

Preparatory Template Activation during Search for Alternating Targets

Anna Grubert¹ and Martin Eimer²

Abstract

■ Visual search is guided by representations of target-defining features (attentional templates). We tracked the time course of template activation processes during the preparation for search in a task where the identity of color-defined search targets switched across successive trials (ABAB). Task-irrelevant color probes that matched either the upcoming relevant target color or the previous now-irrelevant target color were presented every 200 msec during the interval between search displays. N2pc components (markers of attentional capture) were measured for both types of probes at each time point. A reliable probe N2pc indicates that the corresponding color template is active at the time when the probe appears. N2pcs of equal size emerged from 1000 msec before search display onset for both

relevant-color and irrelevant-color probes, demonstrating that both color templates were activated concurrently. Evidence for color-selective attentional control was found only immediately before the arrival of the search display, where N2pcs were larger for relevant-color probes. These results reveal important limitations in the executive control of search preparation in tasks where two targets alternate across trials. Although the identity of the upcoming target is fully predictable, both task-relevant and task-irrelevant target templates are coactivated. Knowledge about target identity selectively biases these template activation processes in a temporally discrete fashion, guided by temporal expectations about when the target template will become relevant. ■

INTRODUCTION

During visual search, observers have to detect and identify a target object that appears at unpredictable locations among other task-irrelevant distractor objects. Because the identity of the looked-for target is usually known in advance, search can be controlled by attentional templates (Duncan & Humphreys, 1989). Such search templates are mental representations of target-defining features (e.g., a specific color, shape, or orientation). They are believed to be maintained in visual working memory (e.g., Olivers, Peters, Houtkamp, & Roelfsema, 2011; Duncan & Humphreys, 1992) and to guide selective attention toward objects with template-matching features (e.g., Wolfe & Horowitz, 2004, 2017). It is often assumed that attentional templates are activated in advance, during the preparation for an impending search episode (e.g., Desimone & Duncan, 1995). However, there is so far only little direct evidence for the existence of such preparatory search template activation processes, their time course, and their sensitivity to strategic top-down control. Because the preparation for search takes place endogenously, in the absence of overt behavior, it is difficult to assess with conventional performance-based measures. Some evidence for the existence of preparatory attentional templates comes from neurophysiology. For example,

single-cell recording studies on monkeys, conducted by Chelazzi, Duncan, Miller, and Desimone (1998), showed that representations of known upcoming target objects are actively maintained before the presentation of a search display.

In a recent study from our laboratory (Grubert & Eimer, 2018), we employed a new rapid serial probe presentation (RSPP) paradigm and used EEG measures to track the time course of search template activation processes in human participants. Search displays contained a color-defined target object among distractors in different nontarget colors, so that search had to be guided by a color-specific target template. Critically, task-irrelevant displays containing a color singleton probe were flashed sequentially, every 200 msec, in the interval between successive search displays. These color probes matched either the current target color or a different task-irrelevant color. Our prediction was that target-color matching probes would capture attention when they are presented during the time when a corresponding preparatory search template is active, but not at times when this template is switched off. Measuring the ability of target-color and nontarget-color probes to attract attention at particular moments in time should therefore reveal the time course and the feature selectivity of preparatory template activation processes.

To assess attentional capture by color singleton probes, we recorded ERPs during task performance and extracted

¹Durham University, ²University of London

N2pc components elicited by target-color and nontarget-color probes presented at different time points between two search displays. The N2pc is an enhanced negativity at posterior scalp electrodes contralateral to attended objects in visual search displays with a poststimulus onset latency of 180–200 msec that is generated in ventral extrastriate visual areas (Hopf et al., 2000). This component reflects the rapid allocation of attention to target objects in visual search displays (e.g., Woodman & Luck, 1999; Eimer, 1996; Luck & Hillyard, 1994; see Eimer, 2014, for a review) and is also elicited by nontarget objects with features that match a currently active search template (e.g., Eimer & Kiss, 2008; Lien, Ruthruff, Goodin, & Remington, 2008). Thus, the presence of an N2pc component to a particular color singleton probe would demonstrate that this probe captured attention and that a corresponding search template was activated at the time the probe was presented. We found that target-color probes did indeed trigger reliable N2pc components. However, these N2pcs only emerged for probes that were presented from about 1000 msec before the onset of the next search display, but not for probes that appeared earlier during the interval between two search displays. Nontarget-color probes did not trigger N2pcs at any point during this interval. These results indicate that the preparation of search was guided by a color-selective target template and that this template did not remain active in a sustained fashion across multiple trials but was activated anew during the preparation for each upcoming search episode (see also Olmos-Solis, van Loon, Los, & Olivers, 2017, for converging eye movement results). An additional experiment (Grubert & Eimer, 2018, Experiment 3) revealed that the moment when a template was activated could be flexibly adjusted in line with temporal expectations about the arrival of the next search display. When the predictable interval between two search displays was short, N2pcs to target-color probes were triggered much earlier during the preparation period than in blocks where this interval was longer.

These results suggest that the activation of attentional templates during the preparation for an upcoming search episode is regulated in a flexible fashion by top-down control processes. These processes are sensitive to target-defining features and to the moment when a feature-selective task set will become relevant and thus ensure that a search template is activated for the right object, at the right time.

In our previous study (Grubert & Eimer, 2018), search targets were defined by one specific color that remained constant across blocks of trials. Participants therefore had to activate the same color-specific search template during each preparation period, which makes it likely that, after some initial training, relatively little executive attentional control was required (e.g., Grubert, Carlisle, & Eimer, 2016; Carlisle, Arita, Pardo, & Woodman, 2011). The goal of the present experiment was to assess how flexibly template activation processes can be regulated in a task

where color-defined targets change between individual trials, so that search has to be guided by a different color-selective search template on each trial. Participants searched for one of two possible color-defined targets among distractors in multiple different colors. Critically, target colors alternated in a fully predictable fashion between successive search displays (e.g., red, green, red, green). In this two-color ABAB task, participants knew with 100% certainty which color target object would be response relevant in the next search episode. This knowledge should maximize the incentive to selectively activate the corresponding search template during the preparation for each search episode. Because a switch between the previously active and the currently relevant color template was required on each trial, this task placed higher demands on top-down executive control than a task where observers search for the same color target throughout. Thus, the question was whether preparatory target template activation processes measured before each search display would show an analogous time course and the same degree of color selectivity as was previously found for constant-color search (Grubert & Eimer, 2018).

To assess this, we tracked the time course of search template activation processes by employing the RSPP procedure described earlier. Color singleton probes were presented every 200 msec during the interval between two search displays. Each of these probes matched one of the two possible target-defining colors, and this color was randomly selected for each probe display (see Figure 1). Thus, the color of any given singleton probe matched either the known color of the target in the upcoming search display (relevant-color probes) or the color of the search target on the previous trial that had to be ignored in the next search display (irrelevant-color probes). N2pc components were computed separately for these two types of probes and for each successive time point between two search displays. If executive attentional control processes were able to selectively activate only the currently relevant search template for the upcoming target and to switch off the other target template that was active on the preceding trial, N2pc components should only be elicited by relevant-color probes, but not by irrelevant-color probes. In our previous study with constant target colors (Grubert & Eimer, 2018), such search template activation processes were evident from about 1000 msec before the arrival of the next search display (i.e., from Probe 3 onwards). The need to switch templates between trials in the present experiment could result in a systematic delay of template activation. In this case, significant N2pcs may only emerge for later relevant-color probes. Alternatively, the executive control of search template activation processes may not be fully target-selective under conditions where target identity alternates between successive trials. In this case, reliable N2pcs might also be found for irrelevant-color probes at some point during the interval between search displays, indicating that both search templates were

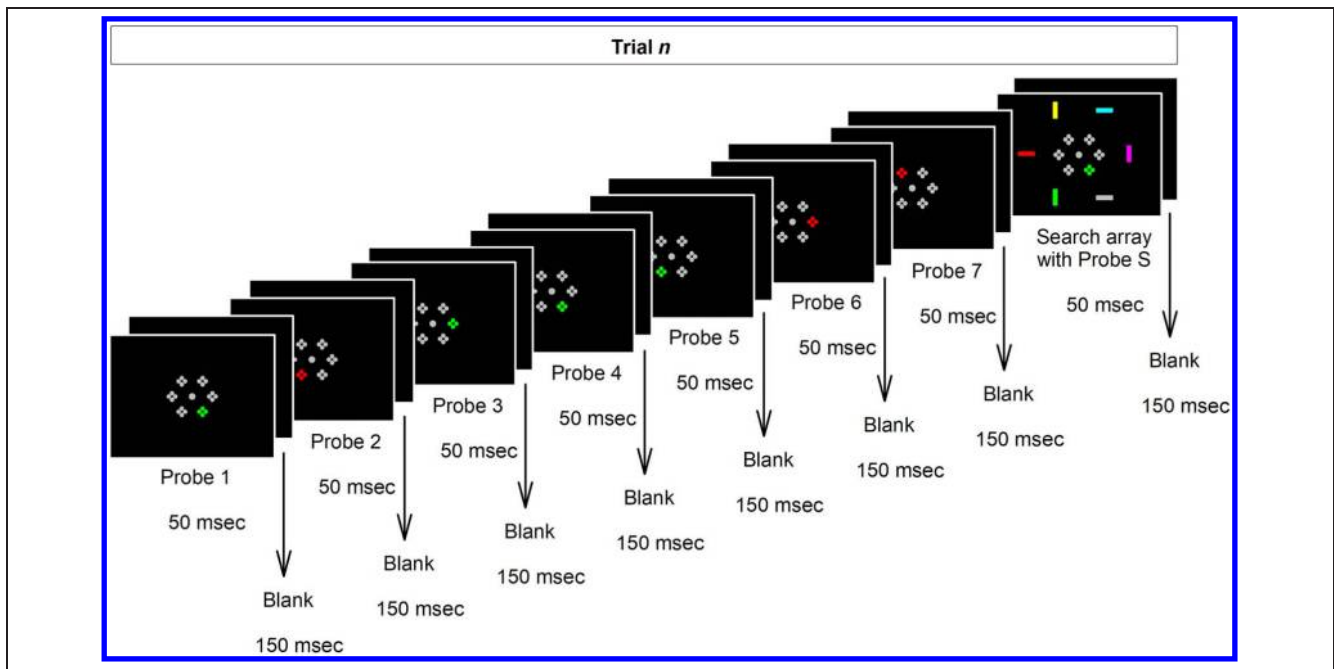


Figure 1. Schematic illustration of the time course of stimulus events in one trial. Search displays contained one bar in the currently relevant target color (red), one bar in the other possible target color (green) that was not relevant on this trial, and four distractor bars in four different nontarget colors (yellow, pink, cyan, and gray). In probe displays, a singleton probe in either of the two possible target colors appeared among five gray items. Probe displays were presented every 200 msec in the interval between two search displays (Probes 1–7) and simultaneously with a search display (Probe S). The interval between the search display of a given trial (n) and the onset of the first probe display on the next trial ($n + 1$) was also 200 msec, resulting in a continuous serial presentation stream of stimuli within each block (12 trials). The items in the probe and search displays were arranged in a circular fashion, at an eccentricity of 0.5° (probe displays) and 1.4° (search displays) from central fixation.

activated concurrently. For example, such N2pcs might emerge during early but not later phases of the preparation for the next search episode, suggesting that search templates matching the previous target are transiently reactivated (after the target was found) before they are switched off.

METHODS

Participants

Sixteen participants were paid to take part in this experiment. The study was conducted in accordance with the Declaration of Helsinki and was approved by the Psychology Ethics Committee at Birkbeck, University of London. All participants gave informed written consent before testing. One participant was excluded because of exceedingly high error rates ($>40\%$). The remaining 15 participants were aged between 25 and 42 years ($M = 31.4$, $SD = 5.2$). Eight were female, three were left-handed, and all participants had normal or corrected-to-normal vision and normal color vision (tested with the Ishihara color vision test; Ishihara, 1972). The required sample size of 15 was determined based on an a priori power analysis (G*Power; Faul, Erdfelder, Lang, & Buchner, 2007) with an assumed alpha of .05, a power (1- β) of .95, and an effect size (f) of 1.08 (determined according to Cohen, 1988). This effect size was originally measured in Experiment 1 of Grubert and Eimer (2018,

$p = .9532$; $\eta_p^2 = .54$) for N2pc amplitudes triggered by target-color probes (main effect of laterality across all successive probes) in the RSPP paradigm.

Stimuli and Procedures

Participants were seated in a dimly lit and sound-attenuated Faraday cage. They viewed the stimuli on a 17-in. Samsung wide Syncmaster 753S CRT monitor (resolution: 1280×1024 pixels, 100-Hz refresh rate) at a distance of approximately 100 cm. An LG Pentium PC running under Windows XP controlled stimulus presentation, timing, and response collection, using MATLAB and the Cogent 2000 toolbox. Figure 1 illustrates the time course of stimulus events. All stimuli were presented on a black background that contained a constant central gray fixation point (CIE x/y color coordinates: 0.287/0.312; $0.2^\circ \times 0.2^\circ$ of visual angle). Each trial included eight consecutive circular stimulus displays that were each presented for 50 msec and were separated by a blank 150-msec interval (200-msec SOA). The first seven displays in each trial were probe displays (Probes 1–7). The eighth display contained both the task-relevant search display and a probe display (simultaneous probe/search: Probe S). The blank interval between the offset of the probe/search display on the preceding trial and the onset of the first probe display on the next trial was also 150 msec, resulting in a continuous serial

presentation stream of stimuli within each block. Probe displays were presented simultaneously with target displays (Probe S) to make probe onset completely regular (every 200 msec) within each experimental block. Probe displays appeared at a different eccentricity (closer to fixation) than the target displays, as pilot testing had revealed that presenting multiple successive color singleton probes at the same eccentricity as the target displays distracted participants and made it hard to find and discriminate target items in the search displays. When the probe displays were presented at a different eccentricity, they were much easier to ignore, and none of the participants reported being distracted by these displays.

Search displays contained six vertical or horizontal bars ($0.2^\circ \times 0.6^\circ$ each) at the 1-, 3-, 5-, 7-, 9-, and 11-o'clock positions of an imaginary clock face, at an eccentricity of 1.4° from central fixation. The six bar orientations in each trial were selected independently and randomly. Each bar was shown in a different color. There were seven possible stimulus colors: red (0.609/0.327), green (0.296/0.581), blue (0.174/0.149), yellow (0.389/0.512), cyan (0.227/0.376), pink (0.216/0.110), and gray (0.287/0.312). All colors were equiluminant (~ 10.9 cd/m²). In each search display, participants searched for one of two possible color targets (e.g., red or green). Importantly, the sequence of search displays that contained one or the other of the two color-defined targets was fully predictable and alternated in an ABAB fashion across successive trials (e.g., red in Trial 1, green in Trial 2, red in Trial 3, green in Trial 4). To ensure that participants kept track of this sequence of target colors, all search displays contained both a target-color bar (e.g., red in Trial 1) as well as a bar in the other possible target color that was not relevant for the current trial (e.g., green in Trial 1), together with four bars in four different nontarget colors (e.g., yellow, pink, cyan, and gray). There were no cues indicating the relevant target color for the upcoming search display, but in each break between two successive blocks, participants received a reminder about the target color sequence and about the first relevant target color in the first trial of the new block. One participant reported that he or she lost track of the target color sequence in multiple blocks. This participant was excluded from analysis, as their accuracy rate was below 60% (see above). None of the other participants reported similar issues. Always five participants searched for one of three possible target color pairs (red or green, red or blue, or green or blue). The other four colors (yellow, cyan, pink, and gray) always served as nontarget colors. The target color sequence at the start of each block was counterbalanced across participants (e.g., red first, then green, or vice versa) but remained the same for each participant during the whole experiment. The location of both the response-relevant and response-irrelevant target color bars was selected randomly in each trial, with the constraint that, within each block of trials,

response-relevant target bars appeared equally often in the left and right hemifields. Participants' task was to report the orientation of the target-color bar in the search display (vertical, horizontal) by pressing the respective one of two vertically aligned (custom-built) response keys. The response-to-key mapping (vertical/horizontal response on the top/bottom key) and the hand-to-key mapping (left/right hand on the top/bottom key) were counterbalanced across participants but were kept constant for each participant for the duration of the whole experiment.

Probe displays that were presented between (Probes 1–7) and together with (Probe S) the search displays contained six items composed of four closely aligned dots ($0.1^\circ \times 0.1^\circ$ each; two on the vertical axis and two on the horizontal axis; total size of each four-dot probe item: $0.25^\circ \times 0.25^\circ$). They were presented at the 1-, 3-, 5-, 7-, 9-, and 11-o'clock positions of an imaginary clock face, at an eccentricity of 0.5° from central fixation. One of the items in each probe display was a target-color singleton; the other five items were uniformly gray. These singletons randomly and equiprobably matched either of the two possible target colors, that is, the color of the upcoming search target (relevant-color probes) or the color of the search target on the previous trial that had to be ignored in the next search display (irrelevant-color probes). The color probe location was selected independently for each probe display, with the restriction that there were no immediate location repetitions across consecutive displays and that successive probes would equally likely appear on the same or opposite display side (to ensure that, on average, each probe was preceded equally often by a probe on the same or opposite display side). Participants were informed that probe displays were response irrelevant and should be entirely ignored.

The experiment contained 40 blocks, each with 12 trials. Blocks were short to minimize the presence of blinks within each block. In each block, the 12th search display was followed by seven additional probe displays to keep stimulus conditions during the posttarget response interval identical across all trials in a block. Each block thus contained 12 search displays and 103 probe displays (13 for Probes 1–7 and 12 for Probe S, which was presented together with the search display). Before each task condition, participants received two practice blocks where EEG was not recorded.

EEG Recording and Data Analyses

EEG was DC-recorded from 27 scalp sites (standard positions of the extended 10–20 system), sampled at 500 Hz, and digitally low-pass filtered at 40 Hz (no other filters applied after data acquisition). Impedances were kept below 5 k Ω . The left earlobe served as online reference during data acquisition, but all channels were rereferenced offline to linked earlobes. EEG was segmented into 500-msec time windows including a 100-msec prestimulus

baseline and a 400-msec ERP time window after the onset of a particular stimulus display (Probes 1–7, search display, and Probe S). Data from the first and last seven probe displays in each block were excluded, as search templates may not be active before the first response to targets and may be deactivated when participants realize that the preceding search display was the last within a block (blocks always included exactly 12 search displays). Trials with anticipatory (<200 msec), very slow (>1500 msec), and missing or incorrect responses did also not enter analysis. Furthermore, data contaminated with artifacts (eye movements exceeding $\pm 30 \mu\text{V}$ in the bipolar horizontal EOG channel; blinks exceeding $\pm 60 \mu\text{V}$ at FPz; muscular movements exceeding $\pm 80 \mu\text{V}$ in all other channels) were excluded from EEG analyses. Artifact rejection resulted in an exclusion of 6.7% ($SD = 6.6\%$) of all epochs (ranging between 0.1% and 22.9% across participants). Of the remaining epochs, averages were computed for all probe displays (Probes 1–S, where Probe 1 was the probe that immediately followed the preceding search display and Probe S was the probe that was presented simultaneously with the search display in a trial), separately for displays with probes in the left or right hemifield. Separate averages were computed for relevant-color probes that matched the upcoming target color and irrelevant-color probes that matched the previous target color that had to be ignored in the next search display. In addition, averages were also computed for search displays with a target in the left or right hemifield.

N2pc components to probes were quantified based on ERP mean amplitudes obtained at lateral posterior electrodes PO7 and PO8, contralateral and ipsilateral to the side of a probe, within an 80-msec time window starting at 200 msec after the respective probe display onset. As in our previous work using analogous RSPP procedures (Grubert & Eimer, 2018), the start of this time window was determined by measuring the point in time (rounded to the nearest 10) when the ascending flank of the averaged probe N2pc (pooled across all relevant-color and irrelevant-color probes) reached 50% of the peak amplitude (at $-0.13 \mu\text{V}$). N2pc components to target bars in the search displays were computed within the same 200- to 280-msec poststimulus time window used for the probe N2pc analyses. All t tests reported are two-tailed. Effect sizes are reported in terms of Cohen's d (Cohen, 1988), with a confidence interval of 95%, for t tests, and partial eta squared (η_p^2), for F tests.

RESULTS

Behavioral Results

Less than 0.1% of all trials were excluded from the analysis because RTs were exceedingly slow (>1500 msec). There were no anticipatory RTs (<200 msec). Mean RT on trials with correct responses was 626 msec. Error rate was 6.6%.

N2pc Components

The overall pattern of ERP activity elicited at posterior electrode sites PO7/8 in response to search displays and probe displays is illustrated in Figure 2, which shows grand-averaged ERPs to two successive search displays and intermediate probe displays across all trials. Waveforms are shown separately for electrodes contralateral and ipsilateral to the response-relevant target-color bar in the second search display. Large visual P1 and N1 components were triggered by both search displays, and much smaller P1 and N1 components were elicited by each of the seven probe displays in the interval between successive search displays (probe display onsets are indicated by vertical lines). The amplitude differences of P1/N1 components to search versus probe displays reflects the fact that probe displays were much smaller, were presented in rapid succession at identical locations, and could be ignored throughout. Because the locations of two successive targets and the location of all intermediate color probes were determined independently, an N2pc to search targets is only visible in Figure 2 for the second search display, but not for probes or for targets in the first search display. The target N2pc was reliable, as reflected by an enhanced negativity at contralateral versus ipsilateral electrodes, $t(14) = 9.7, p < .001, d = .51$.

N2pcs elicited by target-color probes that matched either the relevant upcoming target color or the irrelevant previous target color were extracted by computing ERPs at posterior sites PO7/8, contralateral and ipsilateral to the side of a probe, separately for each of the eight successive probes in a trial (Probes 1–S). The resulting ERP waveforms are shown in Figure 3. To visualize the time course of successive probe N2pcs in these two task conditions more intuitively, Figure 4 depicts probe N2pc difference waveforms (obtained by subtracting ipsilateral from contralateral ERPs at PO7/8) in a temporally continuous fashion, separately for relevant-color probes that matched the upcoming target color (top) and irrelevant-color probes that matched the target color on the previous trial (bottom). For each probe, except Probe 1, the time interval shown ranges from 150 to 350 msec after probe onset. For Probe 1, the complete interval from 100 msec before to 350 msec after probe onset is displayed. In these plots, data from two different successive probe intervals are interpolated between adjacent data points. The onset of each probe is marked with vertical lines, and the N2pc time windows for each probe (200–280 msec poststimulus) are indicated with gray bars. Because probes were presented every 200 msec, the onset of each individual probe coincides with the N2pc time interval for the preceding probe.

As shown in Figure 4, relevant-color probes did not elicit any N2pc components when they appeared simultaneously with or immediately after a search display (Probes S, 1, and 2). N2pcs to these probes started to emerge from Probe Display 3 onward and were largest



Figure 2. Grand-averaged ERPs elicited at electrodes PO7/8 in response to two successive search displays and the probe displays presented in the interval between these displays, collapsed across all trials. Waveforms are shown for electrodes contralateral and ipsilateral to the response-relevant target-color bar in the second search display. The shaded areas indicate the target N2pc time window (200–280 msec poststimulus).

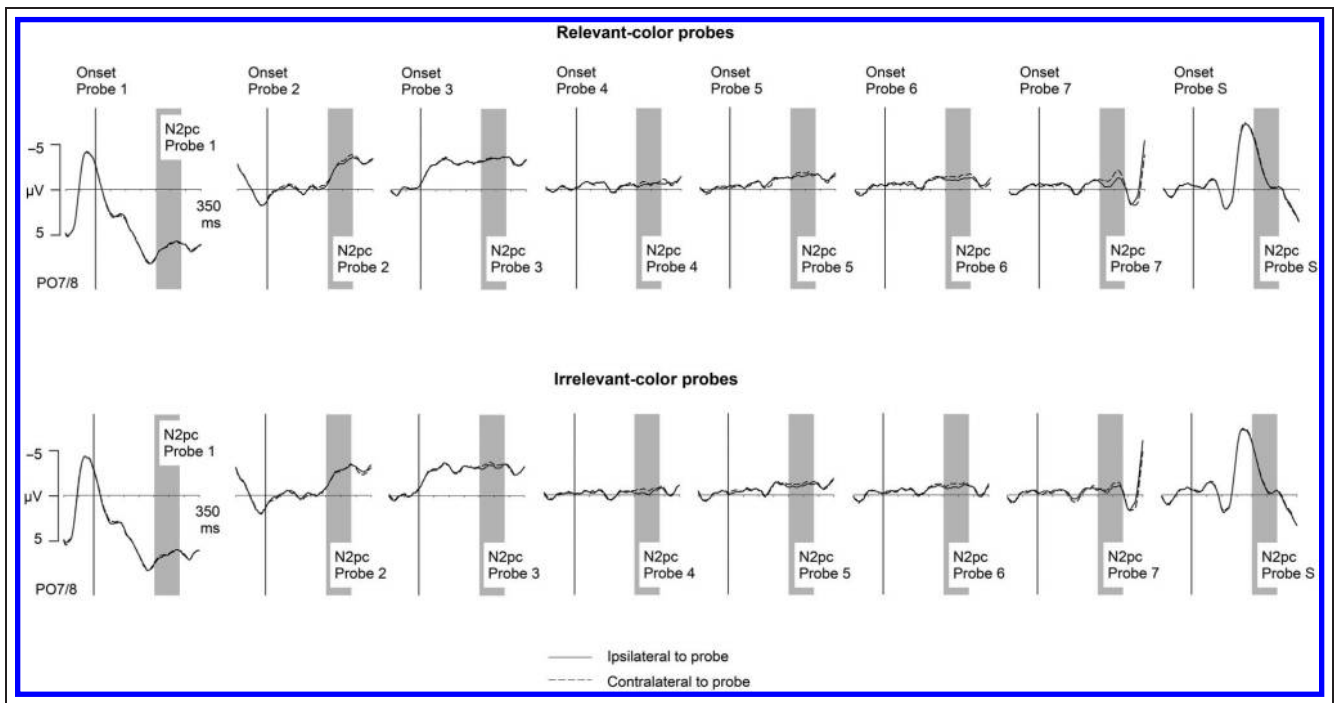


Figure 3. Grand-averaged ERPs elicited at electrodes PO7/8 contralateral and ipsilateral to singleton probes that matched either the relevant upcoming target color (relevant-color probes; top) or the color that defined the target in the preceding search display (irrelevant-color probes; bottom). ERPs are shown separately for each temporal position of these probe displays (from Probe 1 to Probe 8). The shaded areas indicate the probe N2pc time windows (200–280 msec poststimulus).

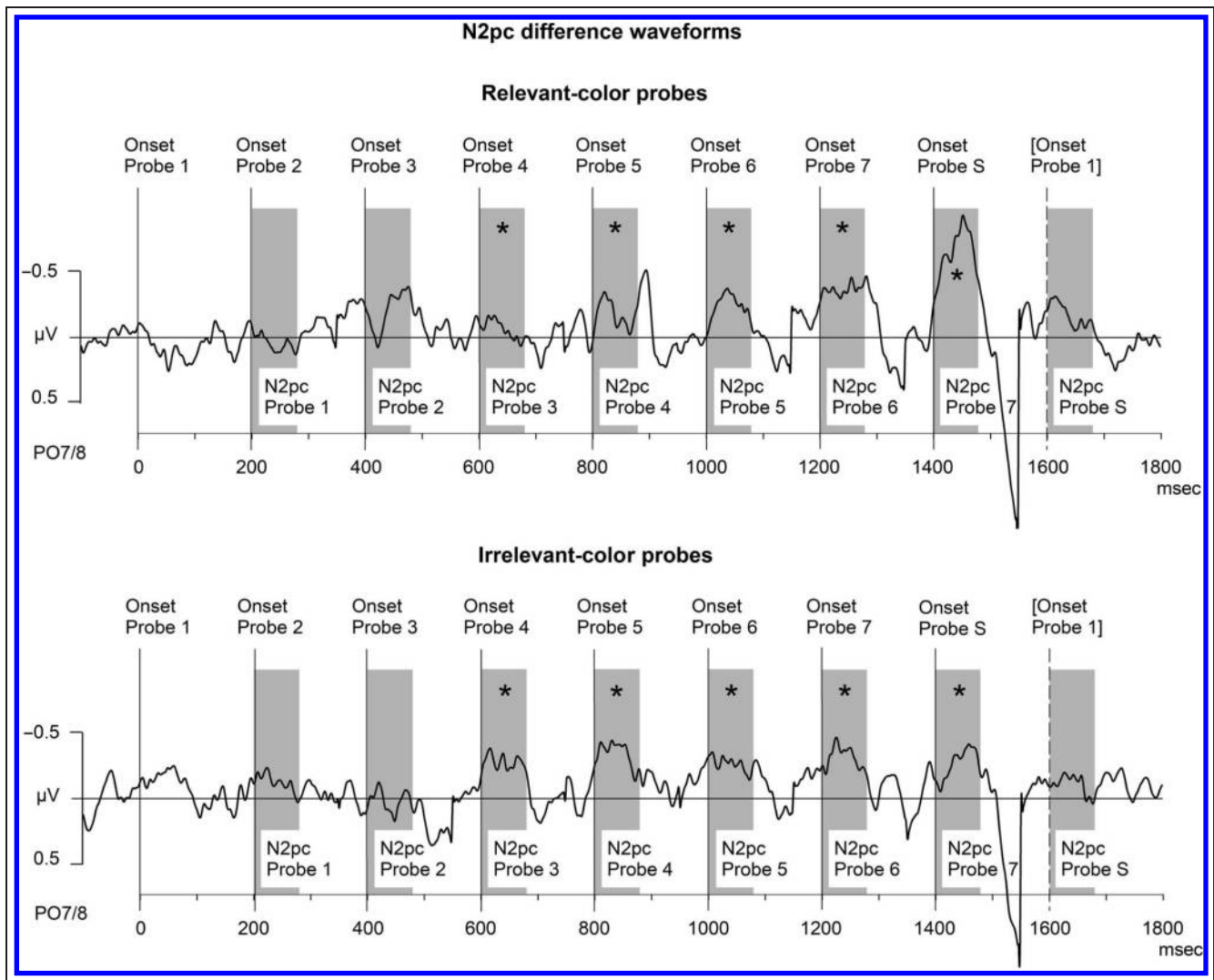


Figure 4. N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for each successive color singleton probe, shown separately for relevant-color probes (top) and irrelevant-color probes (bottom). Difference waves for all successive probes are shown in a temporally continuous fashion, as 200-msec time segments for each probe (150–350 msec after probe onset). Probe onsets are indicated by vertical lines; and probe N2pc time windows, by shaded areas (200–280 msec poststimulus). Note that the onset of each probe coincides with the N2pc window for the preceding probe. Statistically reliable probe N2pcs are marked by asterisks.

in amplitude for Probe Display 7, immediately before the onset of the upcoming search display. Surprisingly, probe N2pcs appear to be present not only for relevant-color probes but also for probes that matched the other irrelevant target color that had to be ignored in the next search display. These irrelevant-color probe N2pcs emerged at the same time as the N2pcs to relevant-color probes and were initially also similar in size. However, N2pc amplitude differences between these relevant-color and irrelevant-color probes were evident immediately before search display onset (Probe 7), where N2pcs were substantially larger for probes that matched the predictable color of the upcoming search target.

These informal observations were substantiated by statistical analyses. A repeated-measures ANOVA with the factors Probe type (relevant-color vs. irrelevant-color

probe), Probe number (Probe 1, 2, 3, 4, 5, 6, 7, or S), and Laterality (electrode contralateral vs. ipsilateral to the side of a color probe) was conducted for ERP mean amplitudes at PO7/8 in the probe N2pc time window (200–280 msec after probe display onset). A main effect of Laterality, $F(1, 14) = 10.0, p = .007, \eta_p^2 = .42$, confirmed the presence of reliable probe N2pcs. There was also an interaction between Laterality and Probe number, $F(7, 98) = 3.5, p = .002, \eta_p^2 = .20$, confirming that N2pc amplitudes differed between probes at different temporal positions. Laterality and Probe type did not interact, $F(1, 14) = 0.1, p = .749, \eta_p^2 = .01$, which suggests that there was no overall N2pc amplitude difference between relevant-color and irrelevant-color probes. However, and importantly, an interaction between Laterality, Probe type, and Probe number was present, $F(7, 98) = 2.3, p = .034, \eta_p^2 = .14$.

To investigate this three-way interaction in more detail, repeated-measures ANOVAs were conducted separately for each probe position (Probes 1–7, Probe S), with the factors Probe type and Laterality. For Probes 1, 2, and S, no significant effects involving the factor Laterality were found, all $F_s(1, 14) \leq 2.3$, $p \geq .155$, $\eta_p^2 \leq .14$, indicating that these probes failed to trigger N2pc components, regardless of their color. In contrast, main effects of Laterality were found for Probes 3–7, all $F_s(1, 14) \geq 4.8$, $p \leq .046$, $\eta_p^2 \geq .26$, which indicates that N2pc components emerged first for probes that were presented 1000 msec before the onset of the next search display (i.e., 600 msec after the preceding search display) and remained present for all successive probes during the interval between search displays. Notably, there were no interactions between Laterality and Probe type for Probes 3, 4, 5, and 6, all $F_s(1, 14) \leq 3.0$, $p \geq .106$, $\eta_p^2 \leq .18$. This indicates that, during this period, N2pc components were triggered by both relevant-color and irrelevant-color probes and that they were similar in size for both types of probes. In contrast, and importantly, an interaction between Laterality and Probe type was present for Probe 7, $F(1, 14) = 5.9$, $p = .030$, $\eta_p^2 = .30$. In line with the temporal pattern of N2pc components shown in Figure 4, this confirms that, immediately before the onset of the next search display, N2pc amplitudes were larger for relevant-color probes as compared with irrelevant-color probes. Of the 15 participants tested, 11 showed this difference, whereas the remaining four had equal N2pc amplitudes for both types of probes or slightly larger N2pcs for irrelevant-color probes. However, follow-up t tests revealed that reliable N2pcs to Probe 7 were elicited not only when these probes had the relevant color, $t(14) = 3.6$, $p = .003$, $d = .35$, but also by irrelevant-color probes, $t(14) = 2.2$, $p = .043$, $d = .14$.

On the basis of the analyses for individual probe positions, which revealed reliable N2pcs for Probes 3–7, we conducted additional ANOVAs across these probes, separately for relevant-color and irrelevant-color probes. For relevant-color probes, an interaction between Laterality and Probe number was found, $F(4, 56) = 6.3$, $p < .001$, $\eta_p^2 = .31$, confirming that probe N2pc amplitudes increased toward the end of the preparation interval (see Figure 4). In contrast, no such N2pc amplitude increase was present for irrelevant-color probes, $F(4, 56) < 1$, $p = .961$, $\eta_p^2 = .01$.

The presence of reliable N2pcs to both relevant-color and irrelevant-color probes could in principle be because of color priming across successive probe displays. This would be in line with a previous suggestion by Moore and Weissman (2010, 2014) that distractors matching one of two possible target colors will activate a corresponding search template even when this color is not currently task relevant. To test this possibility, we computed probe N2pcs for each probe position, separately for probes that matched the color of the immediately preceding probe (color repetition) and probes that were

preceded by a probe in a different color (color change). An ANOVA of resulting probe N2pc amplitudes was then conducted, including the factors Laterality, Probe type, and Probe number, and the new additional factor Color priming (color repetition vs. change). Priming should generally enhance probe N2pcs for color repetitions as compared to color changes, for both relevant-color and irrelevant-color probes, and this should be reflected in a significant interaction between Laterality and Color priming. However, no such interaction was found, $F(1, 14) = 2.0$, $p = .175$, $\eta_p^2 = .13$, and there was also no three-way interaction involving the additional factor Probe type, $F(7, 98) < 1$, $p = .816$, $\eta_p^2 = .04$. The same results were obtained when only probes that produced reliable N2pcs (Probes 3–7) were included in the analysis (Laterality \times Color Priming: $F(1, 14) = 2.1$, $p = .174$, $\eta_p^2 = .13$; three-way interaction: $F(4, 56) < 1$, $p = .799$, $\eta_p^2 = .03$). To test whether the N2pc amplitude difference for Probe 7 between relevant-color and irrelevant-color probes was specifically affected by priming, we ran an additional analysis involving the factor Color priming for Probe 7 only. As in our original analysis, there was a significant interaction between Laterality and Probe type, $F(1, 14) = 4.9$, $p = .043$, $\eta_p^2 = .26$, reflecting larger N2pcs for relevant-color probes, but no three-way interaction involving the factor Color priming, $F(1, 14) = 1.2$, $p = .286$, $\eta_p^2 = .08$. These results show that probe N2pcs were not produced or reliably affected by task-unspecific color priming effects. An informal inspection of probe N2pcs for probe color repetitions and changes indicated that there even was a numerical tendency for N2pc amplitudes to be larger for color changes.

DISCUSSION

During visual search, attentional templates represent features that are relevant for the selection of upcoming target objects. Our previous study (Grubert & Eimer, 2018) demonstrated that, when observers search for a color-defined target that remains constant throughout, search templates are not maintained in a sustained fashion but are activated anew during the preparation for each successive search episode. Search templates were color specific, and their activation was regulated in line with the predictable onset of the next search display. In this study, we investigated the time course and target selectivity of preparatory template activation processes in a task where color targets were no longer constant but alternated in a fully predictable fashion between successive search displays (ABAB). Thus, participants now had to switch between color templates on each trial, thereby increasing the demands on the top-down control mechanisms that regulate search template activation. Because target identity was fully predictable on each trial, efficient executive control should ensure that only the template representing the color of this target is activated during the

preparation period, whereas the template for the other currently irrelevant target color is switched off.

To assess this, we measured N2pc components to relevant-color and irrelevant-color singleton probes that were presented every 200 msec during the interval between successive search displays. As expected, reliable N2pc components were triggered by relevant-color probes, demonstrating that an attentional template for the upcoming target color was activated in a preparatory fashion. These N2pcs again emerged from about 1000 msec before the onset of the next search display, as in our previous study with constant color targets (Grubert & Eimer, 2018). This indicates that search templates were transiently activated during each preparation period and that the need to switch search templates across successive trials did not delay the onset of these activation processes.¹ Critically, and in marked contrast to this earlier study, significant N2pcs were now also elicited by irrelevant-color probes. Notably, the N2pcs to relevant-color and irrelevant-color probes emerged at the same time during the preparation period and were initially identical in size. These observations demonstrate that both color templates were activated in parallel, although only one of them matched the known upcoming target color. However, and importantly, N2pc components triggered by Probe 7, which appeared immediately before the onset of the next search display, were reliably larger for relevant-color as compared with irrelevant-color probes. This result indicates that top-down control processes were in fact sensitive to knowledge about the identity of the upcoming target object but that this sensitivity affected template activation processes only during the final phase of preparation, just before the relevant template would become relevant for the guidance of attention in the next search episode.

Whereas our previous study (Grubert & Eimer, 2018) demonstrated that preparatory search templates are selectively tuned to the known identity of an upcoming target when this target remains constant throughout, the current results show that this selectivity is strongly reduced when search targets change predictably across successive trials. The activation of the template for the previous target color before search displays where a different color is known to be relevant raises the question why executive top-down control processes are not more effective in biasing search preparation selectively toward the currently task-relevant color. It is possible that the cognitive demands of selectively prioritizing the template for the upcoming target and suppressing the template that was involved in the selection of the preceding target outweigh any benefits that might result from such a strategy. With this respect, the observation that a search template for the preceding but currently irrelevant target color is coactivated in parallel with the template for the upcoming target color is relevant for current debates about whether only a single or multiple search template(s) can be active at any given time. Although there

is some evidence for the single-template account (see Olivers et al., 2011, for a discussion), the present results, as well as previous behavioral and electrophysiological research, suggest that at least two color-specific target templates can be maintained simultaneously and that the costs associated with maintaining two as compared with only a single target template are relatively small (e.g., Ort, Fahrenfort, ten Cate, Eimer, & Olivers, 2019; Grubert & Eimer, 2013, 2015, 2016; Beck, Hollingworth, & Luck, 2012; Irons, Folk, & Remington, 2012). In this case, it might be more effective to coactivate templates for all objects that are relevant in a given task context than to selectively prioritize only the current target, especially if two known targets alternate predictably across successive trials, as in the present experiment. Here, the fact that the currently irrelevant color target will have to be selected again in the subsequent search display may have been a sufficient reason to coactivate both target templates on all trials.

An alternative possibility is that the concurrent activation of both color templates observed here does not reflect a deliberate strategy but is an unavoidable consequence of having to switch target templates across trials. This would be reminiscent of analogous findings from experiments studying switches between task sets (i.e., stimulus-response mappings) across successive trials. In these task-switching experiments, performance on switch trials is impaired relative to performance on trials where the same task set is repeated, and these switch costs remain present even when observers are given ample time to prepare the task that will have to be executed on the next trial (e.g., Rogers & Monsell, 1995). Such switch costs have been attributed to task-set inertia (i.e., the residual activation of a task set that has been active on a preceding trial; e.g., Allport, Styles, & Hsieh, 1994), although other factors are also known to be involved (see Monsell, 2003, for a review). The activation of a search template for the previous target during the preparation for a different target could represent a new type of task-set inertia in attentional control. In contrast to the inertia described in task-switching research, which reflects a sustained activation of previously relevant task sets, the absence of reliable N2pcs for early relevant-color and irrelevant-color probes (i.e., Probes 1 and 2) shows that both corresponding templates were temporarily switched off.² Thus, any search template inertia would not reflect the sustained activation of a previously relevant template but, instead, the reactivation of this template at the moment when the other currently relevant template becomes active. Moreover, whereas previous S-R mappings are maintained in a residual (i.e., attenuated) fashion, the current N2pc results suggest that both color templates were activated equally until immediately before the next search display was presented. These two differences might suggest that the pattern of template activation processes found here does not reflect the same type of task-set inertia as observed in typical task-switching experiments

but instead a deliberate top-down strategy. These alternatives will need to be investigated more systematically in future research. For example, performance costs associated with switches between task sets are known to disappear as soon as a new task has been executed once (Monsell, 2003; Rogers & Monsell, 1995). If this also applies to switches between search templates, template activation processes should become color-specific in tasks where the same target color is repeated at least once (e.g., in a two-color AABB task).

It is important to note that, in the present experiment, search displays contained both the color-defined target and a distractor object in the other possible target color. Therefore, participants could not simply adopt the simple strategy of activating both target color templates equally during search preparation and search execution, because this would have left them unable to select the target object and ignore this other distractor in the search displays. For this reason, the observation that N2pcs to relevant-color probes were larger than N2pcs to irrelevant-color probes that appeared at Position 7,

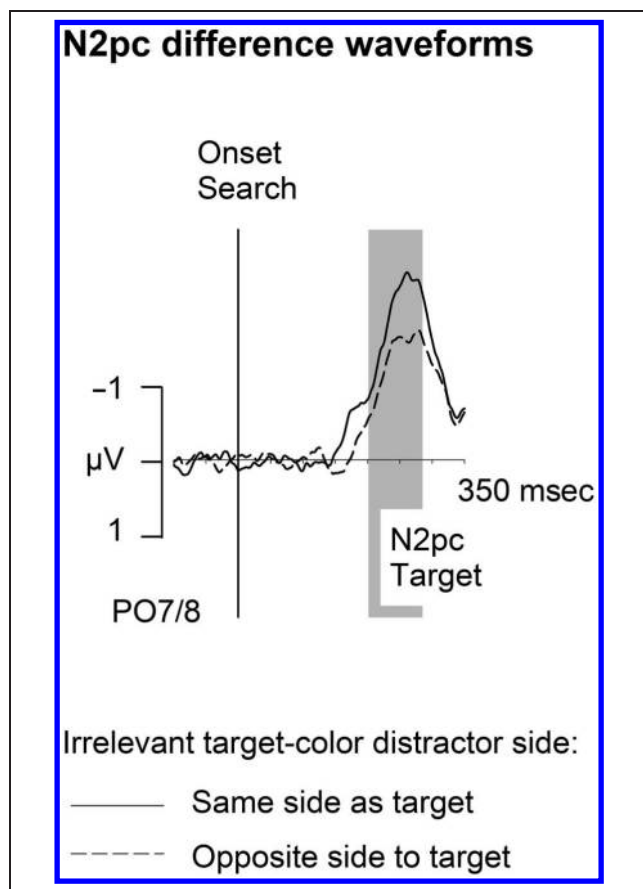


Figure 5. N2pc difference waveforms in response to search displays, obtained by subtracting ERPs at electrodes PO7/8 ipsilateral to the search target from contralateral ERPs. Difference waves are shown separately for search displays where the target and the distractor that matched the now-irrelevant color of the preceding target appeared on the same side or on opposite sides. The shaded area indicates the target N2pc time windows (200–280 msec poststimulus).

immediately before the next search display, is particularly relevant. It suggests that temporal expectations about when a specific template will be needed to guide target selection determine the point in time when parallel template activation processes are biased in favor of the target-matching template. However, even at this moment, the search template for the other target color was not completely suppressed, as demonstrated by the fact that a reliable N2pc was still elicited when Probe 7 appeared in the irrelevant color. If this template was active during the late phase of search preparation, it is likely that this activation persisted up to the point when the next search display was presented. In this case, the distractor in this search display that matched the currently irrelevant target color should also have attracted attention to some degree. To assess this, we computed target N2pc components separately for displays where the target and this distractor appeared on the same side or on opposite sides, as shown in Figure 5. These N2pcs were smaller for opposite-side as compared with same-side displays, as confirmed by an interaction between Laterality and Distractor side, $F(1, 14) = 20.0, p = .001, \eta_p^2 = .59$. This indicates that these distractors did indeed capture some attention in search displays, independently of and in parallel with the much stronger attentional enhancement to target objects, resulting in an increase of target N2pc amplitudes in same-side search displays and in a decrease in opposite-side displays.

Overall, the current study has demonstrated that, when the identity of color-defined search targets switches between successive trials, both corresponding search templates are activated during the preparation for all search episodes. Knowledge about the identity of the next search target biases the strength of these template activations, but this effect is temporally discrete and only emerges immediately before the next search episode commences.

Acknowledgments

This work was supported by the Economic and Social Research Council, UK (ES/L016400/1).

Reprint requests should be sent to Anna Grubert, Department of Psychology, Durham University, South Road, Durham, DH1 3LE, United Kingdom, or via e-mail: anna.k.grubert@durham.ac.uk.

Notes

1. Because the RSPP paradigm involves the successive presentation of multiple probe displays during search preparation periods, it is not yet entirely clear whether the transient nature of template activation processes revealed by these findings applies in the same way to more typical search tasks where no such probes are present. It is conceivable that observers might have deliberately deactivated search templates at the start of each new trial to avoid distraction by the color singleton probes. However, such distraction effects were minimized by

presenting probe and search displays at different eccentricities, and participants did not report any difficulties in ignoring these probes. This makes it unlikely that transient template activation results from distraction that is specific to the RSPP paradigm. To rule this out conclusively, the potential for distraction could be further reduced by presenting only a single probe display on each trial, at different temporal positions relative to search display onset. If template activation remains transient under these conditions, N2pcs should be elicited only for later but not for early probes.

2. This “silent period” during the early phase of search preparation does not reflect an attentional blink caused by the processing of the target in the preceding search display (e.g., Raymond, Shapiro, & Arnell, 1992). We previously demonstrated that target-color probes presented during this early phase still failed to trigger N2pc components when no target was present in the previous search display (Grubert & Eimer, 2018, Experiment 2).

REFERENCES

- Allport, D. A., Styles, E. A., & Hsieh, S. (1994). Shifting intentional set: Exploring the dynamic control of tasks. In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV: Conscious and nonconscious information processing* (pp. 421–452). Cambridge, MA: MIT Press.
- Beck, V. M., Hollingworth, A., & Luck, S. J. (2012). Simultaneous control of attention by multiple working memory representations. *Psychological Science*, *23*, 887–898.
- Carlisle, N. B., Arita, J. T., Pardo, D., & Woodman, G. F. (2011). Attentional templates in visual working memory. *Journal of Neuroscience*, *31*, 9315–9322.
- Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *Journal of Neurophysiology*, *80*, 2918–2940.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Hillsdale, NJ: Erlbaum.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, *96*, 433–458.
- Duncan, J., & Humphreys, G. W. (1992). Beyond the search surface: Visual search and attentional engagement. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 578–588.
- Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, *99*, 225–234.
- Eimer, M. (2014). The neural basis of attentional control in visual search. *Trends in Cognitive Sciences*, *18*, 526–535.
- Eimer, M., & Kiss, M. (2008). Involuntary attentional capture is determined by task set: Evidence from event-related brain potentials. *Journal of Cognitive Neuroscience*, *20*, 1423–1433.
- Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavioural Research Methods*, *39*, 175–191.
- Grubert, A., Carlisle, N. B., & Eimer, M. (2016). The control of single-template and multiple-colour visual search by attentional templates in working memory and in long-term memory. *Journal of Cognitive Neuroscience*, *28*, 1947–1963.
- Grubert, A., & Eimer, M. (2013). Qualitative differences in the guidance of attention during single-colour and multiple-colour visual search: Behavioural and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception and Performance*, *39*, 1433–1442.
- Grubert, A., & Eimer, M. (2015). Rapid parallel attentional target selection in single-color and multiple-color visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *41*, 86–101.
- Grubert, A., & Eimer, M. (2016). All set, indeed! N2pc components reveal simultaneous attentional control settings for multiple target colors. *Journal of Experimental Psychology: Human Perception and Performance*, *42*, 1215–1230.
- Grubert, A., & Eimer, M. (2018). The time course of target template activation processes during preparation for visual search. *Journal of Neuroscience*, *38*, 9527–9539.
- Hopf, J. M., Luck, S. J., Girelli, M., Hagner, T., Mangun, G. R., Scheich, H., et al. (2000). Neural sources of focused attention in visual search. *Cerebral Cortex*, *10*, 1233–1241.
- Irons, J. L., Folk, C. L., & Remington, R. W. (2012). All set! Evidence of simultaneous attentional control settings for multiple target colors. *Journal of Experimental Psychology: Human Perception and Performance*, *38*, 758–775.
- Ishihara, S. (1972). *Tests for color-blindness*. Tokyo: Kanehara Shuppan.
- Lien, M. C., Ruthruff, E., Goodin, Z., & Remington, R. W. (2008). Contingent attentional capture by top-down control settings: Converging evidence from event-related potentials. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 509–530.
- Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 1000–1014.
- Monsell, S. (2003). Task switching. *Trends in Cognitive Sciences*, *7*, 134–140.
- Moore, K. S., & Weissman, D. H. (2010). Involuntary transfer of a top-down attentional set into the focus of attention: Evidence from a contingent attentional capture paradigm. *Attention, Perception, & Psychophysics*, *72*, 1495–1509.
- Moore, K. S., & Weissman, D. H. (2014). A bottleneck model of set-specific capture. *PLoS One*, *9*, e88313.
- Olivers, C. N., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in visual working memory: When it guides attention and when it does not. *Trends in Cognitive Sciences*, *15*, 327–334.
- Olmos-Solis, K., van Loon, A. M., Los, S. A., & Olivers, C. N. (2017). Oculomotor measures reveal the temporal dynamics of preparing for search. *Progress in Brain Research*, *236*, 1–23.
- Ort, E., Fahrenfort, J. J., ten Cate, T., Eimer, M., & Olivers, C. N. (2019). Humans can efficiently look for but not select multiple visual objects. *eLife*, *8*, e49130.
- Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 849–860.
- Rogers, R., & Monsell, S. (1995). Costs of a predictable switch between simple cognitive tasks. *Journal of Experimental Psychology: General*, *124*, 207–231.
- Wolfe, J. M., & Horowitz, T. S. (2004). What attributes guide the deployment of visual attention and how do they do it? *Nature Reviews Neuroscience*, *5*, 495–501.
- Wolfe, J. M., & Horowitz, T. S. (2017). Five factors that guide attention in visual search. *Nature Human Behavior*, *1*, 1–8.
- Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature*, *400*, 867–869.