A bilateral N2pc (N2pcb) component is elicited by search targets displayed on the vertical midline.

Mattia Doro[1], Francesco Bellini[1], Sabrina Brigadoi[1], Martin Eimer[2], Roberto Dell'Acqua[1,3*]

[1] *Department of Developmental Psychology, University of Padova*

[2] *Department of Psychological Sciences, Birkbeck University of London*

[3] *Padova Neuroscience Center, University of Padova*

*Correspondence to:

Roberto Dell'Acqua

Department of Developmental Psychology and Socialization

Via Venezia, 8

35131 Padova, Italy

Email: dar@unipd.it

Abstract

The study of visually-elicited event-related potentials (ERPs) detected at posterior recording sites during visual search has enormously advanced our knowledge about how and when visuo-spatial attention locks onto one or more laterally presented target objects. The N2pc component to lateral targets has been pivotal to further our understanding of the mechanisms and time-course of target selection in visual search. However, the N2pc cannot track visuo-spatial attention deployment to targets displayed along the vertical midline. Here, we introduce a new ERP marker (N2pcb component) that is elicited during the selection of such midline targets. In line with retinal and callosal projections from striate to ventral extrastriate cortex, this component reflects an enhanced negativity elicited by midline targets over both posterior hemispheres. By comparing the attentional selection of lateral and midline targets in a singleton search condition and a feature search condition, we show that the N2pcb is triggered at the same time as the N2pc to lateral targets, and shows the same onset latency difference between singleton and feature search. We conclude that the N2pcb and N2pc components reflect the same attentional target selection processes in visual search.

Keywords: Visual search, N2pc, midline targets.

Introduction

A major turning point in the long history of studies on visual search has been the advent of the event-related potential (ERP) approach to the analysis of electrophysiological data (e.g., Mangun, 2013). Owing to its temporal resolution, the ERP approach has allowed researchers to track with millisecond precision the time-course of mental events that occur substantially earlier than a typical target present/absent response. The ERP component that has proved most informative in answering at least some of the long-standing questions about how visual search is accomplished under diverse conditions has been N2pc. This component reflects an enhanced negativity usually unfolding in a 200–300 ms post-stimulus time-window at parieto-occipital sites contralateral to the visual hemifield in which a search target is displayed (e.g., Luck & Hillyard, 1994; Eimer, 1996). The N2pc component is generally interpreted as an electrophysiological marker of the attentional selection of candidate target objects in visual search displays (see Luck, 2012; Eimer, 2014, for details). Measuring the N2pc in visual search tasks can provide novel insights into the time course of such target selection processes. Consider, for instance, the assumption of a subclass of attention models (e.g., Treisman & Gelade, 1980) that the function relating reaction times (RTs) to the number of searched items, the so-called search slope, reflects the speed with which attention travels across a visual display until a target is (or is not) found. Though plausible, the underlying question is truly whether the human brain is endowed with neural mechanisms enabling this serial search strategy. ERP evidence compatible with this assumption has been provided by Woodman and Luck (2003), who displayed two distinct red shapes among grey shapes, and instructed subjects to search for a specific shape between the red ones. One red shape was displayed in one visual hemifield nearby fixation, to prioritize it for search. The second red shape was displayed in the

opposite visual field and farther from fixation. The ERP results were clear-cut in revealing a first N2pc contralateral to the red shape close to fixation, followed 100 ms later by a second N2pc contralateral to the red shape farther from fixation, suggesting that attention is deployed serially to the two red shapes in this design.

Consider also the long raging debate about how attention is deployed to successive targets displayed in distinct spatial locations, the underlying question being whether the attention focus is unitary and allocated serially to each target in turn in this condition, or can be split and allocated separately and independently to two or more targets (Jans, Peters, & De Weerd, 2010). To answer this question, Eimer and Grubert (2014) exposed subjects to two successively displayed pairs of colored alphanumeric characters arrayed on opposite sides of fixation. The stimulus onset asynchrony (SOA) between the successive pairs was varied in a 10–100 ms range, and subjects had to report the identity of two sequential characters in a given color. The condition of interest was when the two targets were displayed on opposite visual hemifields, a condition in which Eimer and Grubert (2014) observed two sequential N2pcs, the first contralateral to the first target and the second contralateral to the second target. Of relevance, the latency difference between the two N2pcs matched the SOA between the sequential targets, even at 10 ms SOA, suggesting that attention can indeed be separately and independently deployed to two sequential targets (see Benavides-Varela, Basso Moro, et al., 2018, for a similar conclusion using static multi-target displays).

The two seminal N2pc studies succinctly summarized above illustrate a common feature of all studies employing N2pc to track visual attention. In most visual search studies that measured N2pc components, targets are usually displayed laterally relative to fixation and embedded in sensory balanced multi-element arrays of distractors (but see Hickey, Di

Lollo, & McDonald, 2009; Mazza, Turatto, & Caramazza, 2009b, for exceptions). This is done because the spatial information conveyed by N2pc is limited to activation differences between posterior cortical hemispheres and, in fact, parametrically estimated as the difference between ERPs recorded contralaterally and ipsilaterally relative to the visual field containing the target. For this reason, the N2pc is deemed unsuited to track attention shifts within the same visual hemifield and, importantly for the present context, is also practically blind to attention deployment to targets displayed along the vertical (i.e., sagittal) midline. Midline targets project to both posterior cerebral hemispheres, as they fall in a narrow strip of the visual space where the receptive fields of homologous striate neurons in each occipital hemisphere marginally overlap (Wandell, Dumoulin, & Brewer, 2007; Zeki, 1993) and are bilaterally connected by particularly thick and myelinated axonal fibers that traverse the caudal part of the corpus callosum (Innocenti 1986; Nakamura, Chaumon, Klijn, & Innocenti, 2007). For this reason, attentional responses to midline targets cannot be measured with N2pc components computed by subtracting ipsilateral from contralateral ERPs, although different EEG analysis methods have been effectively used to track visuo-spatial attention dynamics affecting midline targets (e.g., Fahrenfort, Grubert, Olivers, & Eimer, 2017).

Imagine a situation analogous to those typically designed to monitor N2pc. When a target is lateralized, it is safe to say that the contralateral posterior hemisphere receives sensory input predominantly consisting of target and surrounding distractors, whereas the opposite hemisphere receives input consisting of just distractors. In this case, an N2pc — an increment in negativity in the N2 range recorded over the posterior scalp contralateral to the target — would obviously be expected. Imagine however a target displayed along the vertical midline in an otherwise analogous visual display. As argued above, the target

would be represented bilaterally in both posterior cerebral hemispheres, each of which would also receive input separately from contralateral distractors. In principle, this target would be expected to trigger a bilateral N2pc, that is, a bilateral increment in negativity in the N2 range recorded over the posterior scalp. Because each posterior hemisphere would separately and independently react to a pattern of stimuli (i.e., target plus contralateral distractors) equivalent to that received by the contralateral hemisphere when a target is lateralized, the amplitude and latency of this bilateral component should not differ from the contralateral portion of a typical N2pc elicited by a lateralized target. We propose to label this component N2pcb, where the added 'b' in the component's acronym stays for 'bilateral.'[1]

To test whether this hypothetical N2pcb component does actually exist, we exposed participants to circular arrays of colored disks arranged at equal retinal eccentricity around fixation, and asked them to perform, in different blocks of trials, two types of visual search tasks while recording EEG. Participants alternated between blocks of feature search, in which a disk in a pre-specified (target) color had to be searched among equally salient and differently colored disks, and blocks of singleton search, in which a colored disk had to be detected among less salient and homogeneously colored grey disks. In both feature and singleton search blocks, a target, when present, was displayed either in one of the lateral positions to the left or right of fixation, or in one of the positions along the vertical midline

[1] Replacing the 'c' in N2pc with a 'b' so as to refer to this component as "N2pb" would have perhaps appeared more natural to some readers. However, an ERP component labelled N2pb has already been described in a prior study by Luck and Hillyard (1994), who use this label to refer to a posterior bilateral negativity, which differs in terms of functional origin and properties from the N2pc. The acronym N2pcb is intended to avoid any possible confusion between these different ERP components.

(above/below fixation). The N2pc to lateral targets was computed in the usual way, by comparing contralateral and ipsilateral ERPs. For midline targets, ERPs measured at lateral posterior electrodes over the left and right hemisphere were collapsed, and compared to the ERPs elicited by lateral targets at corresponding contralateral and ipsilateral electrodes. If midline targets elicit a bilateral negativity, the ERP waveforms observed during the N2pc time window for these targets should be more negative than the ipsilateral ERPs triggered by lateral targets, but should not differ from contralateral ERPs. Therefore, we quantified the hypothetical N2pcb component by subtracting ipsilateral ERPs for lateral targets from bilateral ERPs to midline targets.

While this analysis method can potentially reveal the presence of an N2pcb component to midline targets that reflects the same attentional selection processes than the N2pc to lateral targets, it is important to note that a bilateral negativity to targets presented on the midline could in principle also reflect processes that are not exclusively linked to target selection (see the Discussion section for further details). It is therefore essential to demonstrate that the hypothetical N2pcb component derived by this method shows the same sensitivity as the N2pc to factors that affect the speed with which search targets can be selected. For this reason, we interleaved blocks of feature search, in which target and distractors were equally salient, with blocks of singleton search, in which all distractors were homogeneously grey and the target was a salient color singleton. Search for such unique feature singleton targets presented together with uniform distractors is typically faster than search for non-unique targets that appear among heterogeneous distractors, and this is also reflected by corresponding N2pc onset latency differences. A number of previous studies have shown that N2pc tends to emerge earlier for singleton targets than for feature targets (e.g., Callahan-Flintoft & Wyble, 2017; Feldmann-Wüstefeld & Schubö,

2015; Mazza, Turatto, & Caramazza, 2009a). The same result was also expected for the N2pc to lateral targets in the present study, which should be triggered earlier in singleton search as compared to feature search blocks. The critical question was whether the N2pcb component, calculated as described earlier, would show the same onset latency difference between these two types of blocks. If the N2pcb elicited by midline targets reflects the same attentional target selection process as the N2pc elicited by lateralized targets, this component should also emerge earlier during singleton search, and the N2pcb onset latency difference between singleton and feature search should be equivalent to the onset latency difference observed for the N2pc component.

Method

Participants

Twelve participants (6 males; mean age = 31 years, SD = 6 years) took part in the present experiment. All participants had normal or corrected-to-normal vision. Written informed consent was obtained for all participants. The experiment was approved by the local ethics committee.

Stimuli and procedure

An example of the stimuli and a schematic illustration of the sequence of events on a trial in the singleton search condition and in the feature search condition are shown in Figure 1. Visual arrays composed of eight colored disks (radius = .5° of visual angle) regularly spaced at equidistant (3.5° of visual angle) locations from fixation were displayed against a black background (CIE coordinates: 0.174/0.005; luminance: 0.2 cd/m^2) of a 25” LCD computer monitor with 100 Hz refresh rate, at a viewing distance of about 100 cm.

Two positions were located along the vertical midline (i.e., top and bottom positions), whereas the other six positions were symmetrically located to the left/right of fixation. The colors used were equiluminant (luminance: 10.5 cd/m^2) and relative CIE coordinates were blue (0.616/0.338), brown (0.505/0.412), cyan (0.211/0.309), lilac (0.478/0.161), orange (0.518/0.453), pink (0.302/0.271), red (0.217/0.109), green (0.261/0.558), or yellow (0.399/0.476). The colors used to define the target disk could be either red, green, or yellow with equal probability, and each participant was informed about the target color at the beginning of each block. Participants had to report the presence or the absence of the target-color disk by pressing, as fast and accurately as possible, one of two keys of the numeric keypad of the computer keyboard (i.e., '1' or '2'), using the index or middle finger, respectively, of their right hand. The response mapping was counterbalanced across participants. Each participant alternated between singleton search and feature search blocks, for a total of 10 blocks of 96 trials each. The starting search block was counterbalanced across participants. Distractor colors varied depending on the search condition. In singleton search blocks, all distractors were grey disks (0.288/0.316), whereas in feature search blocks the distractor colors were chosen among the set of non-target colors.

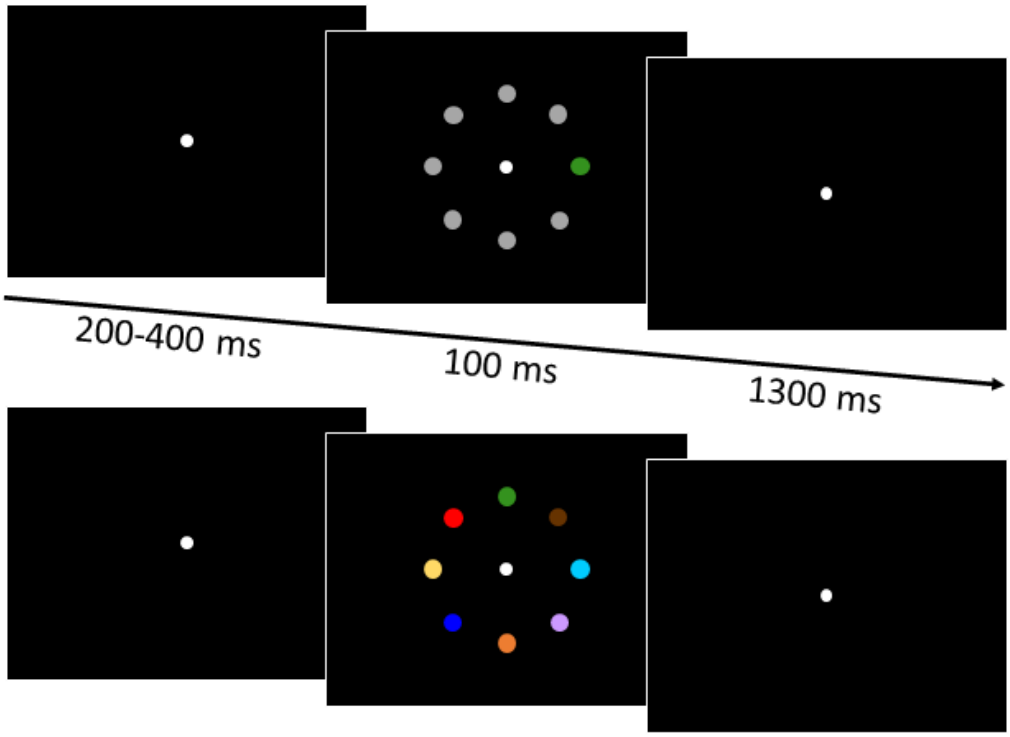

Figure 1. Schematic of the experimental paradigm employed for singleton search (upper panels) and for feature search (lower panels). Both are examples of target present trials, in which the target — the green disk — is displayed in a lateral position in singleton search, and in a midline position in feature search.

Each trial began with the presentation of a fixation point for a randomly jittered interval of 200–400 ms, followed by the presentation of the visual search array, displayed for 100 ms. Targets were presented on one third of all trials in one of the two positions along the vertical midline (i.e., above/below fixation), on another third of trials in one of the three possible lateral positions (to the left/right of fixation), or targets were absent in the other third of trials. The maximum time for responding was 1300 ms. Participants were instructed to keep central fixation throughout each trial and respond as fast and accurately

as possible. To familiarize with the task in both search block types, 6 practice trials were performed at the beginning of the first two blocks.

EEG recording and pre-processing

EEG was recorded continuously from 27 scalp electrodes placed on an elastic cap according to the International 10-10 system position (Fpz, F7, F8, F3, F4, Fz, FC5, FC6, T7, T8, C3, C4, Cz, CP5, CP6, P9, P10, P7, P8, P3, P4, Pz, PO7, PO8, PO9, PO10, and Oz), referenced to the left earlobe. Horizontal electrooculogram (HEOG) activity was recorded from two electrodes positioned on the outer canthi of both eyes. All electrode impedances were kept below 5 KΩ. The EEG activity was amplified, low-pass filtered at 40 Hz, digitized at a sampling rate of 500 Hz, and then referenced offline to the average of the left and right earlobes. Continuous EEG was segmented in epochs starting 100 ms before the visual array onset and ending 500 ms after. Epochs were baseline corrected by using the average activity in the time interval starting from -100 ms and the visual array onset. Trials contaminated by artifacts (i.e., eye-blinks and vertical eye movements exceeding 60 μV at Fpz, horizontal eye movements exceeding 30 μV in the HEOG channel or muscular artifacts exceeding 80 μV in all other channels) were excluded from EEG analyses by means of a sliding window approach with steps of 10 ms (e.g., Adam, Robison, & Vogel, 2018).

EEG epochs were then averaged to obtain four distinct ERPs in each search condition, that is, the contralateral and the ipsilateral portions of the N2pc elicited by lateral targets (i.e., the average between PO7 activity elicited by a right presented target and PO8 activity elicited by a left presented target for the former, and vice versa for the latter), and a bilateral ERP (obtained by averaging the activity of PO7 and PO8) for both midline targets

and target absent trials. The amplitude of N2 components of these averaged ERPs was estimated in a 200–300 ms interval from the onset of the visual search array.

The mean amplitude of the N2pc elicited by lateral targets was computed as the subtraction of the ipsilateral activity from the contralateral activity. The mean amplitude of the N2pcb elicited by midline targets was computed as the subtraction of the ipsilateral activity elicited by lateralized targets from the averaged bilateral activity elicited by a midline target. The mean latency of the subtracted N2pc and N2pcb components was estimated using the jackknife approach (Kiesel, Miller, Jolicœur, & Brisson, 2008), correcting *F*, *t* and *p* values using the solution proposed by Miller, Patterson, and Ulrich (1998). Corrected values are indicated as F_c and t_c, respectively. Onset latency values were calculated as the time-point when individual jackknife waveforms reached the absolute threshold of -1 µV. Greenhouse-Geisser adjustments were applied on *p* values when appropriate and all the *t* tests were corrected using the false-discovery rate method (Benjamini & Hochberg, 1995). Mean amplitudes of subtracted N2pc and N2pcb were also compared by means of mixed models. Bayes factors (Bf_{01}) have been reported when an estimate of the relative probability of a result under the null hypothesis against the probability of the result under each of the possible alternative hypotheses was appropriate.

Results

EEG and behavioral data from all participants were retained in the following analyses, since no participant reached the 50% of discarded trials due to EEG artifacts, which was the only criterion adopted for exclusion.

Behavior

Participants were highly accurate in both search tasks, reaching a mean accuracy level of 96% (range: 94% to 100%). Given the low frequency of response errors, the behavioral analyses considered only correct reaction times (RTs) shorter than 1300 ms.

A bar-plot summarizing the mean RTs is reported in Figure 2. Mean RTs were submitted to a 2 × 3 ANOVA considering search condition (singleton search vs. feature search) and target condition (lateral vs. midline vs. absent) as within-subject factors.

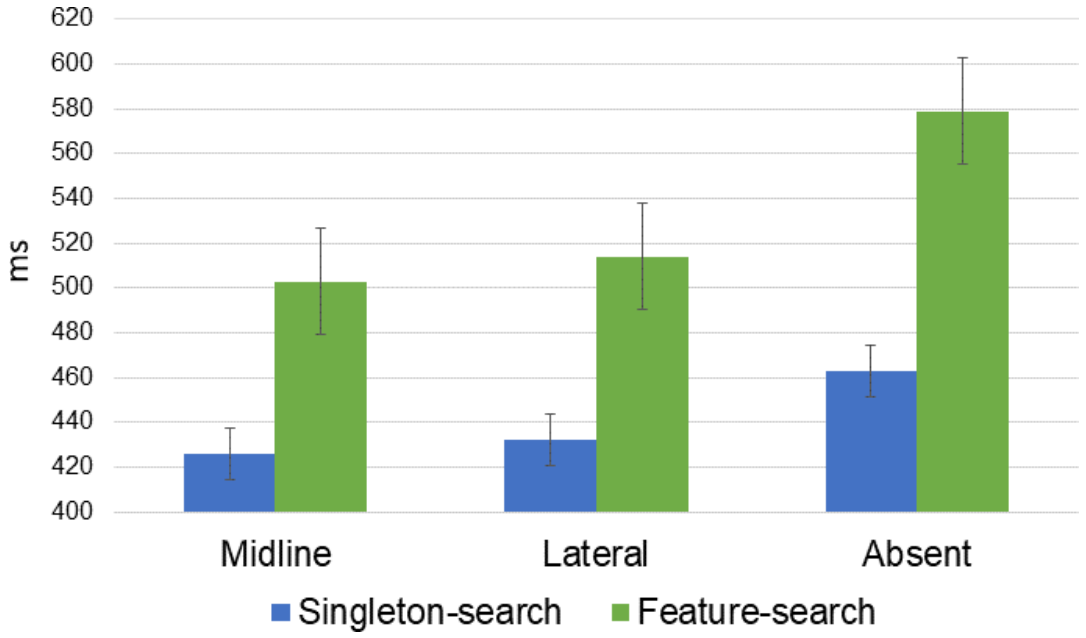

Figure 2. Mean RTs for singleton search and feature search as a function of target presence (midline vs. lateral) vs. absence. Error bars represent standard error.

As Figure 2 suggests, participants were generally faster in singleton search compared to feature search ($F(1, 11) = 112.8$, $\eta_p^2 = .911$, $p < .001$), and faster in detecting the presence of a target (i.e., midline and lateral) rather than its absence ($F(2, 11) = 59.1$, $\eta_p^2 = .843$, $p < .001$). These two effects combined non-linearly ($F(2, 22) = 10.3$, $\eta_p^2 = .483$, $p < .001$), reflecting the fact that RT differences between singleton and feature search were

largest on target-absent trials (see Figure 2). To identify possible RT differences on target-present trials with targets at lateral versus midline positions, a further a 2 × 2 ANOVA was carried out, excluding the RT data from target-absent trials, and including the factors search condition and target position (lateral, midline). A main effect of search condition ($F(1, 11) = 69.5$, $\eta_p^2 = .863$, $p < .001$) confirmed that participants were faster in singleton search relative to feature search. There was also a main effect of target position ($F(1, 11) = 8.4$, $\eta_p^2 = .464$, $p = .014$), as participants were faster in detecting a midline target compared to a lateral target (see Figure 2). The interaction between these factors was not significant ($F(1, 11) = .4$, $p = .524$).

ERPs in the singleton and feature search conditions

Figure 3 shows ERPs elicited at PO7/8 in response to lateral targets (separately for electrodes ipsilateral and contralateral to the side of these targets), as well as for midline targets and target-absent trials (both collapsed across PO7/8). ERPs are presented separately for the singleton search condition (top panel) and the feature search condition (bottom panel). Following the presentation of a lateral target, a greater negativity was recorded at contralateral sites compared to ipsilateral sites in both singleton search (1.11 µV vs. 2.12 µV, respectively; $t(11) = -3.3$, $p = .025$) and feature search (1.17 µV vs. 2.21 µV, respectively; $t(11) = 6.1$, $p = .005$), confirming that reliable N2pcs were present in both search conditions. Following the presentation of a midline target, the bilateral negativity at PO7/8 was more pronounced than the negativity recorded ipsilaterally in response to lateral targets in both singleton search (.92 µV vs. 2.12 µV, respectively; $t(11) = -2.70$, $p = .04$) and feature search (.69 µV vs. 2.21 µV, respectively; $t(11) = 3.3$, $p = .025$), suggesting the presence of a reliable N2pcb component for midline targets. In line with this interpretation,

there were no significant differences between contralateral ERPs elicited by lateral targets and bilateral ERPs for midline targets for either singleton or feature search in the N2pc time window (black versus green lines in Figure 3; $t(11) < 1$, both $p > .351$). When the target was absent, a bilateral negativity was elicited specifically in the singleton search condition during the N2pc time window. Here, ERP mean amplitudes were reliably more negative for target-absent trials relative to bilateral ERPs for midline targets and contralateral and ipsilateral ERPs for lateral targets (all $t(11) > 2.9$, all $ps < .03$). In the feature search condition, there was no such enhanced negativity for target-absent trials relative to bilateral ERPs for midline targets and contralateral ERPs for lateral targets (both $t(11) < 1.5$, both $p > .181$). The difference between the ipsilateral ERP for lateral targets and the bilateral ERP for target-absent trials was significant ($t(11) = 4.0$, $p = .010$).

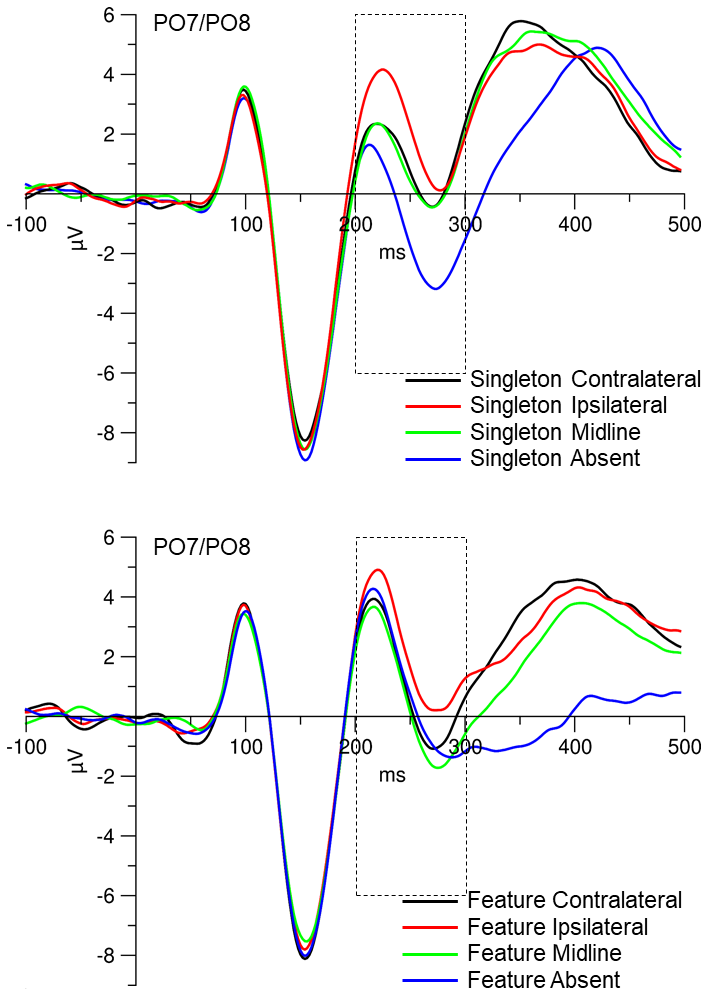

Figure 3. ERPs elicited at electrodes PO7/8 in the singleton (top) and feature (bottom) search conditions. The area delimited by the dashed-line rectangles in both graphs indicates the time-window used for N2pc/N2pcb amplitude analyses.

Analyses of N2pc and N2pcb difference waveforms

Figure 4 shows N2pc and N2pcb difference waveforms (N2pc: red lines; N2pcb: black lines) observed in the singleton search condition (solid lines) and the feature search condition (dashed lines). Figure 5 shows the corresponding scalp topographies. Figure 4 suggests that N2pc and N2pcb components were similar in terms of amplitude, and that both components emerged earlier in the singleton search condition relative to the feature

search condition. Figure 5 suggests a substantial overlap of the voltage distribution of N2pc and N2pcb over the posterior scalp.

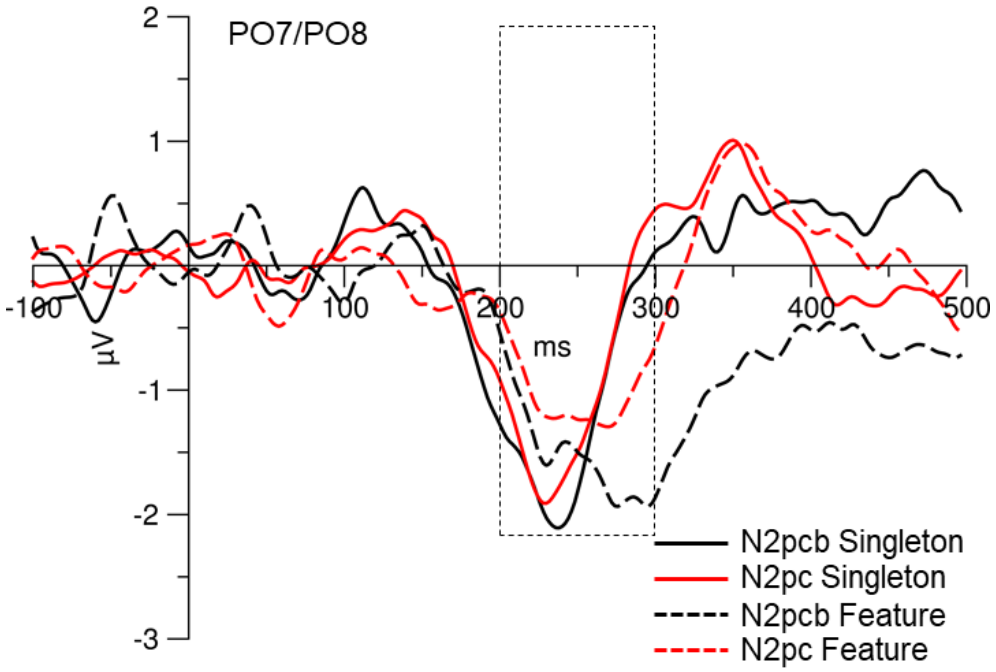

Figure 4. N2pc and N2pcb difference waveforms for the singleton and feature search conditions. The area delimited by the dashed-line rectangles in both graphs indicates the time-window considered for ERP amplitude analyses.

The visual impression of similarity between N2pc and N2pcb was confirmed by separate analyses of N2pc/N2pcb amplitudes and onset latencies. The mean amplitudes of N2pc and N2pcb difference waveforms were submitted to a 2 × 2 ANOVA, with search condition (singleton search vs. feature search) and component (N2pc vs. N2pcb) as within-subjects factors. No main effects or interaction emerged (max $F(1, 11) = .63$, min $p = .44$). Mixed model comparison analysis corroborated this important null result (min Bf_{01} =

2.468), indicating positive evidence of the null model compared to all the possible models which considered the search condition, the component, and their interaction. This suggests that there were no amplitude differences between N2pc and N2pcb components, and also that both components did not differ in size between the singleton and feature search conditions.

An analogous 2 × 2 ANOVA was carried out for the onset latencies of N2pc and N2pcb components, as determined by jackknife-based procedures (see Methods for details). There was a significant main effect of search condition ($F_c(1, 11) = 17.4$, $\eta_p^2 = .994$, $p = .002$), reflecting the fact that these components were triggered earlier in singleton search compared to feature search. Critically, there was no interaction between search condition and component for onset latencies ($F_c(1, 11) = .8$, $p = .390$), suggesting that the onset delay for feature versus singleton search was equally present for the N2pc and N2pcb. Follow-up analyses demonstrated that this onset latency difference between singleton and feature search was reliably present both for the N2pc (178 vs. 206 ms, respectively; $t_c(11) = 3.2$, $p = .018$) and for N2pcb (180 vs. 198 ms, respectively; $t_c(11) = 2.5$, $p = .029$). There was also no reliable main effect of component ($F_c(1, 11) = .3$, $p = .595$), indicating that N2pc and N2pcb components did not differ in terms of their onset latencies. For the sake of symmetry with the amplitude analysis, it would have been desirable to confirm this result with mixed models. Unfortunately, this was not possible, due to the absence in the literature of a proposal to correct the *Bf* estimated with jackknifed data, in line with the *F* and *t* correction (Miller et al., 1998).

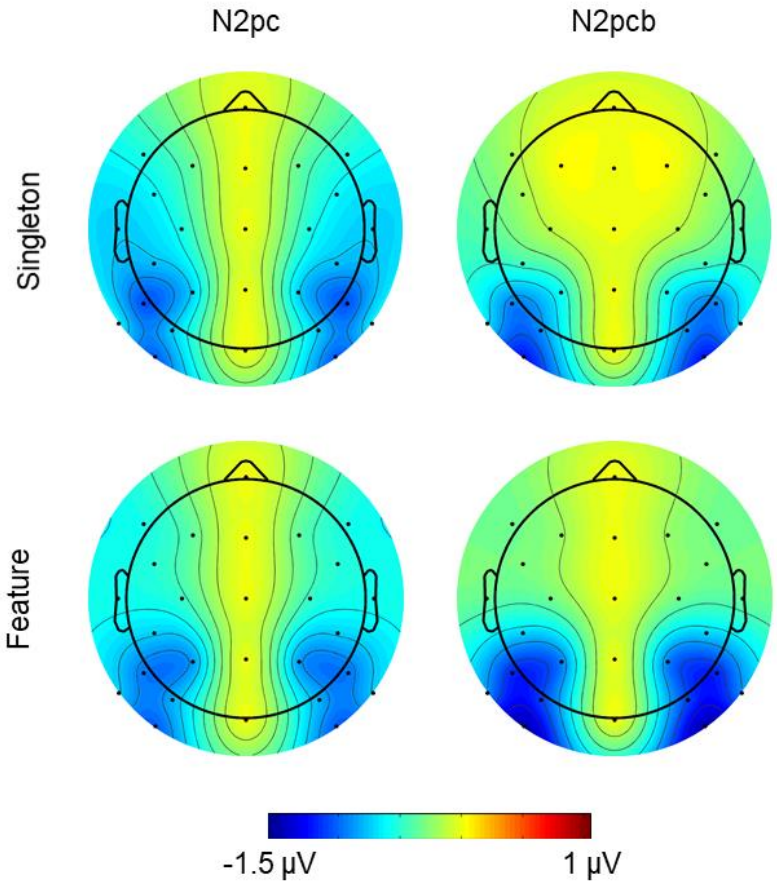

Figure 5. Scalp topographies of N2pc (left plots) and N2pcb (right plots) difference waveforms, shown for singleton (top) and feature (bottom) search conditions in the 200–300 ms time window. The components are plotted mirrored in both the hemiscalps.

Two additional tests were performed in the optic to strengthen the hypothesis of a common neural and functional source of N2pc and N2pcb. One test explored whether the amplitude of N2pcb varied as a function of the vertical elevation of the midline target (upper/lower visual field), based on prior observations indicating that N2pc amplitude is often larger for lateral targets displayed below the horizontal meridian than for lateral targets displayed above the horizontal meridian (e.g., Luck, Girelli, McDermott, & Ford, 1997; Perron, Lefebvre, Robitaille, Brisson, Gosselin, Arguin, & Jolicœur, 2009). The

N2pcb waveforms elicited by midline targets presented at the top versus bottom position are shown in Figure 6. Midline targets below the horizontal meridian elicited N2pcb activity of larger amplitude relative to midline targets displayed above the horizontal vertical meridian (-2.36 µV vs. -.37 µV, respectively; $t(11) = -4.4$, $p < .001$)[2].

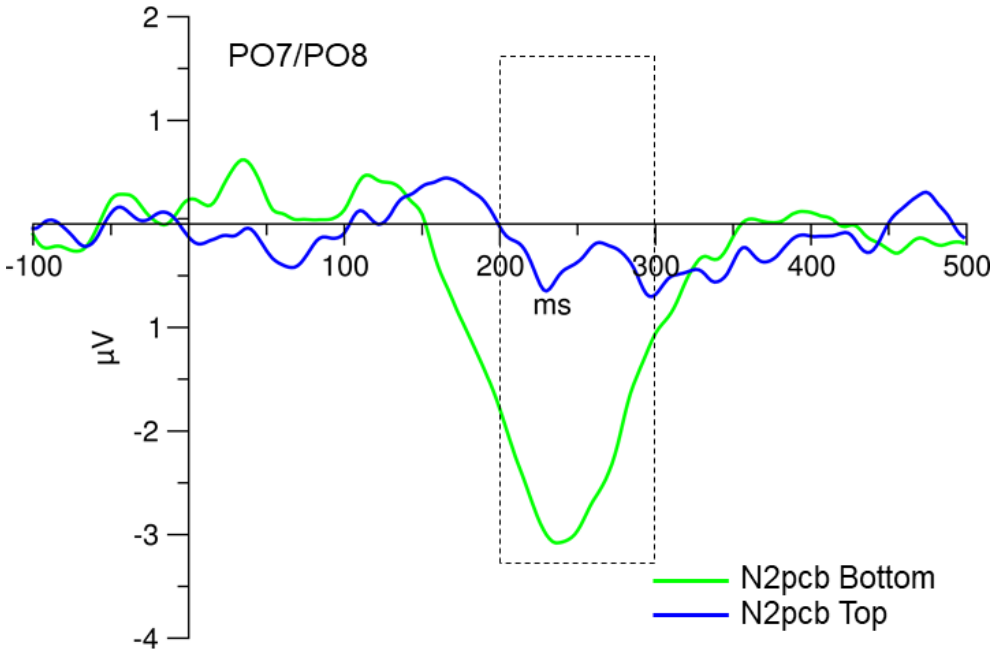

Figure 6. N2pcb difference waveforms for midline targets presented at the top and bottom positions. The area indicated by the dashed-line rectangles in the graph represents the time-window considered for ERP amplitude analyses.

A different test explored whether a measure of attention allocation efficiency to lateral targets could predict attention allocation efficiency also to midline targets, at the

[2] An analogous analysis comparing N2pc amplitudes for lateral targets in the upper versus lower visual hemifield was unfortunately not possible, as our EEG marking scheme did not specify the exact vertical elevation of these targets.

individual level. To do so, individual measures of attention allocation efficiency to lateral and midline targets were estimated by subtracting, for both N2pc and N2pcb, the onset latency in the singleton search condition from the onset latency detected in the feature search condition, separately for each participant. The scatterplot reporting these individual values is reported in Figure 7. A possible correlation between these sets of values was tested by adopting a robust correlation approach (Pernet, Wilcox, & Rousselet, 2013), indicating that the correlation was indeed reliable (r = .68, p = .015). Participants who showed a greater N2pc latency delay in the feature as compared to the singleton search task also showed a greater N2pcb latency difference between these tasks.

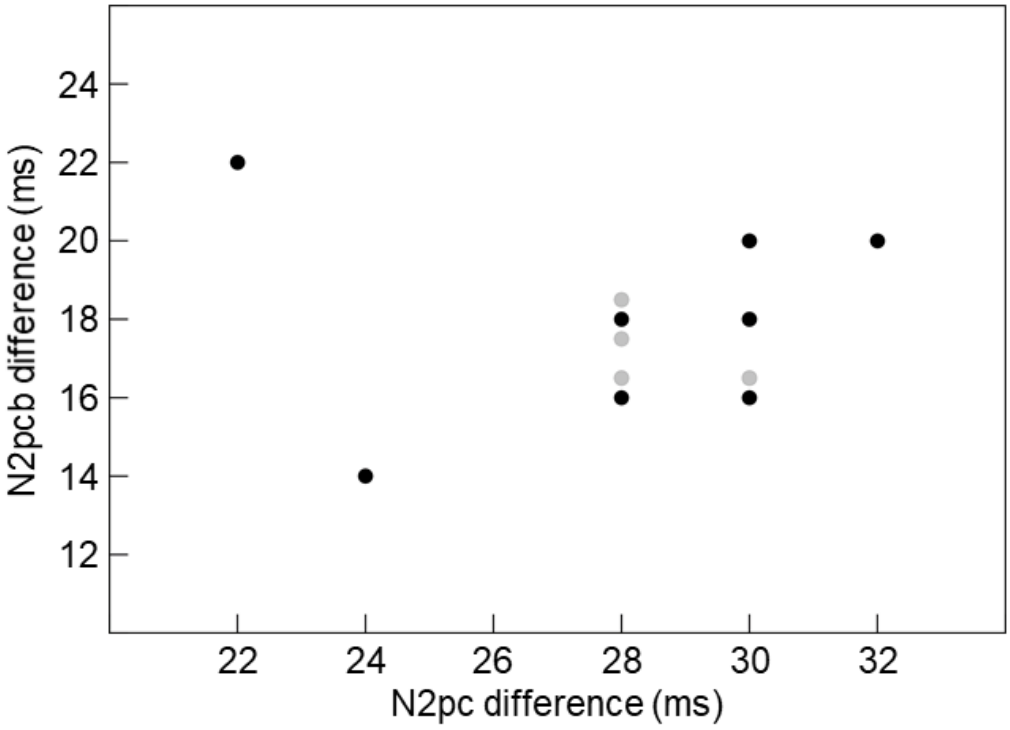

Figure 7. Correlation between latencies differences (feature search minus singleton search) of N2pc (horizontal axis) and N2pcb (vertical axis). Given the overlap of some data points, four dots (plotted in grey) have been slightly moved from their real position for graphical purposes.

Discussion

In the present study, we measured ERP responses to visual search targets displayed laterally or along the vertical midline. The goal was to investigate whether the attentional selection of midline targets would be reflected by a bilateral negativity at lateral posterior electrodes between 200 and 300 ms after search display onset, analogous to the well-known N2pc component to lateral targets. We assumed that the difference between the N2pc and N2pcb components should reflect the difference in how lateral and midline targets are hypothesized to be represented in striate and extrastriate regions of the visual cortex. Whereas lateral targets fall in receptive fields of neurons localized in the contralateral occipital cortex of a single hemisphere, midline targets fall in partially overlapping receptive fields of tightly interconnected neurons bilaterally distributed in both hemispheres (Innocenti, 1986; Nakamura et al., 2008 Wandell et al., 2007; Zeki, 1993). If the selection of lateral targets elicits a contralateral negativity (N2pc) and the selection of midline targets a bilateral negativity (N2pcb), these two components should show the same temporal profile when the difficulty of target selection is manipulated.

We therefore measured N2pc and N2pcb components to salient color singleton targets (singleton search) and less salient feature-defined targets (feature search). As expected, RTs were faster for singleton as compared to feature search, confirming that the attentional selection of search targets was indeed easier when these targets were color singletons. For lateral targets, the deployment of attention was indexed by a contralateral increment in negativity, i.e., a prototypical N2pc component. Importantly, this N2pc emerged reliably earlier during singleton as compared to feature search, confirming previous observations (e.g., Callahan-Flintoft & Wyble, 2017; Feldmann-Wüstefeld &

Schubö, 2015; Mazza, Turatto, & Caramazza, 2009a), and demonstrating that attention was allocated more rapidly to color singleton targets as compared to feature-defined targets. The critical new result was that a very similar onset latency difference between singleton and feature search was also observed for the N2pcb component that was quantified by subtracting ipsilateral ERPs to lateral targets from bilateral ERPs to midline targets. The N2pc onset delay for lateral feature as compared to singleton search targets was 28 ms, and the corresponding N2pcb delay for midline targets was 18 ms, and these two onset delays were statistically indistinguishable. Moreover, the individual onset delays of N2pc and N2pcb showed a reliable correlation. These findings provide novel evidence for the existence of an N2pcb component for search targets presented on the vertical midline, and also strongly suggest that this component reflects the same attentional selection mechanisms that are responsible for generating N2pc components in response to lateral targets.

The behavioral results also revealed an RT benefit for midline as compared to lateral targets in both search tasks (see Figure 2). This finding is congruent with the hypothesis of a bilateral early sensory representation for midline targets. Such bilateral representations have been shown to give rise to the so-called ‘stimulus redundancy gain’ effect (Miller & Van Nes, 2007; Shim, Jiang, & Kanwisher, 2013), namely, the faster detection speed for identical stimuli displayed in both visual hemifields relative to when a single stimulus is displayed in either visual hemifield. In spite of its intuitive appeal of this hypothesis, it should be noted that there was no direct correspondence between this particular behavioral effect and the ERP findings reported in the present study. The results of previous ERP studies exploring the locus of stimulus redundancy gain are quite mixed. Using punctuate stimuli and comparing conditions in which stimuli were unilaterally vs.

bilaterally displayed, Miniussi, Girelli, and Marzi (1998) found an amplitude enhancement of P1 and N1 ERP components for bilateral vs. unilateral stimuli, suggesting an early, sensory locus of stimulus redundancy gain effects. When the inherent sensory imbalance of the uni- vs. bilateral presentation was avoided by displaying two lateral stimuli on opposite sides of fixation among homogeneous distractors, Akyürek and Schubö (2013) found an initial P3b amplitude enhancement followed by a P3b amplitude reduction for identical vs. deviant stimuli, suggesting a late, response-related locus of stimulus redundancy effects. In the present study, a sensory origin of possible redundancy gain effects can be excluded based on the absence of P1/N1 modulations that is visible in Figure 3 by comparing midline and contralateral ERPs. In addition, we performed several tests (not reported for brevity) comparing midline and contralateral ERPs across centro-parietal (where P3b usually peaks) and frontal regions of the scalp, which found no evidence for an origin of redundancy gain effects at later post-perceptual stages. Future work will need to clarify the role of redundancy gains for performance benefits in response to midline targets and possible ERP correlates of such effects (e.g., by including conditions in which ERPs for midline targets are compared directly with bilateral targets).

As can be seen in Figure 4, there were no amplitude differences for either the N2pc or the N2pcb component between the singleton and the feature search conditions. This is important, in particular with respect to the N2pcb component. Previous work has shown that to-be-ignored distractors in a search display can elicit a contralateral positivity (Pd component; e.g., Hickey et al., 2009), which has been linked to distractor suppression. In search displays where a target appeared on the midline, this target was accompanied by distractor objects in the left and right visual field. These distractors could have elicited bilateral inhibition-related Pd components, which could have overlapped with the N2pcb,

thereby attenuating or possibly even eliminating this component. This type of distractor inhibition should have occurred primarily in the feature search condition, where distractors in different nontarget colors were more likely to interfere with target selection, but not in the singleton search condition, where targets were salient color singletons and all distractors were uniformly grey. In this case, an overlap with inhibition-related Pd components should have resulted in a clear reduction of N2pcb amplitudes in the feature search condition, but this was not observed. The apparent absence of distractor inhibition, as reflected by Pd components in the feature search condition, may have been due to the fact that participants searched for a single fixed target color, and search could therefore be guided by a strong color-specific top-down task set, thereby reducing or eliminating any competition from distractors that did not match this task set (e.g., Desimone & Duncan, 1995). In this context, and in contrast to situations where targets and distractors have at least one feature in common (e.g., Sawaki & Luck, 2011), no inhibitory mechanism may have to be recruited to suppress any possible 'attend-to-me' signal.

A comment is in order concerning our choice to treat the ipsilateral ERPs for lateral targets — i.e., activity commonly held to be related to distractor processing — as the algebraic invariant in the equations for the calculation of N2pc and N2pcb, and to consider similarities and differences between N2pc and N2pcb as arising from activity related to target processing. The choice to treat ipsilateral ERPs as a common 'baseline' to assess N2pc and N2pcb was primarily motivated by the need to preserve the maximum degree of analogy of the parameters considered for their respective calculations. It must be stressed however that our choice rested on the assumption that ipsilateral ERPs are not influenced by target position (lateral vs. midline). Direct empirical support for this assumption is structurally impossible to provide, because ipsilateral activity can by definition only be

recorded in trials with a lateral target. On the other hand, a number of classic N2pc studies seem to support the general claim that manipulations of a variety of target dimensions are primarily reflected in variations of contralateral ERPs, but have no such effects on ipsilateral ERPs, which remained largely invariant across conditions. This has been shown to be the case for target color (Luck, Fuller, Braun, Robinson, Summerfelt, & Gold, 2006), target vs. nontarget feature selection (Luck & Hillyard, 1994), target position relative to the horizontal midline (Luck et al., 1997; Perron et al. 2009), target numerosity (Benavides-Varela et al., 2018; Mazza & Caramazza, 2011), and target selection difficulty (Luck et al., 1997). Although these studies provide only indirect support for the assumption of ipsilateral ERPs invariance made in the present study, primarily because target objects were always lateralized, their results strongly suggest that treating ipsilateral ERPs as a common baseline for the calculation of both N2pcb and N2pc is a conceptually plausible solution. In relation to this argument, one may wonder whether ERPs in response to target-absent displays could be considered as another plausible baseline for the assessment of N2pc and N2pcb in the present context. However, the results shown in Figure 3 indicate that subtracting ERPs in the target-absent condition from contralateral and midline ERPs in the singleton search condition would yield sizable *positive* N2pc and N2pcb components. In the feature search condition, a small lateralized *negative* ERPs would be found for ipsilateral ERPs. This strongly suggests that the absence versus presence of a target gives rise to additional ERP components, and that target-absent displays can therefore not be employed as neutral baselines for the computation of N2pcb components. Other visual search studies that have measured ERPs to target-absent displays have also reported a larger bilateral negativity to target-absent displays as compared to target-present displays (e.g., Mazza et

al., 2009b, Schubö, Wykowska, & Müller, 2007; Wykowska and Schubö, 2011), although the processes that are reflected by this negativity have so far not been identified.

While the onsets of N2pcb and N2pc components were very similar in both search tasks, and the duration of both components was similar in the singleton task, the N2pcb remained present for longer than the N2pc in the feature task (see Figure 4). This discrepancy could in principle reflect a longer duration of focal attentional processing for midline as compared to lateral targets in this task. However, the fact that RTs were faster for midline targets appears inconsistent with this possibility. Another possibility is that late stages of the N2pcb components in the feature search task do not exclusively reflect the attentional selection of midline targets, but also other processes that are associated with the analysis and/or suppression of heterogeneous distractor objects in both hemifields. Due to the way it is computed, such processes would not be picked up by the N2pc to lateral targets. This further underlines the importance of further work investigating whether and up to which point in time the N2pcb, as defined in this study, and the N2pc component reflect the same cognitive and neural mechanisms of attentional target selection.

Previous studies have observed a selection negativity (SN) component in response to attended target objects (e.g., Hillyard & Münte, 1984) which, similarly to the N2pc and the N2pcb, is typically observed in a 200–350 ms time-window after stimulus presentation. It is unlikely that N2pc/N2pcb and SN components reflect the same attentional processes. First, the N2pc and N2pcb components found in our experiment were localized over lateral temporo-parieto-occipital scalp sites, whereas the SN is usually much more broadly distributed across posterior scalp areas, peaking at centro-parietal electrodes closer to the midline than N2pc and N2pcb (Busch, Fründ, & Herrmann, 2010). Moreover, the SN is

normally elicited in paradigms which require the detection of more than a single attribute of the target (e.g., Anllo-Vento & Hillyard, 1996).

To conclude, the present study has provided new evidence that target objects that appear on the vertical midline within visual search displays trigger a bilateral negativity in the N2 time window (N2pcb component). By contrasting singleton and feature search tasks, we demonstrated that the onset of this component in response to midline targets and the onset of the much better-known N2pc component elicited by lateral targets are equally sensitive to the speed with which attention is allocated to these targets. We propose that the N2pcb and the N2pc are functionally equivalent ERP markers for the attentional selection of target objects in visual search displays.

References

Adam, K. C. S., Robison, M. K., & Vogel, E. K. (2018). Contralateral delay activity tracks fluctuations in working memory performance. *Journal of Cognitive Neuroscience, 30*, 1229–1240. DOI: https://doi.org/10.1162/jocn_a_01233

Akyürek, E.G., & Schubö, A. (2013). The electrophysiological locus of the redundant target effect on visual discrimination in a dual singleton search task. *Brain Research, 1537,* 180–190. DOI: https://doi.org/10.1016/j.brainres.2013.09.014

Anllo-Vento, L., & Hillyard, S. A. (1996). Selective attention to the color and direction of moving stimuli: Electrophysiological correlates of hierarchical feature selection. *Perception & Psychophysics, 58*, 191–206. DOI: https://doi.org/10.3758/BF03211875

Benavides-Varela, S., Basso Moro, S., Brigadoi, S., Meconi, F., Doro, M., Simion, F., Sessa, P, Cutini, S., & Dell'Acqua, R. (2018). N2pc reflects two modes for coding the number of visual targets. *Psychophysiology, 55*, e13219. DOI: https://doi.org/10.1111/psyp.13219

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 289–300. DOI: https://doi.org /10.1111/j.2517-6161.1995.tb02031.x

Busch, N. A., Fründ, I., & Herrmann, C. S. (2010). Electrophysiological evidence for different types of change detection and change blindness. *Journal of Cognitive Neuroscience, 22*, 1852–1869. DOI: https://doi.org/10.1162/jocn.2009.21294

Callahan-Flintoft, C., & Wyble, B. (2017). Non-singleton colors are not attended faster than categories, but they are encoded faster: A combined approach of behavior, modeling

and ERPs. *Vision Research, 140*, 106–119. DOI: https://doi.org/10.1016/j.visres.2017.06.013

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193–222. DOI: https://doi.org/10.1146/annurev.ne.18.030195.001205

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology, 99*, 225–234. DOI: https://doi.org/10.1016/0013-4694(96)95711-9

Eimer, M. (2014). The neural basis of attentional control in visual search. *Trends in Cognitive Sciences, 18*, 526–535. DOI: https://doi.org/10.1016/j.tics.2014.05.005

Eimer, M., & Grubert, A. (2014). Spatial attention can be allocated rapidly and in parallel to new visual objects. *Current Biology, 24*, 193–198. DOI: https://doi.org/10.1016/j.cub.2013.12.001

Fahrenfort, J. J., Grubert, A., Olivers, C. N., & Eimer, M. (2017). Multivariate EEG analyses support high-resolution tracking of feature-based attentional selection. *Scientific Reports, 7*, 1886. DOI: https://doi.org/10.1038/s41598-017-01911-0

Feldmann-Wüstefeld, T., & Schubö, A. (2015). Target discrimination delays attentional benefit for grouped contexts: An ERP study. *Brain Research, 1629*, 196–209. DOI: https://doi.org/10.1016/j.brainres.2015.10.018

Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience, 21*, 760–775. DOI: https://doi.org/10.1162/jocn.2009.21039

Hillyard, S. A., & Münte, T. F. (1984). Selective attention to color and location: An analysis with event-related brain potentials. *Perception & Psychophysics*, *36*, 185–198. DOI: https://doi.org/10.3758/BF03202679

Innocenti, G. M. (1986). General organization of callosal connections in the cerebral cortex. In E. G. Jones & A. Peters (Eds). *Cerebral Cortex: Vol. 5* (291–353). New York: Plenum. DOI: https://doi.org/10.1007/978-1-4613-2149-1_9

Jans, B., Peters, J. C., & De Weerd, P. (2010). Visual spatial attention to multiple locations at once: The jury is still out. *Psychological Review*, *117*, 637–684. DOI: https://doi.org/10.1037/a0019082

Kiesel, A., Miller, J., Jolicœur, P., & Brisson, B. (2008). Measurement of ERP latency differences: A comparison of single-participant and jackknife-based scoring methods. *Psychophysiology*, *45*, 250–274. DOI: https://doi.org/10.1111/j.1469-8986.2007.00618.x

Luck, S. J. (2012). Electrophysiological correlates of the focusing of attention within complex visual scenes: N2pc and related ERP components. In Luck S. J. & Kappenman E. S. (Eds.), *The Oxford Handbook of Event-Related Potential Components*. Oxford (UK): Oxford University Press. DOI: https://doi.org/10.1093/oxfordhb/9780195374148.001.0001

Luck, S. J., & Hillyard, S. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, *31*, 291–308. DOI: https://doi.org/10.1111/j.1469-8986.1994.tb02218.x

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. DOI: https://doi.org/10.1006/cogp.1997.0660

Luck, S. J., Fuller, R. L., Braun, E. L., Robinson, B., Summerfelt, A., & Gold, J. M. (2006). The speed of visual attention in schizophrenia: Electrophysiological and behavioral evidence. *Schizophrenia Research*, *85*, 174–195. DOI: https://doi.org/10.1016/j.schres.2006.03.040

Mangun, G. R. (2013). *Cognitive electrophysiology of attention: Signals of the mind*. New York (USA): Academic Press. DOI: https://doi.org/10.1016/C2011-0-09640-0

Mazza, V., & Caramazza, A. (2011). Temporal brain dynamics of multiple object processing: The flexibility of individuation. *PLoS ONE*, *6*, e17453. DOI: https://doi.org/10.1371/journal.pone.0017453

Mazza, V., Turatto, M., & Caramazza, A. (2009a). Attention selection, distractor suppression and N2pc. *Cortex*, *45*, 879–890. DOI: https://doi.org/10.1016/j.cortex.2008.10.009

Mazza, V., Turatto, M., & Caramazza, A. (2009b). An electrophysiological assessment of distractor suppression in visual search tasks. *Psychophysiology*, *46*, 771–775. DOI: https://doi.org/10.1111/j.1469-8986.2009.00814.x

Miller, J., Patterson, T., & Ulrich, R. (1998). Jackknife-based method for measuring LRP onset latency differences. *Psychophysiology*, *35*, 99–115. DOI: https://doi.org/10.1111/1469-8986.3510099

Miller, J., & Van Nes, F. (2007). Effects of response task and accessory stimuli on redundancy gain: Tests of the hemispheric coactivation model. *Journal of Experimental Psychology: Human Perception and Performance*, *33*, 829–844. DOI: https://doi.org/10.1037/0096-1523.33.4

Miniussi, C., Girelli, M., & Marzi, C.A. (1998). Neural site of the redundant target effect: Electrophysiological evidence. *Journal of Cognitive Neuroscience, 10*, 216–230. DOI: https://doi.org/10.1162/089892998562663

Nakamura, H., Chaumon, M., Klijn, F., & Innocenti, G. M. (2007). Dynamic properties of the representation of the visual field midline in the visual areas 17 and 18 of the ferret (Mustela putorius). *Cerebral Cortex, 18*, 1941–1950. DOI: https://doi.org/10.1093/cercor/bhm221

Pernet, C. R., Wilcox, R. R., & Rousselet, G. A. (2013). Robust correlation analyses: False positive and power validation using a new open source Matlab toolbox. *Frontiers in Psychology*, *3*, 606. DOI: https://doi.org/10.3389/fpsyg.2012.00606

Perron, R., Lefebvre, C., Robitaille, N., Brisson, B., Gosselin, F., Arguin, M., & Jolicœur, P. (2009). Attentional and anatomical considerations for the representation of simple stimuli in visual short-term memory: Evidence from human electrophysiology. *Psychological Research, 73*, 222–232. DOI: https://doi.org/10.1007/s00426-008-0214-y

Sawaki, R., & Luck, S. J. (2011). Active suppression of distractors that match the contents of visual working memory. *Visual Cognition*, *19*, 956–972. DOI: https://doi.org/10.1080/13506285.2011.603709

Schubö, A., Wykowska, A., & Müller, H. J. (2007). Detecting pop-out targets in contexts of varying homogeneity: Investigating homogeneity coding with event-related brain potentials (ERPs). *Brain Research*, *1138*, 136–147. DOI: https://doi.org/10.1016/j.brainres.2006.12.059

Shim, W. M., Jiang, Y. V., & Kanwisher, N. (2013). Redundancy gains in retinotopic cortex. *Journal of Neurophysiology*, *110*, 2227–2235. DOI: https://doi.org/10.1152/jn.00175.2013

Treisman, A. M., & Gelade, G. (1980). A feature integration theory of attention. *Cognitive Psychology*, *12*, 97–136. DOI: https://doi.org/10.1016/0010-0285(80)90005-5

Wandell, B. A., Dumoulin, S. O., & Brewer, A. A. (2007). Visual field maps in human cortex. *Neuron*, *56*, 366–383. DOI: https://doi.org/10.1016/j.neuron.2007.10.012

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. DOI: https://doi.org/10.1037/0096-1523.29.1.121

Wykowska, A., & Schubö, A. (2011). Irrelevant singletons in visual search do not capture attention but can produce nonspatial filtering costs. *Journal of Cognitive Neuroscience*, *23*, 645–660. DOI: https://doi.org/10.1162/jocn.2009.21390

Zeki, S. M. (1993). *A vision of the brain*. Oxford (UK): Blackwell Scientific Publications.