [28].

Compared to the large number of ERP studies focusing on the functional interpretation of attentional processes indicated by N2pc and P_D, there have been relatively few attempts to determine whether N2pc and P_D reflect different manifestations of the same neural circuit or whether they involve distinct neural processes that can be distinguished at the neural level. Sawaki, Geng, and Luck [29] analyzed the topographical scalp distribution of N2pc and P_D and suggested that both components reflect the action of a single neural mechanism, with N2pc enhancing and P_D suppressing the neural representation of target and distractor, respectively. However, source localization analyses using magnetoencephalography (MEG) have identified subtle but significant differences in the field distributions of N2pc and P_D. Specifically, N2pc has been associated with an early source in the inferior intra-parietal sulcus (IPS) and a later source in the ventral extra-striate and infero-temporal (IT) cortices [30–33]. A recent MEG study by Donohue, Schoenfeld, and Hopf [34] added to these findings, showing that P_D is generally associated with a more dorsal field distribution, despite sharing an early source with N2pc.

Of critical importance for the present context, the more ventral source of N2pc and the more dorsal source of P_D have been raised to explain an often overlooked aspect of how N2pc and P_D modulate as a function of the position of targets and distractors relative to the horizontal midline. Previous research has shown that N2pc is fully-fledged when targets are displayed below the horizontal midline (i.e., in the lower visual hemifield) and substantially attenuated, or even reversed in polarity, when targets are displayed above the horizontal midline (i.e., in the upper visual hemifield, [2, 35–40]). P_D shows the opposite pattern in response to distractor vertical elevation. In their original demonstration of P_D, Hickey et al. [13] showed that P_D was fully-fledged for distractors displayed in the upper visual hemifield and attenuated for distractors displayed in the lower visual hemifield. Speculations proposed in past work (e.g., [34]) concerning the opposite reactions of N2pc and P_D to vertical elevation have been referred to the retinotopic organization of the ventral and dorsal visual pathways. In short, N2pc would be 'missed' for targets in the upper visual hemifield because this field is represented by a ventral portion of the striate visual cortex that is anatomically distant from the parieto-occipital electrode sites (i.e., PO7/8) where N2pc is usually most prominent. Conversely, N2pc would be fully-fledged for targets in the lower visual hemifield because this field is represented by a portion of the ventral visual cortex closer to these electrode sites (e.g., [41]). Although explaining the attenuation of P_D for distractors in the lower visual hemifield has proven slightly more challenging, it is generally believed that a similar explanation applies to P_D with reference to retinotopy. P_D would be 'missed' for distractors in the lower visual hemifield because this field is represented by deep intrasulcular portions of the dorsal V4 cortex, making the electrical activity from these regions harder to detect compared to that from the upper visual hemifield (e.g., [42]; see also [43]).

Scope of the present investigation is to revisit the issue of vertical elevation as a modulatory factor of N2pc and P_D using the additional-singleton paradigm shown in Fig. 1 in the present Experiment 1. The underlying motivation is related to the demonstration of Hickey et al. [13] and the specific visual stimulation used in their investigation. Hickey et al. [13] used very sparse search arrays in which a salient target shape and a line equal in brightness to the background were displayed one laterally and the other along the vertical midline. This stimulation is not ideal for ruling out sensory imbalance, perceptual asymmetry, and the reduced number of objects comprising the search arrays as possible causes of the opposite modulation of N2pc and P_D amplitude in relation to vertical elevation. Although a proposal for how such factors might modulate N2pc and P_D as a function of vertical elevation is beyond the scope of the present work, the paradigm illustrated in Fig. 1 should address all these potentially problematic aspects. The stimuli composing the search arrays were arranged along a notional circle centered at fixation, as is typical in most recent visual search studies. Furthermore, the search arrays in the present context were composed of eight stimuli, equidistant from each other. This number was intentionally chosen to avoid the potential confounds associated with sparse arrays, where fewer items might introduce variability in sensory processing and attention dynamics [26]. A display with eight stimuli, while not overwhelming in terms of visual load, ensures that the attentional mechanisms at play are comparable to typical visual search paradigms, allowing for a clearer interpretation of the effects of vertical elevation manipulation. As a preview, Experiment 1 allowed us to faithfully replicate the opposite pattern of N2pc and P_D modulation by vertical elevation shown by Hickey et al. [13] — thus ruling out all the aforementioned peculiar aspects of Hickey et al.'s [13] design among the possible causes — while also providing important additional information on the polarity reversal of N2pc, which turned to a paradoxical target-induced positivity (i.e., the post-N2pc positivity (PNP) component, see below), for targets displayed in the upper visual hemifield.

In Experiment 2, we used the same stimuli as in Experiment 1 with one critical modification. We eliminated all bars within the shapes shown in Fig. 1 to eliminate an additional potential source of the opposite pattern of N2pc and P_D modulation by vertical elevation originally shown by Hickey et al. [13] and replicated in Experiment 1. Although physically identical in geometrical structure, the way in which target and distractor singletons had to be processed in Experiment 1 was substantially different. The target had to be examined in all its features, including the inscribed bar, because the bar tilt was the relevant dimension for a response. One obvious suspect is that the distractor could instead be suppressed on the basis of color alone. By removing the bars in Experiment 2 and displaying the target shape in only half of the trials for target detection, we made it less likely that the opposite pattern of N2pc and P_D modulation by vertical elevation could be attributed to the involvement of different neuronal populations in target and distractor processing. Straight segments are known to be visual primitives encoded by neurons in V1, whereas color additionally involves different extrastriate areas (e.g., [44]). Despite this important change in stimuli and task, we replicated in Experiment 2 the pattern observed in Experiment 1. In addition, Experiment 2 provided us with the opportunity to test whether N2pc and P_D are not only neurally separable (at least on the basis of retinotopy) but also functionally dissociable. Although prior research (e.g., [45,46]) has shown that P_D is not modulated by target presence and that N2pc is observed in both target-absent and distractor-absent trials (e.g., [47]), our study sought to extend this work by focusing on the modulation of these components by vertical elevation. By manipulating the vertical position of targets and distractors, we aimed to show that N2pc and P_D responded differently to vertical elevation even when each of these components was triggered independently of each other, thus reinforcing the hypothesis of distinct neural mechanisms for target selection and distractor suppression. As a preview, the results of Experiment 2 were reassuring in this regard, as we observed N2pc in response to a lateral target in distractor-absent trials and a P_D in response to a lateral distractor in target-absent trials. Of import, N2pc and P_D in these trials were influenced by vertical elevation in a manner similar to N2pc and P_D in Experiment 1, as N2pc reversed in polarity for targets displayed in the upper visual hemifield, and P_D was attenuated for distractors displayed in the lower visual hemifield.

2. Experiment 1

2.1. Participants

Twenty-two students at the South China Normal University (10 males; mean age = 22 years, SD = 2.8) were recruited in the present experiment after providing written informed consent. All participants had normal or corrected-to-normal visual acuity, and all reported normal color vision and no history of neurological disorders. The experiment was vetted by the local ethics committee (No: SCNU-PSY-2022-148).

2.2. Stimuli and procedure

An example of the stimuli is reported in Fig. 1. The stimuli were line drawings of circles and diamonds displayed at equidistant locations (3° of visual angle) from central fixation against the black background (CIE in xyY color space: 0.312/0.329, 1.0 cd/m^2) of a 17’ CRT computer monitor with a refresh rate of 60 Hz and controlled by a computer running E-prime 3.0 software. At a viewing distance of about 60 cm, each circle subtended 1.4°×1.4° of visual angle, and each diamond subtended 1.6°×1.6° of visual angle. Each search array was composed of 8 shapes, at least 6 of which were green (CIE:

0.237/0.261, 25 cd/m^2) non-target circles and one was always a green diamond (target) shape. In half of the trials, one of the green circles was replaced with a red (CIE: 0.500/0.300, 25 cd/m^2) circle (distractor). Our choice of a red circle as a distractor was aimed at maximizing our chances of observing a reliable P_D component. All else being equal (e.g., luminance), red stimuli tend to elicit a particularly pronounced P_D compared to stimuli of different colors (e.g., [48]).

Each shape included a white (CIE: 0.313/0.329, 100 cd/m^2) straight segment, titled 45° either to the left or right. Target and distractor could appear at any of the six possible locations in the search array, excluding the left and right horizontal positions. These locations included upper-left, upper-right, lower-left, lower-right, middle-upper, and middle-lower positions. When presented simultaneously, if the target occupied a vertical position (e.g., middle-upper or middle-lower), the distractor always appeared in one of the lateral positions (upper-left, upper-right, lower-left, or lower-right). Conversely, if the target occupied a lateral position, the distractor always appeared on the vertical midline. This manipulation ensured that target and distractor never appeared both laterally, on the same or opposite sides, as these configurations would introduce an inherent ambiguity in interpreting ERLs. The probability of target and distractor appearing at each position was balanced and equal, both independently and in relation to each other. Trials in which a target was displayed alone on the vertical midline were retained for behavioral analysis but excluded from EEG processing, as no ERL was expected for bilaterally represented midline stimuli.

Each trial began with the presentation of a fixation point for a randomly jittered 500–800 ms interval, followed by the presentation of a search array for up to 2000 ms or until a response was detected. Participants were instructed to keep their gaze at fixation and to press, as fast and accurately as possible, the ‘Z’ or ‘M’ key of the computer keyboard (standard US keyboard, counterbalanced across participants) to identify the orientation of the tilted bar embedded in the diamond shape. Following the detection of a response, a blank inter-trial interval of 1000 ms elapsed before the presentation of the fixation point indicating the beginning of the next trial.

In Experiment 1, we systematically compared the effects of vertical elevation on N2pc and the P_D amplitude. To this end, N2pc amplitude values were submitted to a 2 × 2 × 2 ANOVA considering target’s laterality (contralateral vs. ipsilateral), distractor presence (present vs. absent), and vertical elevation (upper vs. lower visual hemifield) as within-subject factors. P_D, amplitude values were submitted to a 2 × 2 × 2 ANOVA considering distractor’s laterality (contralateral vs. ipsilateral), target presence (present vs. absent), and vertical elevation (upper vs. lower visual hemifield) as within-subject factors.

Each combination of target and distractor position was repeated in 30 random trials, a number determined based on Marturano et al.’s [49] findings demonstrating that a stable N2pc can be attained by averaging as few as 40 sweeps (i.e., 20 per target side). Participants were exposed to three different search arrays, i.e., target-present arrays with or without a distractor, and target-absent arrays with a distractor. Participants performed 10 blocks of 96 experimental trials, in each of which the ratio of proportions of these search arrays was 2:1:1, respectively.

2.3. EEG recording and pre-processing

EEG activity was recorded continuously from 64 Ag/AgCl electrodes, positioned according to the 10–10 International system [50], using a Neuroscan Curry 9 system (Compumedics USA, Charlotte, NC, USA) set in AC mode and using an electrode located between FPz and Fz as ground. Vertical electrooculogram (VEOG) was recorded from two electrodes positioned 1.5 cm above and below the left eye. Horizontal electrooculogram (HEOG) was recorded from two electrodes positioned on the outer canthi of both eyes. EEG, VEOG, and HOEG signals were band-pass filtered between 0.01 and 30 Hz and digitized at a sampling rate of 1000 Hz. EEG activity was referenced online to the left earlobe and then referenced offline to the average of the left and right earlobes. Continuous EEG was then segmented into 700 ms long epochs, starting 100 ms before the onset of the search array and ending 600 ms after it. EEG epochs were baseline corrected by using the average activity in the time interval -100–0 ms relative to the onset of the search array. After excluding trials associated with an incorrect response in the visual search task, individual trials containing artifacts were also excluded from analysis by using the step-function of ERPLAB (step: 30 ms, VEOG deflection > 50 μV within a time window of 150 ms; HEOG deflection > 35 μV within a time window of 200 ms; or signal exceeding ± 80 μV anywhere in the epoch). The average percentage of rejected trials was 5% (ranging from 0.9 to 21.9%). We applied a 70% artifact-free trial threshold (i.e., less than 20 sweeps per target/distractor side) for data inclusion, and no participants were excluded based on this criterion. The final data retention rate ranged from 87% to 92% trials across conditions.

EEG epochs recorded at PO7/8 electrode sites were then averaged to generate ERPs for each cell of the present design. ERLs were computed as contralateral-minus-ipsilateral difference waves relative to the visual hemifield occupied by a lateral target or a lateral distractor. To avoid selection bias, the selection of time-windows was based on the indications for Luck and Gaspelin [51], using the collapsed localizers approach for consistent and unbiased analyses across conditions. ERLs were initially collapsed across design conditions (i.e., target position, distractor position, and distractor presence/absence) so as to define the relevant 50 and 100 ms time-windows centered on the peaks of ERL deflections of positive and negative polarity, respectively (see [52,53]). These time-windows were then used to isolate the mean amplitude of N2pc, PNP, Ppc (positivity posterior contralateral), and P_D in non-collapsed ERLs for each cell of the present design (see 'Supplementary materials' for the collapsed ERLs).

EEG data in the N2pc, PNP, Ppc, and P_D time-windows were transformed to current source density (CSD) topographic maps using a spherical spline surface Laplacian (order of the splines = 4, regularization parameter $\lambda = 1e\text{-}5$, conductivity of the skin = 0.33 S/m) [54]. We opted for CSD maps because the CSD approach provides a sharper topography compared to spline-interpolated maps of voltage intensity by reducing the blurring effects of volume conduction on the scalp-recorded EEG voltage signal [55]. In particular, CSD maps provide a reference-free mapping of scalp-recorded electrical activity, thus rendering ERP polarity unambiguous. The CSD approach to scalp topography does not make any assumptions about the neuroanatomy or about the number, orientation, or independence of the underlying neuronal generators. The sign of these estimates directly reflects the direction of the global radial currents underlying the EEG topography, with positive values representing current flow from the brain towards the scalp, and negative values representing current flow from the scalp into the brain.

Statistical analyses were performed using R [56] and the ezANOVA function of the ‘ez’ package [57] and anovaBF/ttestBF functions of the ‘BayesFactor’ package [58], which implements the Jeffreys–Zellner–Siow (JZS) default prior on effect sizes [59]. The Greenhouse-Geisser correction for non-sphericity was applied when appropriate [60]. All comparisons via *t*-test were Bonferroni-corrected (adjusted alpha level = 0.0125). We adjusted the alpha level rather than the *p*-values to maintain the integrity of the original statistical evidence and ensure transparency in reporting. This approach allows readers to directly interpret the strength of effects while controlling for Type I errors across multiple comparisons. The correction was based on four planned comparisons, which primarily focused on the interaction effects between laterality and vertical elevation—the key effects of interest in our ERP analyses. We applied Bayes statistics to the null effects from ANOVAs and *t*-tests, offering a more nuanced understanding of whether any meaningful effects were truly absent rather than just non-significant. The Bayes factors (*BF*) provide a complementary estimate of the probability that a given main effect or interaction was present (BF_{10}) relative to the alternative hypothesis of its absence ($BF_{01} = 1/BF_{10}$). For example, in case of non-significant factor effects, a BF_{01} greater than 3 is typically considered as noticeable evidence supporting the absence of such effects. It is important to note that the *BF* and *p*-value are not inherently contradictory. When discrepancies arise between the *BF* and *p*-value, but consistency is observed in post hoc multiple comparisons, this may suggest that the interaction effect in the overall analysis is primarily driven by a subset of specific effects. Consequently, we will conduct further analyses to examine these specific effects in greater detail.

2.4. Results

2.4.1 Behavior

Participants were particularly accurate in the visual search task (range = 91.1–99.8%), and no analysis was conducted on accuracy.

RTs on trials associated with an incorrect response and/or RTs exceeding three standard deviations an individual's mean RT (1.8%) were expunged from analysis. RTs were submitted to an ANOVA that considered target's vertical elevation (2 levels: upper vs. lower visual hemifield) and distractor presence (2 levels: present vs. absent) as within-subjects factors. The ANOVA indicated the main effect of distractor presence ($F(1, 21) = 11.2$, $p = 0.003$, $\eta_p^2 = 0.347$, $BF_{10} = 11.34$), reflecting longer RTs when a distractor was present (649 ms) than when a distractor was absent (637 ms). No other factor or interaction was significant (max $F = 2.1$, min $p = 0.166$). RTs on trials in which a distractor was present were submitted to an additional ANOVA that considered target's vertical elevation (2 levels: upper vs. lower visual hemifield) and distractor's vertical elevation (2 levels: upper vs. lower visual hemifield) as within-subjects factors. No main effect or interaction was significant (max $F = 2.9$, min $p = 0.104$).

Given that null effects of vertical elevation on RTs were critical to support our hypothesis of vertical elevation as a factor influencing the retinotopy of ERP manifestations of search efficiency and not attention functions (i.e., selection vs. suppression) [see also 2,36,37,39], we used the Bayes factor (BF_{01}) to quantify the relative support for the null hypothesis versus the alternative hypothesis. The BF_{01} was 1.10 for the effect of the target's vertical elevation, 5.10 for the effect of the distractor's vertical elevation, and 3.04 for the interaction of target's vertical elevation and distractor's vertical elevation. These findings suggest that the vertical position of the distractor does not exhibit a significant influence on search efficiency, whereas the effect of the target's vertical position remains inconclusive.

2.4.2 ERL to lateral target

Fig. 2 provides a graphical summary of ERLs recorded at PO7/8 in response to the search arrays exemplified to the left of the graphs, separately for trials in which a midline distractor was present (solid ERLs) or absent (dashed ERLs), and for targets displayed in the upper visual hemifield (upper panel) or in the lower visual hemifield (lower panel). As Fig. 2 makes clear, a prototypical N2pc was evident for a lateral target displayed in the lower visual hemifield. In striking contrast, a target displayed in the upper visual hemifield failed to elicit an N2pc and elicited instead what appears to be a PNP [61]. In addition, whether or not a distractor was present in the search array did not seem to alter the effect of polarity reversal caused by vertical elevation.

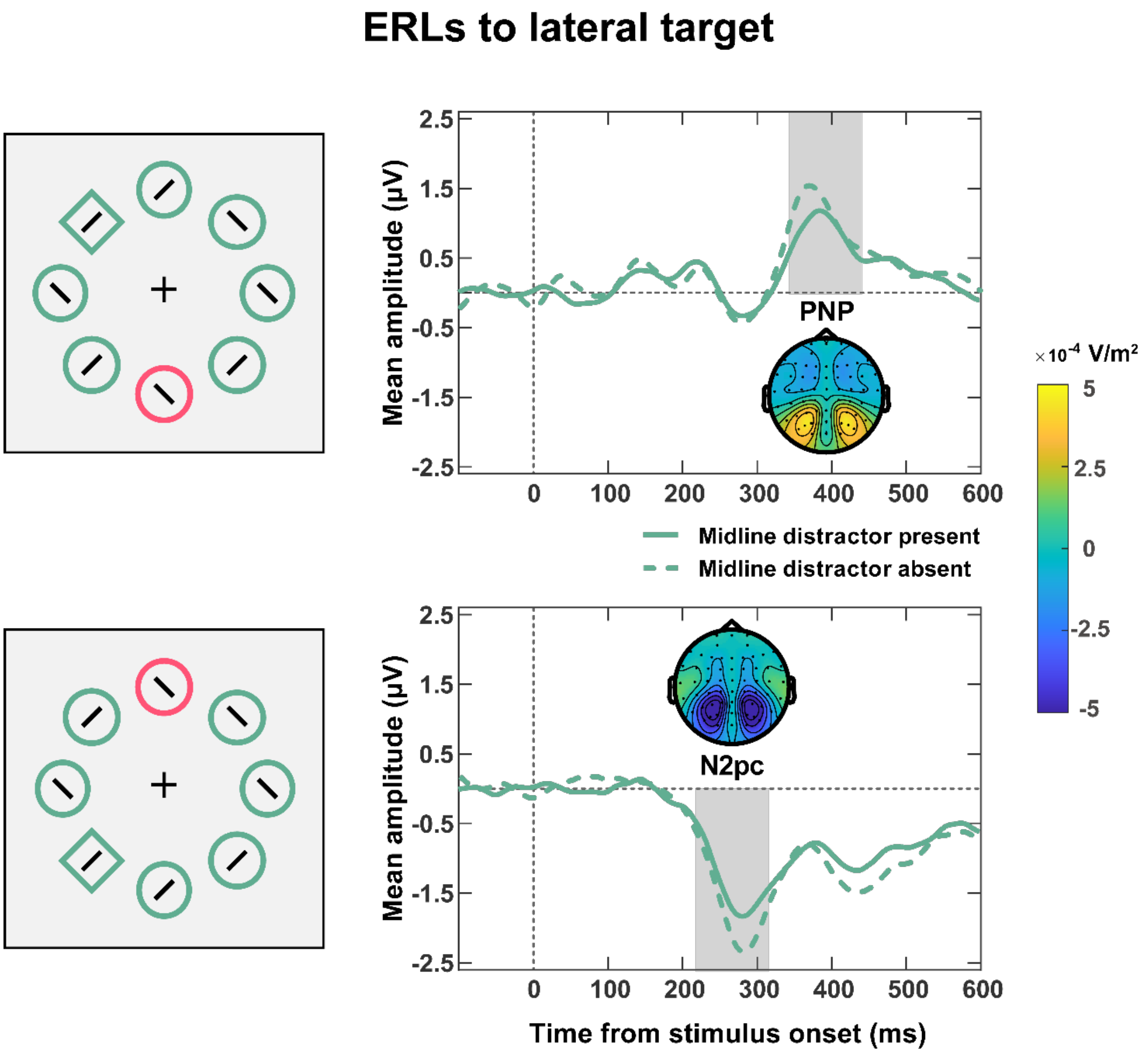

Fig. 2. ERLs (contralateral minus ipsilateral ERPs) elicited by a lateral target in Experiment 1 recorded at electrode sites PO7/8. Mean CSD maps of ERL activity (averaged across distractor-present and distractor-absent trials) in time-windows highlighted with grey shades are reported as insets. ERLs were low-pass filtered at 15 Hz for visualization purposes.

The amplitude values recorded in the N2pc time-window (i.e., 220–320 ms) were first submitted to an ANOVA that considered distractor presence (2 levels: present vs. absent), laterality (2 levels: contralateral vs. ipsilateral) and vertical elevation (2 levels: upper vs. lower visual hemifield) as within-subject factors. The ANOVA indicated a main effect of laterality ($F(1, 21) = 14.7$, $p < 0.001$, $\eta_p^2 = 0.411$, $BF_{10} > 1000$) and an interaction between vertical elevation and laterality ($F(1, 21) = 62.4$, $p < 0.001$, $\eta_p^2 = 0.748$, $BF_{10} > 1000$). N2pc was larger in response to a lateral target displayed in the lower visual hemifield than in the upper visual hemifield (-1.62 μV vs. -0.11 μV). Pairwise comparisons showed that N2pc in response to a lateral target displayed in the lower visual hemifield differed from 0 μV ($t(21) = -6.3$, $p < 0.001$, *Cohen's* $d = -1.081$, $BF_{10} > 1000$), whereas N2pc in response to a lateral target displayed in the upper visual hemifield did not ($t(21) = -0.5$, $p = 0.642$, *Cohen's* $d = -0.074$, $BF_{01} = 5.11$). No other factor or interaction was significant (max $F = 2.1$, min $p = 0.165$), suggesting that N2pc was not influenced by whether a distractor was present (-0.76 μV) or absent (-0.97 μV) in the search array, with both these values differing from 0 μV ($t(21) = -6.7$, $p < 0.001$, *Cohen's* $d = -0.507$, $BF_{10} = 127.65$, and $t(21) = -5.6$, $p < 0.001$, *Cohen's* $d = -0.647$, $BF_{10} = 94.03$, respectively).

Fig. 2 shows that a lateral target displayed in the upper visual hemifield elicited a PNP, whose amplitude was quantified in a 340–440 ms time-window. The amplitude values recorded in this time-window were submitted to ANOVA that considered the same factors as those used for N2pc analyses. The ANOVA indicated an interaction between vertical elevation and laterality ($F(1, 21) = 99.8$, $p < 0.001$, $\eta_p^2 = 0.826$, $BF_{10} > 1000$). Pairwise comparisons showed that a PNP elicited by a lateral target displayed in the upper visual hemifield differed from 0 μV (1.04 μV; $t(21) = 5.8$, $p < 0.001$, *Cohen's* $d = 0.872$, $BF_{10} > 1000$). The negative deflection for a lateral target displayed in the lower visual hemifield, previously described as a sustained posterior contralateral negativity (SPCN; [62]), was also significant (-1.02 μV; $t(21) = -4.4$, $p < 0.001$, *Cohen's* $d = -0.854$, $BF_{10} > 1000$). Although the three-way interaction approached significance ($F(1, 21) = 3.56$, $p = 0.073$, $\eta_p^2 = 0.145$), the BF_{01} was 3.72 indicating positive evidence for the null effect. Further planned comparisons also confirmed that this target-elicited PNP was not influenced by whether a distractor was present or absent (0.91 μV vs. 1.18 μV, $t(21) = -1.25$, $p = 0.225$, *Cohen's* $d = -0.220$, $BF_{01} = 2.25$), with both these values differing from 0 μV ($t(21) = 5.1$, $p < 0.001$, *Cohen's* $d = 0.760$, $BF_{10} = 224.74$, and $t(21) = 4.7$, $p < 0.001$, *Cohen's* $d = 0.986$, $BF_{10} = 595.06$, respectively).

2.4.3 ERL to lateral distractor

Fig. 3 provides a graphical summary of ERLs recorded at PO7/8 in response to the search arrays exemplified to the left of the graphs, separately for trials in which a distractor was displayed in the upper visual hemifield (upper panel) or in the lower visual hemifield (lower panel). Fig. 3 suggests an early positivity in the P1 time interval was evident for a lateral distractor displayed in the upper visual hemifield, which was however absent when a lateral distractor was displayed in the lower visual hemifield. The timing of this early positivity makes it likely that this ERL is a Ppc. The Ppc typically reflects imbalanced saliency or a feature discontinuity [48,63,64]. Albeit small in amplitude, a P_D was however apparent in a later time-window in response to a distractor displayed in the upper visual hemifield.

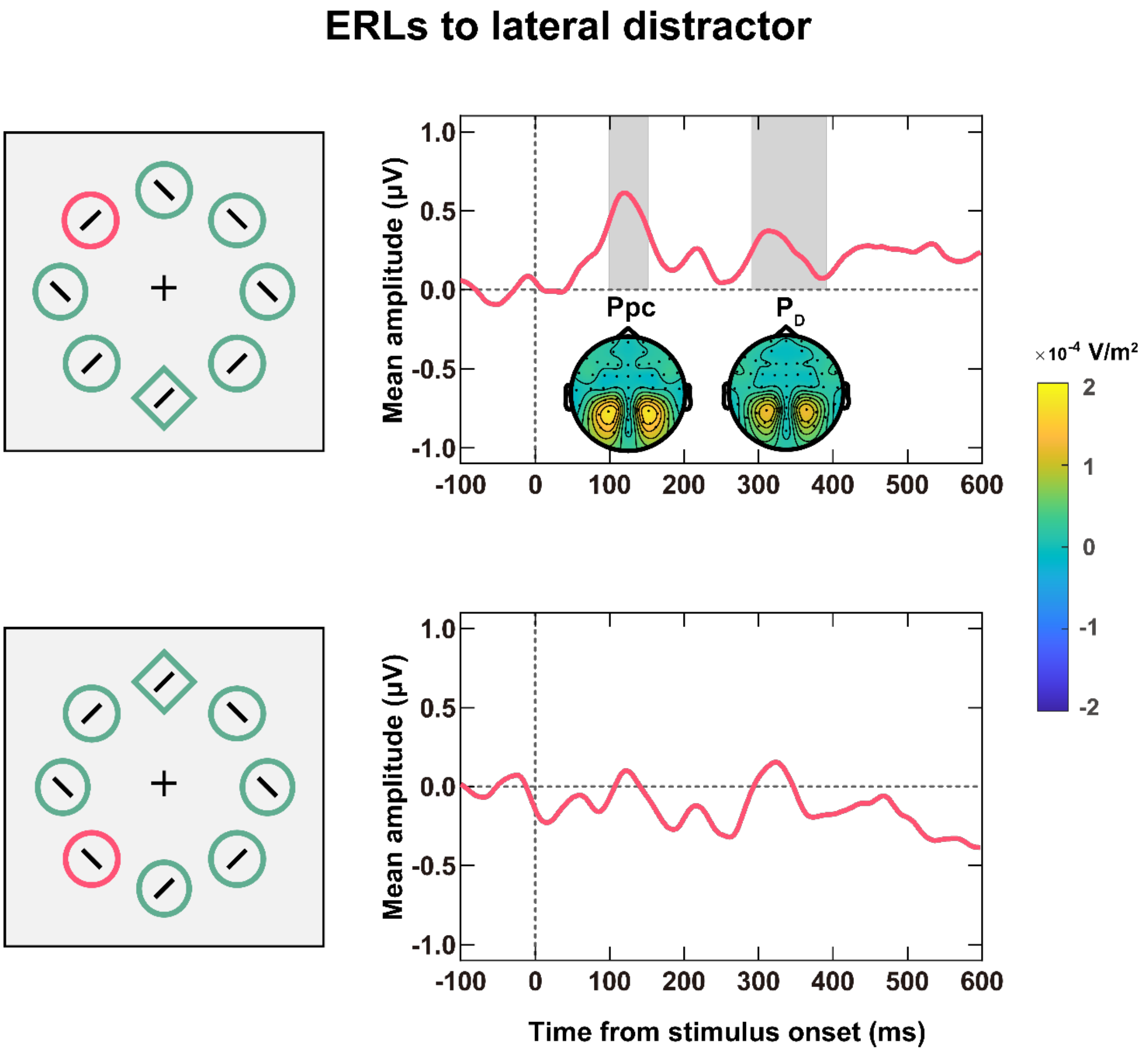

Fig. 3. ERLs (contralateral minus ipsilateral ERPs) elicited by a lateral distractor in Experiment 1 recorded at electrode sites PO7/8. Mean CSD map of ERL activity in the time-window highlighted with grey shade is reported as inset. ERLs were low-pass filtered at 15 Hz for visualization purposes.

One ANOVA was conducted on the amplitude values recorded in the Ppc time-window (i.e., 100–150 ms), with laterality (2 levels: contralateral vs. ipsilateral) and vertical elevation (2 levels: upper vs. lower visual hemifield) as within-subject factors. The ANOVA indicated a main effect of laterality ($F(1, 21) = 58.1$, $p < 0.001$, $\eta_p^2 = 0.735$, $BF_{10} = 11.38$) and an interaction between laterality and vertical elevation ($F(1, 21) = 16.9$, $p < 0.001$, $\eta_p^2 = 0.446$, $BF_{10} = 3.13$). Pairwise comparisons confirmed that the Ppc differed from 0 µV for a distractor displayed in the upper visual hemifield (0.59 µV; $t(21) = 7.3$, $p < 0.001$, *Cohen's d* = 2.880, $BF_{10} > 1000$), but it did not for a distractor displayed in the lower visual hemifield (0.08 µV; $t(21) = 1.1$, $p = 0.297$, *Cohen's d* = 0.370, $BF_{01} = 2.70$).

An additional ANOVA was conducted on the amplitude values measured in the P_D time-window (i.e., 290–390 ms), considering the same within-subject factors as those used for Ppc analyses. The ANOVA indicated an interaction between laterality and vertical elevation ($F(1, 21) = 4.5$, $p = 0.046$, $\eta_p^2 = 0.177$, $BF_{01} = 1.72$). Pairwise comparisons confirmed that the P_D differed from 0 µV for a distractor displayed in the upper visual hemifield (0.26 µV; $t(21) = 2.7$, $p < 0.015$, *Cohen's d* = 0.721, $BF_{10} = 3.63$), but it did not for a distractor displayed in the lower visual hemifield (0.00 µV; $t(21) = 0.0$, $p = 0.978$, *Cohen's d* = 0.008, $BF_{01} = 6.12$).

3. Experiment 2

Experiment 1 extended a previous observation by Hickey et al. [13] concerning the opposite modulation of N2pc and P_D by vertical elevation to a design that addressed the set of issues discussed in the Introduction. In Experiment 2, the tilted bars within the shapes composing the same search arrays as those used in Experiment 1 were removed, and participants had to detect the presence vs. absence of the green diamond shape in the search array, which was unpredictably displayed on a random half of the trials only. Experiment 2 allowed us to test whether the opposite modulation of N2pc and P_D by vertical elevation shown in Experiment 1 could be extended to a search design in which target and distractor were unimodal stimuli (e.g., [65]) and were likely to be inspected on the basis of shape and color alone, without the need for prolonged attentional lingering on the target to encode the bar tilt. This critical manipulation helps further reinforce the conclusion that the effects of vertical elevation are driven by retinal topology and neural functional segregation. In line with this, we focus on a corollary of the hypothesis of distinct neural *and* functional mechanisms underlying N2pc and P_D, in that these ERLs should be detected independently of each other. Given the many demonstrations of target-evoked N2pc in visual search designs without salient distractors and the fact that distractor-evoked P_D can also be observed in the absence of the target, the critical prediction concerned target selection (N2pc) and distractor suppression (P_D) are supported by distinct neural circuits, which we expected the opposite modulation patterns of vertical elevation should be independent of target and distractor presence.

3.1. Participants

Twenty-two students at the South China Normal University (6 males; mean age = 21 years, *SD* = 1.9) took part in the present experiment after providing written informed consent. All participants had normal or corrected-to-normal visual acuity, and all reported normal color vision and no history of neurological disorders. The experiment was vetted by the local ethics committee.

3.2 Stimuli and procedure

An example of the stimuli is reported in Fig. 4. The stimuli were the same as those used in Experiment 1, except that the bars inscribed in the shapes were removed. Participants were instructed to report whether a green diamond was present or absent among green circles by pressing the ‘Z’ or ‘M’ key of the computer keyboard (counterbalanced across participants). Participants could be exposed to four different search arrays, i.e., target-present arrays with or without a distractor, and target-absent arrays with or without a distractor. Participants performed 10 blocks of 102 experimental trials, in each of which the ratio of proportions of these search arrays was 2:1:1:0.025, respectively.

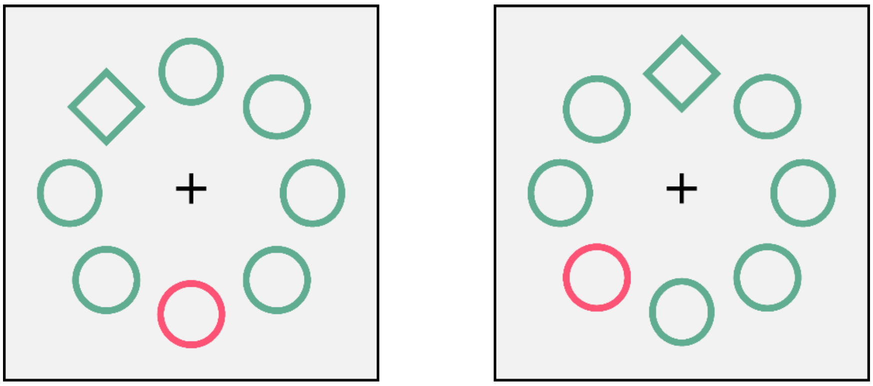

Fig. 4. Examples of search arrays used in Experiment 2. Note that, like in Experiment 1, the background against which the search stimuli were displayed was black in the experiment.

3.3 EEG pre-processing

EEG epochs contaminated by artifacts quantified in the same way as in Experiment 1 were excluded from analysis. The average percentage of rejected trials was 5.1% (ranging from 0.6 to 18.6%). The final data retention rate ranged from 92% to 96% trials across conditions. Unless otherwise reported, N2pc, PNP, Ppc, and P_D were estimated on the basis of the same time-windows as those indicated for Experiment 1.

3.4 Results

3.4.1 Behavior

RTs recorded on trials associated with an incorrect response and/or RTs exceeding three standard deviations an individual's mean RT (1.8 %) were expunged from analysis. Mean RTs were submitted to an ANOVA that considered target status (3 levels: absent vs. present in the upper visual hemifield vs. present in the lower visual hemifield) and distractor status (3 levels: absent vs. present in the upper visual hemifield vs. present in the lower visual hemifield) as within-subject factors. The ANOVA revealed a main effect of target status ($F(2, 42) = 32.6$, $p < 0.001$, $\eta_p^2 = 0.608$, $BF_{10} > 1000$), distractor status ($F(2, 42) = 15.5$, $p < 0.001$, $\eta_p^2 = 0.425$, $BF_{10} = 4.10$), and an interaction between these two factors ($F(4, 84) = 3.5$, $p = 0.022$, $\eta_p^2 = 0.141$, $BF_{01} = 8.06$). Pairwise comparisons showed that target's vertical elevation did not influence RTs when a distractor was absent (upper vs. lower hemifield: 535 vs. 543 ms, respectively; $t(21) = -1.7$, $p = 0.335$, *Cohen's* $d = -0.123$, $BF_{01} = 1.38$), and when a distractor was displayed in the upper visual hemifield (upper vs. lower hemifield: 543 vs. 555 ms, respectively; $t(21) = -2.1$, $p = 0.155$, *Cohen's* $d = -0.188$, $BF_{10} = 1.31$). However, when a distractor was displayed in the lower visual hemifield, RTs were shorter when a target was displayed in the upper than in the lower visual hemifield (upper vs. lower hemifield: 537 vs. 562 ms, respectively; $t(21) = -3.7$, $p = 0.004$, *Cohen's* $d = -0.415$, $BF_{10} = 29.97$). Participants were particularly accurate in the visual search task (range = 95.1–99.8%), and no analysis was conducted on accuracy.

3.4.2 ERL to lateral target

Fig. 5 provides a graphical summary of ERLs recorded at PO7/8 in response to the search arrays exemplified to the left of the graphs, separately for trials in which a midline distractor was present (solid ERLs) or absent (dashed ERLs), and in which a lateral target was displayed in the upper visual hemifield (upper panel) or in the lower visual hemifield (lower panel). Fig. 5 suggests that N2pc was evident for a lateral target displayed in the lower visual hemifield. Like in Experiment 1, a PNP emerged instead when a target was displayed in the upper visual hemifield. The PNP peak was however postponed (and the component more smeared) compared to the PNP found in Experiment 1. Fig. 5

also suggests that another result from Experiment 1 that was replicated in Experiment 2 was the influence of vertical elevation on N2pc, which was largely uninfluenced by whether a midline distractor was present or absent in the search array.

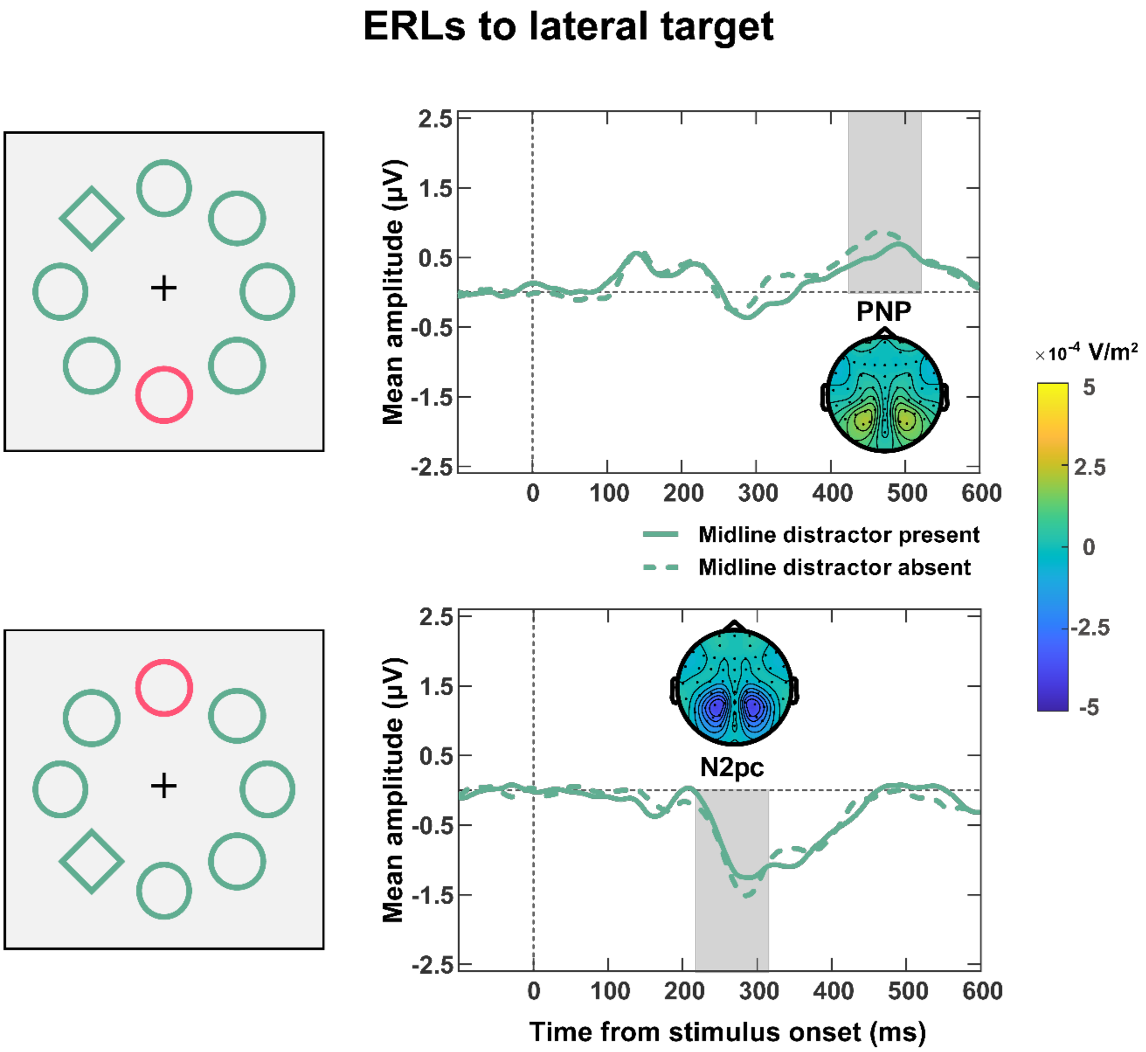

Fig. 5. ERLs (contralateral minus ipsilateral ERPs) elicited by lateral targets in Experiment 2 recorded at electrode sites PO7/8. Mean CSD maps of ERL activity (averaged across distractor-present and distractor-absent trials) in the time-windows highlighted with grey shades are reported as insets. ERLs were low-pass filtered at 15 Hz for visualization purposes.

The amplitude values recorded in the N2pc time-window (i.e., 220–320 ms) were submitted to an ANOVA that considered distractor presence (2 levels: present vs. absent), laterality (2 levels:

contralateral vs. ipsilateral), and vertical elevation (2 levels: upper vs. lower visual hemifield) as within-subject factors. The ANOVA indicated a main effect of laterality ($F(1, 21) = 9.6$, $p = 0.006$, $\eta_p^2 = 0.313$, $BF_{10} = 47.07$), of vertical elevation ($F(1, 21) = 7.4$, $p = 0.013$, $\eta_p^2 = 0.261$, $BF_{10} = 49.81$), and a significant interaction between these two factors ($F(1, 21) = 14.5$, $p < 0.001$, $\eta_p^2 = 0.409$, $BF_{10} = 26.52$). No other factor or interaction was significant (max $F = 2.4$, min $p = 0.140$). Pairwise comparisons confirmed that N2pc elicited by a target displayed in the lower visual hemifield differed from 0 µV (-0.97 µV; $t(21) = -4.1$, $p < 0.001$, *Cohen's d* = -0.888, $BF_{10} > 1000$), both when a distractor was present (-0.90 µV, $t(21) = -3.5$, $p = 0.002$, *Cohen's d* = -0.827, $BF_{10} = 19.47$) and a distractor was absent (-1.04 µV, $t(21) = -3.8$, $p = 0.001$, *Cohen's d* = -0.949, $BF_{10} = 35.64$). In contrast, N2pc did not differ from 0 µV when a target displayed in the upper visual hemifield (-0.05 µV; $t(21) = -0.3$, $p = 0.769$, *Cohen's d* = -0.045, $BF_{01} = 5.70$), both when a distractor was present (-0.08 µV, $t(21) = -0.5$, $p = 0.631$, *Cohen's d* = -0.076, $BF_{01} = 4.03$) and a distractor was absent (-0.01 µV, $t(21) = -0.1$, $p = 0.939$, *Cohen's d* = -0.013, $BF_{01} = 4.47$).

When the amplitude values of the PNP elicited by a target displayed in the upper visual hemifield were measured using the same time-window as Experiment 1 (i.e., 340–440 ms), an ANOVA failed to detect significant effects (all *F*s <= 1.0). However, an ANOVA carried on the amplitude values measured in a slightly later time-window (i.e., 420–520 ms) revealed a main effect of laterality ($F(1, 21) = 5.7$, $p = 0.026$, $\eta_p^2 = 0.213$, $BF_{10} = 1.01$), a main effect of distractor presence ($F(1, 21) = 5.3$, $p = 0.031$, $\eta_p^2 = 0.202$, $BF_{10} = 2.47$), and a significant interaction between laterality and vertical elevation ($F(1, 21) = 8.5$, $p = 0.008$, $\eta_p^2 = 0.288$, $BF_{10} = 3.35$). Pairwise comparisons confirmed that a PNP elicited by a target displayed in the upper visual hemifield differed from 0 µV (0.65 µV; $t(21) = 3.7$, $p < 0.001$, *Cohen's d* = 0.801, $BF_{10} = 123.78$), but it did not when elicited by a target displayed in the lower visual hemifield (-0.07 µV; $t(21) = -0.4$, $p = 0.704$, *Cohen's d* = -0.081, $BF_{01} = 5.53$). Further *t*-tests on whether the amplitude values of PNP were greater than 0 µV revealed that, when a target was displayed in the upper visual hemifield, the PNP differed from 0 µV both when a distractor was present (0.56 µV; $t(21) = 2.8$, $p = 0.012$, *Cohen's d* = 0.692, $BF_{10} = 8.46$) and a distractor was absent (0.74 µV; $t(21) = 3.1$, $p = 0.005$, *Cohen's d* = 0.910, $BF_{10} = 4.35$). However, PNP was clearly absent for a target displayed in the lower visual hemifield, both when a distractor was present (-0.07 µV, $t(21) = -0.4$, $p = 0.733$, *Cohen's d* = -0.079, $BF_{01} = 4.25$) and a distractor was absent (-0.06 µV, $t(21) = -0.3$, $p = 0.758$, *Cohen's d* = -0.084, $BF_{01} = 4.29$).

3.4.3 ERL to lateral distractor

Fig. 6 provides a graphical summary of ERLs recorded at PO7/8 in response to the search arrays exemplified to the left of the graphs, separately for trials in which a midline target was present (solid

ERLs) or absent (dashed ERLs), and in which a lateral distractor was displayed in the upper visual hemifield (upper panel) or in the lower visual hemifield (lower panel). Fig. 6 suggests that a lateral distractor displayed in the upper visual hemifield elicited a Ppc and a P_D peaking within the same time-window as that of Experiment 1, which was however close to nil when a lateral distractor was displayed in the lower visual hemifield. Fig. 6 also suggests that the P_D unfolded as more sustained positivity when a midline target was absent rather than when it was present. This sustained positivity elicited by a lateral distractor was independent of its vertical elevation.

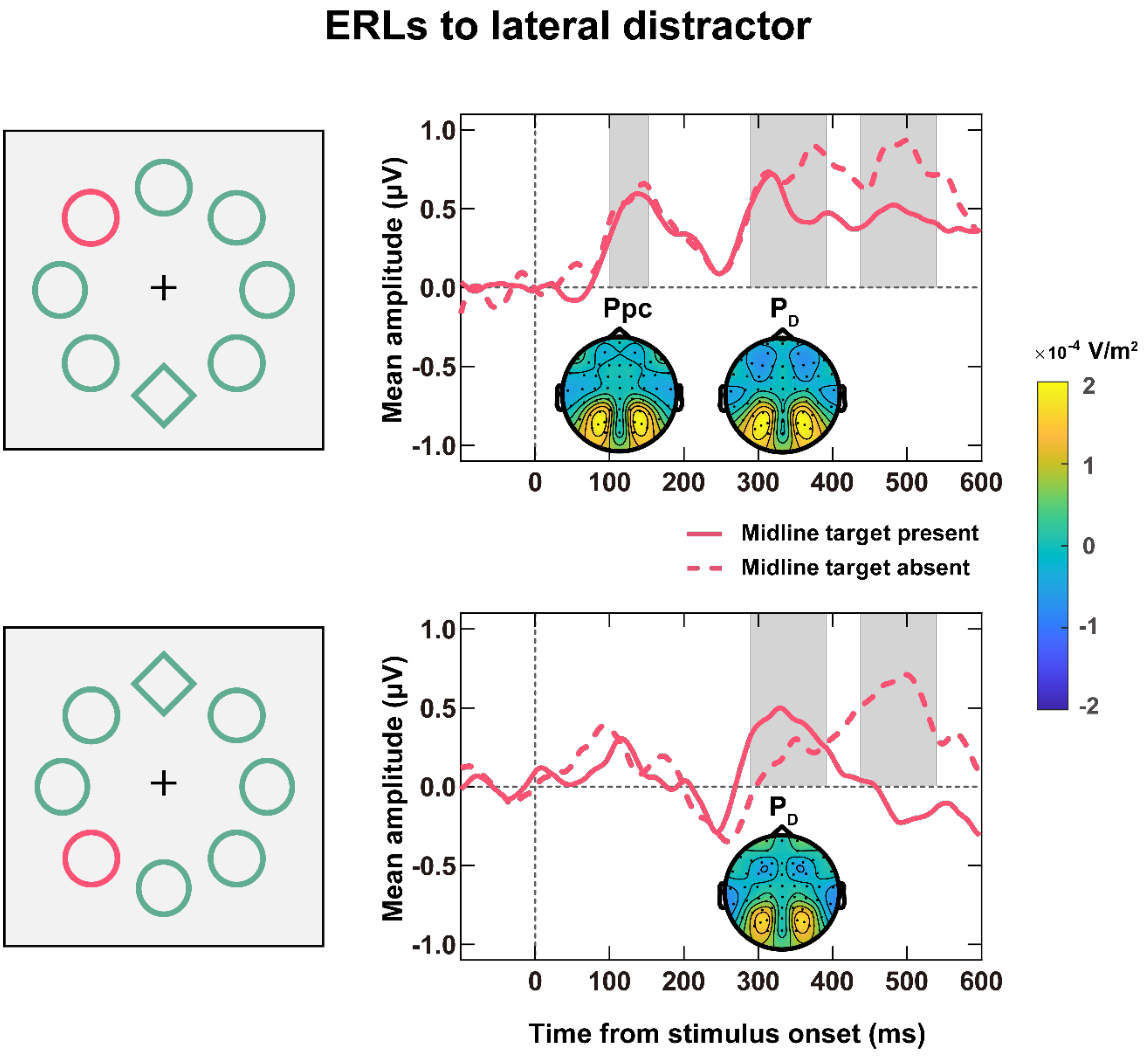

Fig. 6. ERLs (contralateral minus ipsilateral ERPs) elicited by lateral distractors in Experiment 2 recorded at electrode sites PO7/8. Mean CSD maps of ERL activity (averaged across target-present and target-absent trials) in time-windows highlighted with grey shades are reported as insets. ERLs were low-pass filtered at 15 Hz for visualization purposes.

One ANOVA was performed on the amplitude values recorded in the Ppc time-window (i.e., 100–150 ms), considering target presence (2 levels: present vs. absent), laterality (2 levels: contralateral vs. ipsilateral) and vertical elevation (2 levels: upper vs. lower visual hemifield) as within-subject factors. The ANOVA detected a main effect of laterality ($F(1, 21) = 23.6$, $p < 0.001$, $\eta_p^2 = 0.530$, $BF_{10} = 786.99$) and a significant interaction between laterality and vertical elevation ($F(1, 21) = 9.6$, $p = 0.005$, $\eta_p^2 = 0.314$, $BF_{10} = 1.21$). Pairwise comparisons confirmed that the Ppc elicited by a distractor displayed in the upper visual hemifield differed from 0 µV, both when the target was present (0.56 µV; $t(21) = 5.7$, $p < 0.001$, *Cohen's d* = 1.025, $BF_{10} > 1000$) and when it was absent (0.61 µV; $t(21) = 3.5$, $p = 0.002$, *Cohen's d* = 1.121, $BF_{10} = 18.53$). In contrast, the Ppc elicited by a distractor displayed in the lower visual hemifield did not differ from 0 µV, both when a target present (0.25 µV; $t(21) = 1.9$, $p = 0.077$, *Cohen's d* = 0.452, $BF_{01} = 1.04$), and when a target was absent (0.18 µV; $t(21) = 1.2$, $p = 0.236$, *Cohen's d* = 0.334, $BF_{01} = 2.33$).

An additional ANOVA was performed on amplitude values recorded in the time-window of the P_D (i.e., 290–390 ms). The ANOVA detected a main effect of laterality ($F(1, 21) = 15.8$, $p < 0.001$, $\eta_p^2 = 0.429$, $BF_{10} = 13.85$), and a significant interaction between laterality and vertical elevation ($F(1, 21) = 6.2$, $p = 0.021$, $\eta_p^2 = 0.228$, $BF_{01} = 2.77$). Pairwise comparisons confirmed that the P_D elicited by a distractor displayed in the upper visual hemifield differed from 0 µV, both when a target was present (0.55 µV; $t(21) = 4.0$, $p < 0.001$, *Cohen's d* = 0.683, $BF_{10} = 49.49$) and when a target was absent (0.77 µV; $t(21) = 3.4$, $p = 0.003$, *Cohen's d* = 0.956, $BF_{10} = 13.96$). The P_D elicited by a distractor displayed in the lower visual hemifield differed from 0 µV when a target was present (0.42 µV; $t(21) = 2.7$, $p = 0.015$, *Cohen's d* = 0.522, $BF_{10} = 3.64$), but not when a target was absent (0.19 µV; $t(21) = 1.1$, $p = 0.308$, *Cohen's d* = 0.233, $BF_{01} = 2.76$).

A final ANOVA was carried out on the amplitude values of the sustained positivity recorded in a later time-window (i.e., 450–550 ms). The ANOVA detected a main effect of laterality ($F(1, 21) = 15.3$, $p < 0.001$, $\eta_p^2 = 0.421$, $BF_{10} = 2.04$), of vertical elevation ($F(1, 21) = 4.5$, $p = 0.045$, $\eta_p^2 = 0.178$, $BF_{10} = 1.71$), and an interaction between laterality and target presence ($F(1, 21) = 11.5$, $p = 0.003$, $\eta_p^2 = 0.353$, $BF_{01} = 1.90$), an interaction between laterality and vertical elevation ($F(1, 21) = 6.8$, $p = 0.017$, $\eta_p^2 = 0.244$, $BF_{01} = 2.20$). No other factor or interaction was significant (max $F = 1.6$, min $p = 0.210$). Pairwise comparison revealed that the sustained positivity elicited by a distractor displayed in the upper visual hemifield differed from 0 µV, both when a target was present (0.47 µV; $t(21) = 4.6$, $p < 0.001$, *Cohen's d* = 0.644, $BF_{10} = 195.23$) and when a target was absent (0.83 µV; $t(21) = 3.8$, $p = 0.001$, *Cohen's d* = 1.133, $BF_{10} = 33.10$). In contrast, the sustained positivity elicited by a distractor displayed in the lower visual hemifield differed from 0 µV when a target was absent (0.57 µV; $t(21) = 3.1$, $p = 0.006$, *Cohen's d* = 0.780, $BF_{10} = 7.52$), but not when a target was present (-0.15 µV; $t(21) = -0.9$, $p = 0.390$, *Cohen's d* = 0.201, $BF_{01} = 3.18$).

4 General discussion

The present study examined how ERL indices of attention allocation to a searched salient target — typically held to be indexed by N2pc — and suppression of a salient distractor — typically held to be indexed by P_D — responded to vertical elevation, that is, to a manipulation which we leveraged to test whether N2pc and P_D subtended same or different neural circuits. By displaying either target or distractor along the vertical midline, we measured N2pc and P_D independently of each other while relying on a logic that was simple and straightforward. If N2pc and P_D were different manifestations of the same underlying neural circuit mapping stimuli in retinotopic spatial coordinates, we would expect qualitatively (i.e., not necessarily quantitatively) similar responses of N2pc and P_D to the manipulation of vertical elevation. If instead N2pc and P_D originated from distinct neural circuits, we would expect to observe different responses of N2pc and P_D to the manipulation of vertical elevation. As detailed in the Introduction, this logic hinged on prior assumptions about the posterior cortical origins of both N2pc and P_D, the known retinotopic organization of these cortical regions, and past reports of a tendency of N2pc and P_D to respond differently to vertical elevation in work in which vertical elevation was a factor considered in the analysis and interpretation of target-elicited and distractor-elicited ERLs [2,35–40].

The ERL results of both Experiments 1 and 2 were clear-cut in showing that a lateral target displayed in the lower visual hemifield elicited a prototypical N2pc whereas a lateral target displayed in the upper visual hemifield elicited a PNP. A lateral distractor displayed in the upper visual hemifield elicited a prototypical ‘early’ Ppc (i.e., earlier than N2pc) and a ‘late’ P_D (i.e., later than N2pc) whereas a distractor displayed in the lower visual hemifield elicited either no apparent Ppc (Experiment 1) or a P_D that more protracted when a distractor was displayed alone, that is, in a search array without a target (Experiment 2). We argue that this pattern of ERL results is incompatible with the hypothesis of a unitary neural circuit underlying N2pc and P_D processing visual input encoded in one and the same retinotopic map. This conclusion is independent of any specific neuroanatomical explanation for the root cause of vertical elevation effects on N2pc and P_D. To be clear, whether the root cause is the relative distance between the cortical sources of N2pc and P_D and parieto-occipital recording sites, as mentioned in the Introduction, or, in alternative, a change in orientation of an equivalent dipole resulting from cortical folding of the corresponding neural substrate[1] [66,67], the fact that N2pc and

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[1] Exemplary in this respect is the response to vertical elevation of the C1 component of a visual ERP, typically detected bilaterally at occipital electrode sites. C1 manifests itself as a positive ERP deflection for stimuli displayed in the lower visual hemifield and as a negative ERP deflection for stimuli displayed in the upper visual hemifield (e.g., [68,69]). The polarity reversal of the C1 component is due to the folding of V1 cortex into the calcarine fissure. Of import, the effect of vertical elevation on C1 (upper negative, lower positive) is opposite to later effects of vertical elevation (upper positive, lower negative) on N2pc found in both Experiments 1 and 2, and this finding supports past proposals of a

P_D responded in virtually opposite ways to the manipulation of vertical elevation strongly suggests that N2pc and P_D arise from different neural substrates processing visual input encoded in different retinotopic maps. This conclusion dovetails nicely with MEG work showing subtle, albeit consistent, neuroanatomical differences between the cortical sources of the magnetic equivalent of N2pc and P_D recorded using visual search designs [32,34].

One limitation of the present study is the lack of a condition where target and distractor dimensions (i.e., shape and color, respectively) were swapped, and this entails the possibility that the influence of vertical elevation could, at least in part, be due to the distinct neural substrates involved in their processing. However, a strength of the present study is that we provided a demonstration that the opposite modulation of N2pc and P_D by vertical elevation persisted even when the orientation discrimination task used in Experiment 1 was changed with a target detection task in Experiment 2. This consistency suggests that the observed effects arising from the manipulation of vertical elevation were independent of task-specific demands and a likely consequent substantial change in underlying neural circuits. This makes it less likely, in our view, that the present results can be fully explained by differences in feature-specific neural recruitment. Future studies could further dissociate these mechanisms by swapping target/distractor identities (e.g., color-defined target vs. shape-defined distractor) to explicitly test whether retinotopic biases generalize across feature dimensions. Experiment 2, in particular, reinforces our belief that N2pc and P_D reflect distinct neural circuits, as their opposing sensitivity to vertical elevation emerged independently of whether selection required fine-grained feature discrimination (Experiment 1) or mere detection (Experiment 2), dovetailing with evidence that these components can operate independently [45,46,47].

A comment is in order regarding a potential alternative hypothesis for the observed opposite vertical modulation for N2pc and P_D. One might speculate that vertical elevation might alter the topographic expression of these components. Though viable in line of principle, one should note this assumption does not align with previous research indicating distinct functional mechanisms rooted in neuroanatomical organization rather than spatial shifts in cortical activation loci. For instance, Doro et al. [2] demonstrated that when the target is displayed along the vertical midline, a bilateral N2pc (referred to as N2pcb) can be observed at posterior electrode sites. Amplitude and topography of N2pcb closely resembled that of the N2pc observed for lateral targets. Notably, both components exhibited an analogous modulation by vertical elevation, with larger N2pc/N2pcb responses for targets located in the lower visual hemifield. These results suggest that N2pc is not displaced to different electrode sites as a function of stimulus location, but rather is influenced by the retinotopic organization of the visual system. The same logic also applies to the P_D. While our results speak against

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neuroanatomical source of N2pc that extends beyond V1.

major topographic shifts induced by manipulation of vertical elevation, a more plausible hypothesis is that vertical elevation may cause neuronal generators to shift in a way that reduces their perpendicular orientation to the scalp, thereby diminishing their contribution to the recorded EEG. We confess that the present EEG data cannot entirely rule out the coexistence of both mechanisms, i.e., a displacement of neuronal sources contributing to partial amplitude changes, alongside genuine differences in neural activity. Given the limitations of scalp EEG in resolving deep or tangentially oriented sources, high-density EEG (128+ electrodes) or combined EEG-fMRI approaches would be required to definitively disentangle these different anatomical accounts. Additionally, source localization analyses could clarify whether vertical elevation modulates the strength of activity in fixed cortical generators versus recruiting distinct subregions.

A critical issue arises when considering the ERL resulting from averaging the target-elicited ERLs shown in Fig. 2 and Fig. 5 over upper and lower visual hemifields, that is, the target-elicited ERL generated by disregarding vertical elevation as a possible modulatory factor of ERL polarity. The PNP elicited by a lateral target displayed in the upper visual hemifield found in both Experiments 1 and 2 was slightly postponed relative to N2pc elicited by a lateral target displayed in the lower visual hemifield. We confess we do not have an explanation for such PNP postponement. At first blush, this finding seems compatible with findings suggesting generally less reactive responses to visual stimuli displayed in the upper hemifield than in the lower hemifield [70,71], although this may appear to be at odds with the null effect of vertical elevation on search RTs. Over and above this issue, certainly worth further investigation, such ERL would likely be characterized by a so-called polarity flip, namely, an ERL showing a negative deflection (N2pc) trailed by a positive deflection (PNP). Such a polarity flip (some instances of which have been reviewed by Gaspelin et al. [16]; see also [72]) could be taken to reflect a sequence of two processing stages, i.e., attention deployment to the target, indexed by N2pc, followed by the action of some form of terminated mechanism, indexed by PNP. The potential for this interpretation to be incorrect is non-nil in light of the present ERL results suggesting that a lateral target elicits a PNP just because of a variation in retinotopy, without necessarily implying any form of suppression. Search RTs in Experiment 1 were unaffected by target vertical elevation. Search RTs in Experiment 2 were, in fact, *shorter* when the PNP-eliciting target was displayed in the upper visual hemifield relative to when an N2pc-eliciting target was displayed in the lower visual hemifield, implying that no target suppression was underway despite PNP.

It is critical to emphasize that any claim regarding the functional nature of target-elicited positivity, such as a PNP when the target is displayed in the upper visual hemifield, cannot be made without direct comparison to the same target displayed in the lower visual hemifield, who elicits a prototypical, well-characterized N2pc. This comparison is essential, as the stark contrast between these two outcomes highlights the role of vertical elevation in modulating neural responses, and strongly suggests that vertical position alone cannot be ignored in functional interpretations. The same argument applies to distractor-elicited positivities. For instance, while a distractor displayed in the upper hemifield elicits clear and consistent P_D, this response dissipates or even vanishes entirely when the distractor is displayed in the lower hemifield. Any hypothesis regarding the functional connotation of these distractor-elicited positivities must address why these responses fail to appear for distractors in the lower hemifield. While the traditional P_D component is associated with distractor suppression, the PNP appears in conditions unrelated to distractor processing, suggesting a distinct functional origin. We propose that the PNP reflects later stages of attentional allocation or perceptual enhancement specific to target processing [29]. Such processes may involve refining the selection of task-relevant stimuli or consolidating perceptual information to support subsequent decision-making or response execution.

The opposite responses of N2pc and PNP to vertical elevation resemble the findings of Papaioannou and Luck [61], who found a progressive increase in PNP with the decrease in N2pc at the greatest horizontal eccentricity (i.e., 8°). Their findings are consistent with the idea that targets presented farther from the fovea elicit weaker N2pc responses, likely due to the reduced density of receptive fields in ventral visual areas for peripheral stimuli. In contrast, our study manipulated the vertical position of stimuli along the vertical midline, with stimuli positioned in either the upper or lower visual hemifield, both equidistant from the central fixation. A key distinction lies in the neural mechanisms called into play by horizontal and vertical shifts. While horizontal eccentricity effects arise from peripheral receptive field scarcity, vertical elevation effects stem from an anatomical separation between dorsal and ventral cortical maps. This dissociation underscores that attentional selection is constrained not only by the spatial scale of perception but also by the retinotopic organization of distinct visual pathways. In other words, this parallel suggests that both vertical and horizontal spatial constraints impose temporal costs on attentional processes, albeit through distinct cortical pathways, namely, horizontal eccentricity taxes ventral stream resolution, while vertical elevation engages dorsal-ventral anatomical and functional neural pathway segregation. Furthermore, with reference to the postponed PNP in Experiment 2 with that in Experiment 1, it is noteworthy that Papaioannou and Luck [61] found that as horizontal eccentricity increased, the polarity flip point occurred earlier, suggesting prolonged attentional resolution for stimuli requiring greater spatial integration. This explanation may apply to the postponed PNP observed in Experiment 2, where we manipulated the task by removing local features to reduce the amount of attentional dwell time on the target. The removal of these features was thought to reduce the time participants focused on individual features, similar to the decreased demand for attention associated with a more central stimulus in Papaioannou and Luck's study.

Notably, the temporal and spatial overlap between the PNP and the P_D component prompts further consideration of their potential relationship. If the PNP shares characteristics with the P_D, this raises the possibility that P_D-like positivities are not exclusively elicited by distractors but could also arise during target-related processing under certain conditions. This hypothesis aligns with previous findings suggesting that the functional roles of ERPs are influenced by task demands and stimulus context [15,16]. Future research is needed to delineate the boundaries between these components and establish whether the PNP and P_D share a common neural substrate or represent functionally distinct processes. In sum, ERL polarity flips are not uncommon in the literature (e.g., [29][2]) and this compels us to reiterate an invitation we made in a previous attempt at distilling the polarity of ERLs typically recorded in visual search experiments to always take vertical elevation into account lest to incur potentially erroneous interpretation of ERL polarity flips [39].

One issue that deserves comment is the apparent paradox of observing a hallmark of distractor suppression at the ERP level of analysis (i.e., P_D) accompanied by evident and persistent distractor costs at the RT level of analysis. As the recent review from Gaspelin et al. [16] extensively demonstrates, distractor presence costs in reaction times are consistently observed across studies (e.g., [19,73,74]). However, it is also important to note that distractor presence costs tend to be smaller in trials associated with fast than long RTs. This finding suggests that successful proactive suppression — indexed by the early P_D — enables more efficient target processing, whereas residual costs predominantly arise in trials associated with long RTs where suppression mechanisms likely failed, thereby leading to delayed or less efficient target processing. Importantly, the persistence of these costs reinforces the idea that while suppression is often successful, it is not infallible. This temporal pattern — where smaller distractor costs align with faster responses — highlights the variability and dynamic interplay between attentional capture and suppression processes in visual search tasks. That is, suppression, much like attentional activation [75], is not a binary process but operates on a continuum, modulated by factors like stimulus history, task demands, and neural efficiency. Even in tasks where suppression is generally effective (e.g., repeated lab paradigms), residual distractor costs persist, reflecting the inherent fallibility of attentional control [76]. By considering both the RT data and the electrophysiological results, these findings underscore how suppression operates efficiently under many circumstances but still allows for occasional lapses, which manifest as measurable distractor costs in behavior.

The present results have implications for models proposed to explain how attention is controlled when salient targets and distractors compete for attentional resources. Stimulus-driven models claim that a salient distractor automatically captures attention [77]. Using an additional-singleton paradigm

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[2] Do note that Sawaki et al. [29] employed a paradigm in which visual stimuli were aligned to the horizontal midline of a computer monitor intersecting a central fixation point. Their interpretation of the negative/positive polarity flip was therefore devoid of risks associated with confounding polarity reversal owing to variations in retinotopy and positive/negative ERL functional significance.

conceptually identical to that used in the present investigation, Theeuwes ([1]; see also [78]) had participants judge the orientation of a bar tilt inscribed in a circle displayed among diamonds, with or without a uniquely colored distractor. RTs were longer when the distractor was present than when it was absent. The distractor-induced RT slowing was interpreted as evidence that attention was automatically allocated to the distractor, thus slowing the allocation of attention to the target. Signal suppression models claim that a salient distractor, like a salient target, automatically elicits an attend-to-me signal (i.e., one that has the potential to attract attention), but that this signal can be proactively suppressed by top-down inhibitory mechanisms [14,15,17,79,80]. Gaspelin, Leonard, and Luck [81] used an additional-singleton paradigm to track the oculomotor responses of participants instructed to search for a diamond among circles with or without a uniquely colored distractor. When not correctly directed to the target, gaze shifts were less frequently directed to the distractor than to any other circle in the search display. This so-called oculomotor suppression effect suggests that a salient distractor can be proactively suppressed to allow efficient allocation of attention to the target.

Evidence for proactive distractor suppression has so far been provided by ERL studies showing that a lateral distractor elicits an early P_D and either no corresponding N2pc or an N2pc that temporally follows P_D, suggesting that a distractor can indeed be suppressed prior to attentional allocation to a target (see review by [46]; see also [15,18,45,47,72,80,82]). In this vein, the results of Experiment 1 seem to favor a reactive suppression interpretation of the present P_D by showing that a distractor-elicited P_D was observed in a later time-window than N2pc (i.e., in a 290–390 ms time-window), which was more evident when a lateral distractor was displayed in the upper than in the lower visual hemifield. Experiment 2, on the other hand, provides a qualification to the term 'active' (as referred to suppression) that is more cogent because it goes beyond the relative timing of distractor-elicited P_D and target-elicited N2pc. If distractor suppression is preset to be active for a search array containing a distractor, then it would not be implausible to assume that the stimulus eliciting suppression is a distractor *regardless of whether a target is present or absent in the search array*. The ERL results of Experiment 2 were important and unambiguous in these respects, because a distractor-evoked P_D, which was particularly pronounced when the distractor was displayed in the upper visual hemifield, was observed both in target-present and target-absent trials. Thus, taken together, the ERL results of Experiments 1 and 2 strongly suggest that suppression of a distractor and attention allocation to a target are not only likely to be implemented in different neural circuits but also in functionally independent processing stages.

Other results of potential interest in the present study emerged from the comparison between Experiments 1 and 2. Whereas target-elicited ERLs were very similar between Experiments 1 and 2 in terms of N2pc timing and polarity reversal due to the manipulation of vertical elevation, distractor-elicited ERLs differed in one obvious aspect, in that only in Experiment 2 was the early Ppc trailed by a P_D, which, in addition, 'smeared' in the form of sustained positivity when elicited by a lateral distractor displayed alone, without a concomitant target. Crucially, the P_D and sustained positivity showed distinct patterns in the lower visual hemifield. While P_D was exclusively elicited during target-present trials, the sustained positivity was specifically generated during target-absent trials. The observed dissociation in their vertical sensitivity profiles suggested that this late positive complex may reflect more general attentional processing activity but not merely distractor suppression. Late positive ERL deflections similar to those found in the present investigation are not uncommon in the visual search literature and have been interpreted in a variety of ways. A late P_D may, for instance, reflect a reactive shift of attention away from the distractor [83]. In this framework, the particularly late and protracted P_D in target-absent trials found in Experiment 2 can be ascribed to the strong signal produced by a distractor displayed as a unique singleton (without concomitant target singleton), which was more likely to cause such reactive shift. Others have proposed that a subcomponent of late positive ERLs in visual search is influenced by response selection [84], based on the positive correlation between search RTs and timing (and smearing) of P_D. The selection of ipsilateral and contralateral responses to a target in two-alternative forced-choice tasks has also been shown to cause a late positivity contralateral to a salient distractor [85]. RTs in Experiment 2 were in fact generally shorter than RTs in Experiment 1, and one possibility is that a response-related subcomponent arising as late P_D overlapped to a greater extent with processing subtended with stimulus encoding and consequent attention dynamics in Experiment 2. This proposal aligns closely with the findings of Töllner, Rangelov, and Müller [86], who demonstrated that the timing of the N2pc (referred to as PCN in their study) remained constant across distinct visual-search tasks (i.e., localization, detection, discrimination, and compound), whereas the lateralized readiness potential (LRP), reflecting motor-response decisions, varied systematically with task demands. Critically, they concluded that only pre-attentive selection processes generalize across task sets, while post-selective stages — such as response selection and execution — are highly dependent on task-specific requirements (e.g., depth of feature analysis, S-R mapping complexity). The divergence in the P_D — specifically, its interaction with target presence in Experiment 2 — thus echoes Töllner et al.'s observation of task-dependent LRP modulation. The late positivity complex likely reflects processes downstream of focal attention, such as reactive distractor suppression or response competition resolution, which are sensitive to contextual factors like target prevalence and distractor salience. Together, these findings underscore the necessity of dissociating early selection mechanisms from later post-selective processes in both theoretical and experimental designs. We suggest that future work should further explore how vertical spatial attention and task set interact to shape these dynamic neural processes. All in all, it is however hard for us to see this difference between Experiments 1 and 2 as a threat to the main argument and conclusion concerning the neural and functional separability of processing index by N2pc and P_D.

Conclusions

To sum up, we have shown that vertical elevation is key for distinguishing two complementary processes involved in scanning the visual environment in search for a target object, namely, attention allocation to a target, indexed by N2pc, and suppression of a salient distractor, indexed by P_D. The results of the present investigation contribute to the growing body of literature on attentional control by suggesting that target selection and distractor suppression can be distinguished both neurally and functionally.

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