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Effects of top-down and bottom-up attention on post-selection posterior contralateral negativity

Einat Rashal¹ · Elisa Santandrea² · Suliann Ben-Hamed³ · Emiliano Macaluso⁴ · Leonardo Chelazzi² · C. Nico Boehler¹

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Abstract

We examined the effect of combined top-down and bottom-up attentional control sources in easy and difficult visual search tasks. Applying a new analysis on previously acquired data, we focused on the sustained posterior contralateral negativity (SPCN) and the response-locked posterior contralateral negativity (RLpcN), to better understand processes following target selection. We used the signed-area approach to measure the negative area, where the signal was either locked to the target or the response onsets. We further split the RLpcN into an early and a late segment to capture the dynamics of selection and post-selection processes. In Experiment 1, participants reported the orientation of a uniquely tilted target. In Experiment 2, participants reported the position of a small gap within the uniquely tilted target. In both experiments, endogenous cues manipulated top-down attention (valid vs. neutral), and salient color singletons (either the target or a distractor) manipulated bottom-up attention. We hypothesized that the SPCN and the later segment of the RLpcN would be modulated by task difficulty and target salience, as they are associated with post-selection processes, such as response selection and working memory. The early segment of the RLpcN was hypothesized to be modulated by the cueing manipulation and presence of a salient distractor, as they affect target selection. An effect of distractor presence was observed on the early segment of the RLpcN, and our results further supported the hypotheses regarding the SPCN and the later segment of the RLpcN, providing novel insights into post-selection processes in visual search.

Keywords Visual search · Cueing · Salience · Response-locked ERP · Signed area · RLpcN · SPCN

Introduction

Processing our visual surroundings requires the filtering of relevant from irrelevant information. How attentional resources are allocated is often studied through visual search. In visual search studies, often, the search is guided by a defining feature of the target, thus guiding attentional resources in a top-down fashion (e.g., Wolfe et al., 1989). Other times, the target is defined by its salience, and thus

captures attention in a bottom-up fashion (e.g., Itti, 2005). In some studies, the target appears following a spatial cue that narrows down the visual area that needs to be searched and allows the allocation of attention to that area in advance to the onset of the target (e.g., Folk et al., 1992; Posner, 1980; Theeuwes & van der Burg, 2007). These studies often report facilitation effects that are interpreted as facilitation of target selection (see Theeuwes, 2010, for a review). However, much less is known about how the allocation of attention affects the processing of the target once it has been selected.

In the EEG literature, studies of attention in visual search often focus on lateralized activity in posterior areas, particularly in the form of the N2pc component, peaking at approximately 200–300 ms from stimulus onset. This component presumably reflects attentional selection (e.g., Burra & Kerzel, 2013; Eimer, 1996; Luck & Hillyard, 1994); however, it has also been suggested to reflect more detailed processing at the attended location (e.g., Luck & Hillyard, 1994; Zivony et al., 2018). A similarly lateralized

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component is often observed following the N2pc, known as the sustained posterior contralateral negativity (SPCN; also referred to as contralateral delay activity [CDA]) and has been demonstrated to correlate with visual short-term memory (e.g., Jolicœur et al., 2008; Dell'Acqua et al., 2006; Vogel & Machizawa, 2004). Recently, another component, the RLpcN, has been suggested to mark processing at the attended location following target selection (Drisdelle & Jolicœur, 2019, 2020). Though all three components, the N2pc, SPCN/CDA, and RLpcN are defined as the averaged difference ERP between the contralateral and ipsilateral posterior scalp sites relative to the target location, they differ in the viewpoint and information they provide on cognitive processes. Specifically, while the N2pc and SPCN/CDA are measured from stimulus onset (e.g., Eimer, 1996; Hickey et al., 2006; Hopf et al., 2000; Luck & Hillyard, 1990), the RLpcN is aligned with the response onset and is measured in a time window leading up to the response (Drisdelle & Jolicœur, 2019, 2020). The latter provides a measure for post-selection processes that may not be observed clearly when measured from stimulus onset due to variations in the onset times of these processes, some of which are plausibly more closely aligned with response execution rather than stimulus onset, thereby obscuring successive components due to smearing of the EEG signal (Drisdelle & Jolicœur, 2019, 2020).

To support this idea, Drisdelle and Jolicœur (2019) used a task that was likely to require the sustained maintenance of visual information, where participants had to discriminate the target first and then report the location of a gap within the target that was briefly presented at different eccentricities. Time-locking their analysis to the participants' response, they observed a sustained posterior contralateral negativity that was present up until and even beyond response execution. The onset, and thus the duration of the RLpcN, was correlated with reaction times such that earlier onset latencies (i.e., longer durations) were observed for slower responses. Furthermore, by computing partial correlations between the components, they found that the N2pc had a stronger relationship with the early segment of the RLpcN, while the SPCN had a stronger relationship with the peak amplitude of the RLpcN, which occurred at the later segment of the component, closer to the response. Hence, their results suggested that the early segment of the RLpcN reflects the initial deployment of attention, and the later segment reflects the representation and processing of visual information in short-term memory. In a following paper, Drisdelle and Jolicœur (2020) reported the effects of set size and number of response alternatives on the RLpcN; they showed that the number of response alternatives affected the peak latency that occurred closer to the response onset, suggesting that processes related to response selection were reflected in the later segment of the RLpcN. On the other

hand, an effect of set size was observed on RLpcN onset latency, suggesting that search difficulty was reflected in the early part of the component. Thus, the findings of Drisdelle and Jolicœur's investigation into the RLpcN provide a new avenue for studying attentional dynamics in visual search.

In a recent study (Rashal et al., 2022), we examined the effect of task difficulty on the combination of top-down and bottom-up attentional control sources in a visual search task. In two experiments, participants reported the tilt of an orientation-singleton target (Experiment 1) or the position of a gap within the uniquely tilted target (Experiment 2). In the latter, the surrounding nontargets were also tilted and thus more similar to the target, rendering the search in the second experiment more difficult compared with the search in the first one where cardinal directions were used for the nontargets (Barras & Kerzel, 2017). In both experiments, a central cue preceded the search array, either guiding top-down endogenous attention to the target location (valid) or not providing any spatial information (neutral). At the same time, target and distractor salience was manipulated to test for effects of bottom-up deployment of attention when top-down guidance of attention was provided or absent (see Fig. 1A–B for example displays and trial sequence in the two experiments). Not surprisingly, performance was worse in Experiment 2, where the task was more difficult (Table 1). In addition, top-down guidance of attention was more beneficial in the difficult search, reducing interference from the salient distractor following a valid cue, and target salience had a small advantage that was eliminated once top-down guidance of attention was available. Interestingly, in the easy search in Experiment 1, an N2pc was observed only when top-down guidance of attention was absent. In contrast, when the search was more difficult (Experiment 2), an N2pc was observed when top-down guidance of attention was provided, or when the target was salient with no allocation of attention to the target location in advance. This pattern of results suggested that once attention was guided to the target location in the easy task, limited attentional resources were needed for processing the target further, which was not the case in the difficult task. Additionally, since no N2pc was observed in the difficult task when no guidance of attention was available through either the cue or target salience, we speculated that the task in Experiment 2 might have been difficult to the point where participants had to change their search strategy to a serial search.

The different difficulty levels of the tasks in Rashal et al. (2022) could have been a result of (a) search difficulty that differed according to the similarity between the target and the surrounding nontargets in the two experiments, and (b) the task, which was different in the two experiments—in the easy task (Experiment 1), the response involved only one step of reporting the orientation of the target, which was also the feature of the target that guided the search (i.e.,

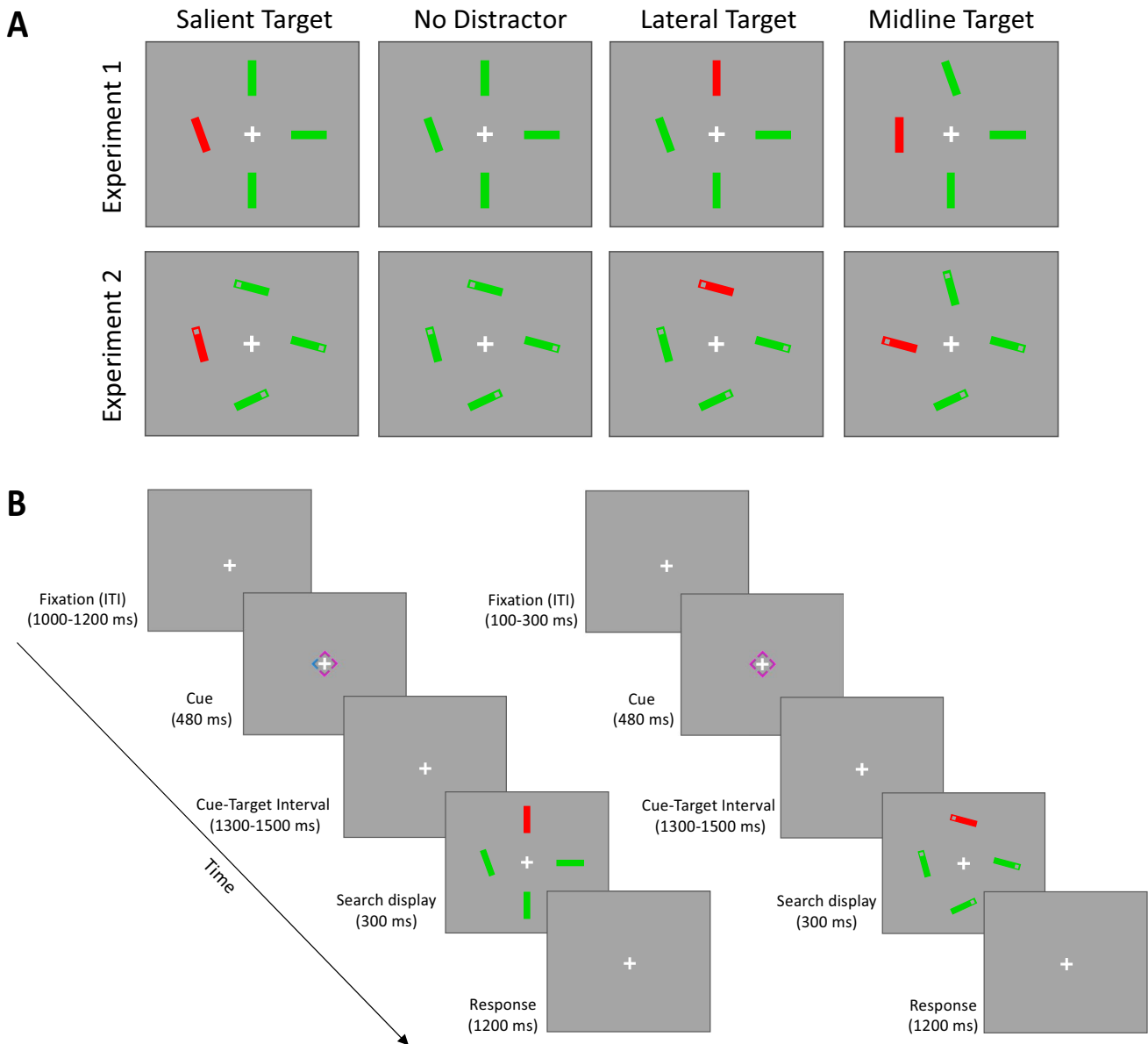


Fig. 1 **A** Illustration of search displays in Experiments 1 and 2. The target was a bar tilted 20° clockwise or counterclockwise from vertical. In the *salient-target* condition, the target appeared laterally and was the only salient item in the display. In the *no-distractor* condition, the target appeared laterally without a salient distractor. In the *lateral-target* condition, the target appeared laterally while a salient distractor appeared at the top or bottom location. In the *midline-target* condition, the target appeared at the top or bottom location, while the salient distractor appeared laterally. The latter condition was not included in the current analysis and is presented only to provide a complete description of the experimental design. In both experi-

ments, the target was the only item tilted clockwise or counterclockwise from horizontal. The task in Experiment 1 was to report the orientation of the tilt, whereas in Experiment 2 the task was to report the location of the gap within the target (top or bottom). In both experiments, on half of the trials the cardinal color was green (salient target and distractors were red), while on the other half of the trials the colors were reversed. The colors were assigned randomly for each trial. **B** The sequence of events in a trial in Experiment 1 (left), depicting a valid cue to the location left of fixation in a lateral-target condition, and in Experiment 2 (right), depicting a neutral cue preceding the same search display condition. (Color figure online)

discrimination task). In contrast, in the difficult task (Experiment 2), there was a second step of locating a gap within the target (i.e., compound task). Töllner et al. (2012) demonstrated differences between discrimination and compound tasks in visual search, such as the ones used in our previous

study. Like in our study, they observed faster responses in a discrimination task compared with a compound task, where the discrimination of the target did not provide the relevant attribute for the response. They found that the task affected components related to response selection over central brain

Table 1 Accuracy (%) and reaction times (ms) in the different cue and display conditions in Experiments 1 and 2 reported in Rashal et al. (2022)

		Experiment 1				Experiment 2			
		Accuracy (%)		Reaction Time (ms)		Accuracy (%)		Reaction Time (ms)	
Cue	Display	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Neutral	No distractor	91.0	7.2	612	115	77.9	10.9	704	139
	Salient target	92.8	5.8	603	111	81.7	9.8	678	123
	Lateral target	91.3	6.4	638	121	73.7	11.3	738	146
	Midline target	92.3	7.5	688	129	65.2	11.2	808	167
Valid	No distractor	95.1	3.6	544	109	88.5	6.2	593	109
	Salient target	94.1	4.3	541	102	89.3	5.7	583	109
	Lateral target	94.9	3.9	557	115	85.8	7.1	599	121
	Midline target	97.1	2.7	561	108	77.9	9.3	659	140

areas (i.e., the lateralized readiness potential, LRP), but did not affect the N2pc (or PCN as it is sometimes referred to, e.g., Töllner et al., 2012), suggesting that the N2pc mostly captures target selection rather than post-selection processing. In a later study, Töllner et al. (2013) showed an increased CDA when the task required more in-depth processing due to lower contrast between the target and its background, indicating the involvement of post-selection processes in difficult tasks.

Considering these and Drisdelle and Jolicœur's findings, it stands to reason that an examination of the RLpcN may be useful in the context of our study as well. Thus, in the current study we turn to analyze the data of Rashal et al. (2022) from a response-locked perspective, specifically targeting the RLpcN that has the advantage of encompassing processes that follow the initial allocation of attention. In addition, since in our previous study the stimulus-locked analysis targeted attentional selection, and thus, focused on the N2pc, in the current study, we also provided a stimulus-locked analysis related to post-selection processes, targeting the SPCN.

Our main predictions focused on the differences between the two experiments—namely, search difficulty and task (discrimination vs. compound). Specifically, as the earlier segment of the RLpcN is thought to reflect search difficulty and initial attentional engagement, we predicted that a larger negativity would be observed for the earlier segment of the RLpcN in Experiment 2, compared with Experiment 1, reflecting a more difficult selection process in the compound task. The later segment of the RLpcN, on the other hand, is thought to reflect post-selection processes, such as processing in working memory and response selection. Thus, differences should be observed in this segment of the component between the two experiments, as the task in the second experiment required further processing of the target, presumably in working memory, and the selection of a response

that was not mapped directly with the search. Hence, we predicted that a larger negativity would be observed for the SPCN and for the later segment of the RLpcN in Experiment 2, compared with Experiment 1.

Since in both experiments other factors were manipulated, for further exploration of the data, some more nuanced hypotheses were made. Specifically, the manipulation of top-down attention control via an endogenous cue facilitated target selection, shifting attention towards the target location in advance, as reflected in the modulations of the N2pc observed for validly and neutrally cued targets reported by Rashal et al. (2022). Thus, the earlier segment of the RLpcN might also be affected by the cueing manipulation.

The presence of a salient distractor was found to interfere with target selection (e.g., Theeuwes, 1991, 1992). In the case that this interference comes from the deployment of attention to the distractor prior to the target, the activity resulting from deployment of attention to the salient distractor will not be captured by the component that is measured for the target, and thus no effect of distractor presence should be observed on the SPCN or any segment of the RLpcN. Still, N2pc amplitudes have been found to increase in the presence of a salient distractor as that leads to an increased difficulty in discrimination (e.g., Boehler et al., 2011; Hopf et al., 2002). We did not observe such an effect in our previous study (Rashal et al., 2022); however, aligning the signal with response onset might recover N2pc-related activity for neutrally cued targets in Experiment 2. We suspected that the participants performed a serial search in those trials. If so, the target would not have been selected first on every trial, and the processes underlying the N2pc to the target could have occurred at various times on different trials and would not have been properly represented in the typical N2pc time window. Hence, response-locking the signal may recover activity related to attentional selection that would be reflected by the stimulus-locked counterpart,

the N2pc, as it would align the N2pc-related activity (with some variation due to noise). Thus, the analysis might show a larger negativity for the earlier segment of the RLpcN for the difficult task.

Lastly, it has been previously found that stimulus-driven attention affects working memory (e.g., Fine & Minnery, 2009; Santangelo & Macaluso, 2013; Wills-Conn et al., 2019), and the effect of salience on working memory was found to increase with task difficulty (Fine & Minnery, 2009). Thus, we predicted an interaction between target salience and task difficulty on the SPCN, and also on the later segment of the RLpcN. Specifically, a larger negativity might be observed with these components for salient compared with nonsalient targets, and this effect should be larger in Experiment 2 compared with Experiment 1.

Methods

The methods reported here are the same as those reported in Rashal et al. (2022), with some modifications pertaining to the aim of the current analysis.

Participants

Twenty-five volunteers participated in Experiment 1 and another 23 participated in Experiment 2. Four participants in Experiment 1 and two in Experiment 2 were excluded from further analysis due to technical issues. Data from three additional participants in Experiment 2 were excluded due to low performance accuracy ($\leq 60\%$), and one due to excessive eye movements. The remaining 21 participants in Experiment 1 (two males, age $M = 22.44$ years, $SD = 3.11$, three left-handed), and 17 participants in Experiment 2 (one male, age $M = 23.43$ years, $SD = 3.94$, one left-handed) were naïve to the purpose of the study and were reimbursed for participation. All had normal or corrected-to-normal vision and reported no neurological deficits. Informed consent was obtained before the experiment, and the protocol was approved by the ethical committee of the Faculty of Psychology and Educational Sciences of Ghent University (Code 2018/13).

Stimuli and design

Stimuli were presented using PsychoPy (Version 1.84.2) software (Peirce, 2007) on a 24in. Benq XL2411Z LED monitor controlled by a Dell Optiplex 9020 tower with Intel Core i5-4590 processor, at 60-Hz refresh-rate. To monitor eye movements, we used a 250-Hz SMI eye tracker (RED250 mobile system; SensoMotoric Instruments, Teltow, Germany). Participants rested their heads on a cushioned chin rest at a viewing distance of 60 cm.

Examples of the different search displays are depicted in Fig. 1A. Search displays consisted of four bars, $2^\circ \times 0.5^\circ$ in size, and were green (RGB: 0, 86, 0; 138.5 cd/m^2) or red (RGB: 170, 0, 0; 64.8 cd/m^2) on a gray background (RGB: 128, 128, 128; 85.5 cd/m^2). The bars were positioned in a diamond-like arrangement centered 7° away from a white fixation cross ($0.5^\circ \times 0.5^\circ$; RGB: 255, 255, 255; 190.2 cd/m^2). The target was tilted 20° clockwise or counterclockwise from vertical. In Experiment 1, the three remaining bars (i.e., distractors) were oriented vertically or horizontally with a constraint that not all three had the same orientation. In Experiment 2, the three distractors were tilted 25° clockwise or counterclockwise from horizontal, and all the bars had a “gap” on one side (i.e., a square with the same color as the background). On half of the displays the principal color was green, while on the other half it was red. The principal color of the display was randomly assigned for each trial.

Overall, there were four conditions, three in which the target appeared laterally and were used here to measure the SPCN and RLpcN. In the *salient-target* condition, the target had a different color than the three distractors (i.e., red target and green distractors, or vice versa). In the *no-distractor* condition, all four bars were in the same color (i.e., green or red). In the *lateral-target* condition, one of the distractors was of a different color while the other two had the same color as the target (i.e., a red distractor in a green display or a green distractor in a red display). Importantly, the salient distractor appeared in the upper or lower location so that the measured lateral activity reflected only target processing. In the *midline-target* condition, the salient distractor appeared on the left or right location, while the target appeared at the upper or lower location. This fourth condition, in which the target appeared on the vertical midline is described here for completion but was not part of the analysis. Each condition was presented equally often. Thus, the targets appeared lateralized on 75% of all trials (25% in each of the three condition) and 25% of the trials it appeared on the vertical midline.

Cues were composed of L-shaped segments forming a $1.2^\circ \times 1.2^\circ$ diamond around the fixation cross. A neutral cue was composed of four magenta segments (RGB: 120, 0, 90; 89.5 cd/m^2). For valid cues, one of the segments was cyan (RGB: 0, 56, 158; 81.1 cd/m^2), pointing to the location of the prospective target. A neutral cue appeared on half of the trials and a valid cue on the other half. Due to the specific arrangement of the target and distractors in the search display, with only one of the four search display conditions with a target on the vertical condition, cues to the left or right locations appeared on 75% of valid-cue trials (37.5% each), while in the other 25% the cue pointed to the upper or lower locations (12.5% each). Note again, that those latter 25% of trials were disregarded here for the analysis.

Procedure

All the conditions were presented in a randomized order. The sequence of events in a trial is depicted in Fig. 1B. A fixation cross was presented continuously at the center of the screen. After a cue presentation of 480 ms and a cue–target interval (CTI) of 1,300–1,500 ms, the search display was presented for 300 ms. The participants' task was to search for the tilted target and indicate its orientation (clockwise or counterclockwise rotation from vertical) with a keypress using the index fingers of the left and right hand (“m” for right tilt and “z” for left) in Experiment 1, or report on which side of it a gap was located within the target in Experiment 2 (i.e., “m” for top and “z” for bottom). Responses were recorded from onset of the search display until 1,200 ms after display offset (i.e., for a total of 1,500 ms). In Experiment 1, once this time window had passed, an intertrial interval displaying only the fixation cross was jittered between 1,000 and 1,200 ms. In Experiment 2, this ITI was shortened to 100–300 ms to reduce the duration of the experiment. Participants were instructed to fixate on the fixation cross that was presented continuously, and to not move their eyes. In Experiment 1, fixation was monitored continuously by the experimenter by means of the online eye-position display of the eye tracker, and the participants were warned in case eye-movements were observed to allow correction. In Experiment 2, a trial was automatically terminated when fixation was broken over a 2° window around fixation. Due to technical issues with the eye tracker, central fixation could not be directly monitored in this way for two of the participants in Experiment 1 and four participants in Experiment 2 but was clearly instructed and monitored via the EEG recording display. Participants performed 10 trials as practice and 12 experimental blocks of 96 trials (1,152 trials in total). Thereby, each condition of cue and display combination was presented for 144 trials.

Electrophysiological recording and analysis

EEG data were recorded using a Brain Products actiCHamp 64-channel system (Brain Products, Gilching, Germany) with 64 active scalp electrodes positioned according to the standard international 10–10 system. The EEG data was analyzed using Brain Vision Analyzer 2 (Brainproducts, Gilching, Germany). Signals were recorded at a 500-Hz sampling rate with Fz as the reference during recording. During the analysis, the data were re-referenced offline to the average of TP9 and TP10, which correspond to the left and right mastoids, and Fz was restored to the dataset. Segments of clearly identifiable bad data were excluded during an inspection of the raw data, and a high-pass filter of 0.1 Hz was applied. Next, independent component analysis (ICA) was used to remove eye blinks from the data. Eye movements

were observed very rarely, and respective ICs were removed from the data. Very noisy electrodes detected during recording or visual inspection of the raw data were interpolated for four participants in Experiment 2 (1–2 electrodes each). Data limited to trials with correct responses only were segmented into epochs from –200 ms to 4,000 ms relative to cue onset, and baseline-corrected with respect to the 200-ms precue period. A semi-automatic artifact rejection blind to the experimental conditions was performed on these segments with a maximal allowed voltage step of 200 μ V/ms, 200 ms before and after the event, and a maximal allowed difference intervals of 250 μ V in a 100-ms interval, 100 ms before and after the event. In the case of an extremely large number of rejected trials ($\geq 25\%$), marked events were recovered during manual inspection where possible. This operation led to the exclusion of 6% of the trials on average in Experiment 1 (range: 0.3%–24%), and 11% in Experiment 2 (range: 0.1%–23%). For the SPCN analysis, data were segmented further into epochs from –200 to 800 ms relative to search display onset, according to the different cues, search display conditions, and the location in which the target appeared (left/right), and baseline corrected relative to the 200-ms presearch display period. For the RLpcN analysis, to capture the complete time-range for search and response processes the data were segmented into epochs from –1,000 ms to 2,000 ms relative to search display onset, according to the different conditions. Then, data were baseline-corrected relative to the 200-ms presearch display period and segmented further into epochs from –800 to 200 ms relative to response onset and averaged per participant. Difference waves were then calculated for each participant in each condition by subtracting their ipsilateral from their contralateral electrode site and then averaged across the two target locations. Statistical analyses reported in the results section were performed on these difference waves. Both components were quantified in each of the three conditions where the target appeared lateralized. The SPCN and RLpcN have been observed in posterior locations (e.g., PO7–PO8), thus, we used the same electrode sites as in our previous paper, in which we also observed the largest negative amplitude for the N2pc at electrode sites PO7–PO8.¹

One concern related to the comparison between our two experiments is the time window in which to quantify the components, since response times were generally slower in

¹ Due to a measurement error in Experiment 1, the cap was placed further to the back, positioning FCz exactly at the Cz site. At the sites that are traditionally considered for the N2pc, which are usually PO7 and PO8, the channel pair that was the closest (~1 cm off) was P3 and P4, which was also found to display the largest negativity. For consistency, the results reported here refer to the correct sites on the head for the two experiments, although they appear under different names in the recorded data.

the second experiment. To address this concern, we used the signed-area approach, measuring the area under the curve ($\mu\text{V}\cdot\text{ms}$) that reflects only negative activity in a wide time window (e.g., Luck, 2014; Sawaki et al., 2012). Using the signed-area approach has the advantage of integrating both latency and amplitude of a component in one measure. Additionally, it allows measuring activity of one polarity without the activity of the opposite polarity, the latter potentially leading to the cancellation of signals when averaged across participants that may vary in their specific onset latencies (Luck, 2014). This approach has been used and validated previously for measuring the N2pc, and also the P_D , a component related to distractor suppression (Gaspelin & Luck, 2018; Hickey et al., 2019; Sawaki et al., 2012; Sawaki et al., 2015; Tay et al., 2019), and should in principle generalize well to both the SPCN and RLpcN, since they have a clear polarity and the end of the relevant time window can be reasonably set around the moment of response execution. Furthermore, since early and late segments of the RLpcN are suggested to reflect different processes, we split the RLpcN into two segments; the first should cover the activity related to the search and corresponding N2pc (up to 300 ms from stimulus onset), while the second should cover activity related to the maintenance of visual information in working memory, response selection, and the corresponding SPCN/CDA (typically observed from ~350 ms from stimulus onset). Importantly, Drisdelle and Jolicœur (2020) observed peak latencies of the RLpcN within the last 300 ms prior to response onset (~250 ms) for response selection in conditions that correspond to the ones employed in our experiments—a set size of four elements and two response alternatives. Hence, we considered a similar time window for the negativity related to response selection. As average RTs in the relevant conditions were around 550–750 ms, we measured the RLpcN area ($\mu\text{V}\cdot\text{ms}$) in two segments of 300 ms each, 600 ms in total relative to the response onset. The SPCN area ($\mu\text{V}\cdot\text{ms}$) was measured between 350 and 700 ms from stimulus onset, to cover post-selection processes following the N2pc time window that was measured in our previous study (Rashal et al., 2022), up until response selection and execution.

Since the signed-area approach is biased for indicating significance in null hypothesis testing against zero, we conducted permutation tests on the area derived for each condition to verify that the polarity of the area we measured was meaningful (e.g., Hickey et al., 2019; e.g., Maris & Oostenveld, 2007; Rashal et al., 2022; Sawaki et al., 2012). We created distributions of negative values taken from the measured components (contralateral minus ipsilateral channels) and their counterparts (ipsilateral minus contralateral times $[-1]$). These distributions were comprised of the means of 100,000 samples equal in size to the corresponding samples in each experiment. If contralateral and ipsilateral

relationship to the stimulus is meaningful, then the observed value of the condition should be in the higher 5% of the distribution of permuted means. Code and results of these permutation tests are available online (<https://github.com/einatr/permutation-test-for-ERP.git>).

All the statistical analyses reported in this paper and data visualization were performed in R (R Core Team, 2016) with ez (Lawrence, 2015), effectsize (Ben-Shachar et al., 2020), and ggplot2 (Wickham, 2016) packages. Analysis of variance (ANOVA) p values were corrected with Greenhouse–Geisser epsilon in cases of significant sphericity violation. Planned comparisons that tested the specific hypotheses described in the introduction were performed using Welch two-samples t tests, two-tailed, unpooled variance for the between-subjects factor of experiment, and paired-sample t tests, two-tailed, for the within-subject factor of search display.

Results

SPCN

Figure 2 depicts mean SPCN difference waves and mean signed area for the different search displays in the two experiments. The results of the permutation tests showed no meaningful lateralization (i.e., the probability of the observed means was more than 5%) in all the conditions of Experiment 1, with only trends evident following a valid cue for the lateral-target and salient-target conditions and following a neutral cue for the no-distractor condition ($p = .07$). On the other hand, in Experiment 2, a meaningful lateralization was found for all conditions following both cue types. This suggests that the emergence of the SPCN in our paradigm depended on the difficulty of the task.

To directly test the hypothesis that the SPCN is modulated by the task and by target salience, but not by the cue or the presence of a salient distractor, a mixed ANOVA was performed on the data from the two experiments with search display (lateral-target, no-distractor, salient target), and cue (valid, neutral) conditions as within-subject factors, and experiment as a between-subjects factor. This analysis revealed a significant main effect of experiment, $F(1, 36) = 6.69, p = .01, \eta_p^2 = 0.16$. No other effect reached significance; however, the interactions between experiment and condition, and the three-way interaction between experiment, condition, and cue were marginally significant, $F(2, 72) = 2.83, p = .07, \eta_p^2 = 0.07$; $F(2, 72) = 2.64, p = .08, \eta_p^2 = 0.07$, respectively.

To test specifically for the hypothesized interaction effect between target salience and task difficulty on the SPCN, we compared the negativity observed in the salient-target and no-distractor conditions in both experiments. A mixed

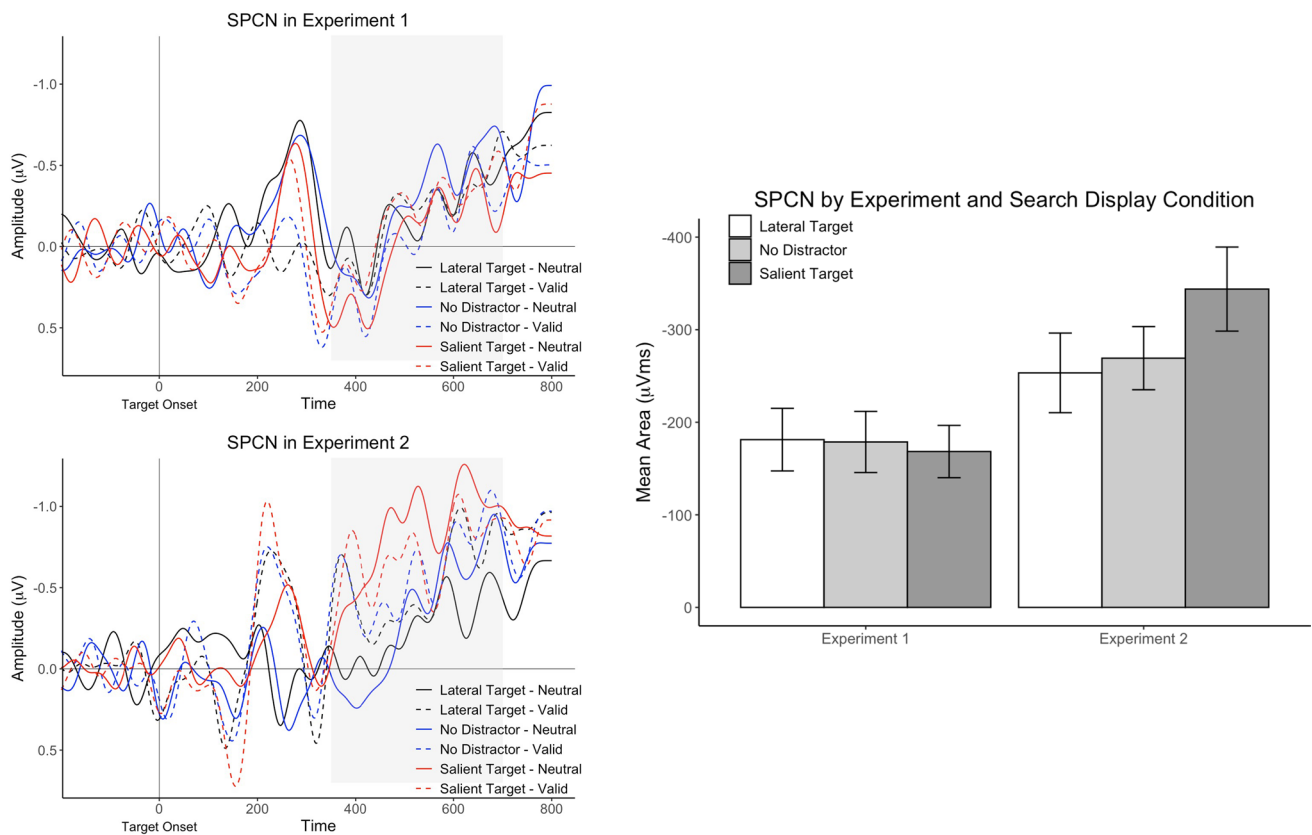


Fig. 2 Left: SPCN difference waves from electrode sites PO7/PO8 for the different cue and search display conditions with lateralized targets in Experiments 1 and 2. Shaded areas represent the time window in which the SPCN area was quantified. A low-pass

filter of 15 Hz was used for visualization purposes. Right: Mean SPCN area in the two experiments as a function of display condition. Error bars indicate standard errors of condition means. (Color figure online)

ANOVA, with search display (no-distractor, salient-target) as a within-subject factor and experiment as a between-subjects factor revealed a main effect of experiment, $F(1, 36) = 8.97, p = .005, \eta_p^2 = 0.20$, and a marginally significant interaction with display condition, $F(1, 36) = 3.64, p = .07, \eta_p^2 = 0.09$. Planned comparisons showed that the SPCN area was larger for the salient-target condition in Experiment 2 (75 $\mu\text{V}\cdot\text{ms}$), while the opposite was observed in Experiment 1 (10 $\mu\text{V}\cdot\text{ms}$). The difference between the conditions did not reach statistical significance in Experiment 1, $t(20) = -0.38, p = .71, d = -0.08$, and was only marginally significant in Experiment 2, $t(16) = 2.03, p = .06, d = 0.49$.

RLpcN

Figure 3 depicts mean RLpcN difference waves as a function of experiment, search display, and cue condition, and the mean signed-area for the different search displays in the two experiments split into first and second 300-ms segments preceding the manual response. The permutation tests showed a meaningful lateralization (i.e., a probability of less than 5%) in Experiment 1 only for the lateral-target

and no-distractor conditions following a neutral cue in both segments. In Experiment 2, a meaningful lateralization was observed in the first segment of the RLpcN for the lateral-target and salient-target conditions following a neutral cue, and a trend was evident in the lateral-target condition following a valid cue ($p = .06$). For the second segment of the RLpcN in Experiment 2, a meaningful lateralization was observed in all conditions following a valid cue and for the no-distractor and salient-target conditions following a neutral cue. A trend was evident in the lateral-target condition following a neutral cue ($p = .06$). Thus, these results indicate a dependency on the search display when the task is easy, but a different pattern when the task is difficult.

To directly test the hypothesized effects of task difficulty, cueing, and search display on both segments of the RLpcN, a mixed ANOVA was performed on the data from the two experiments, with segment (first, second), search display (lateral-target, no-distractor, salient target), and cue (valid, neutral) conditions as within-subject factors, and experiment as a between-subjects factor. This analysis revealed significant main effects of experiment, $F(1, 36) = 8.41, p = .006, \eta_p^2 = 0.19$, and segment, $F(1, 36) = 27.91, p < .0001, \eta_p^2$

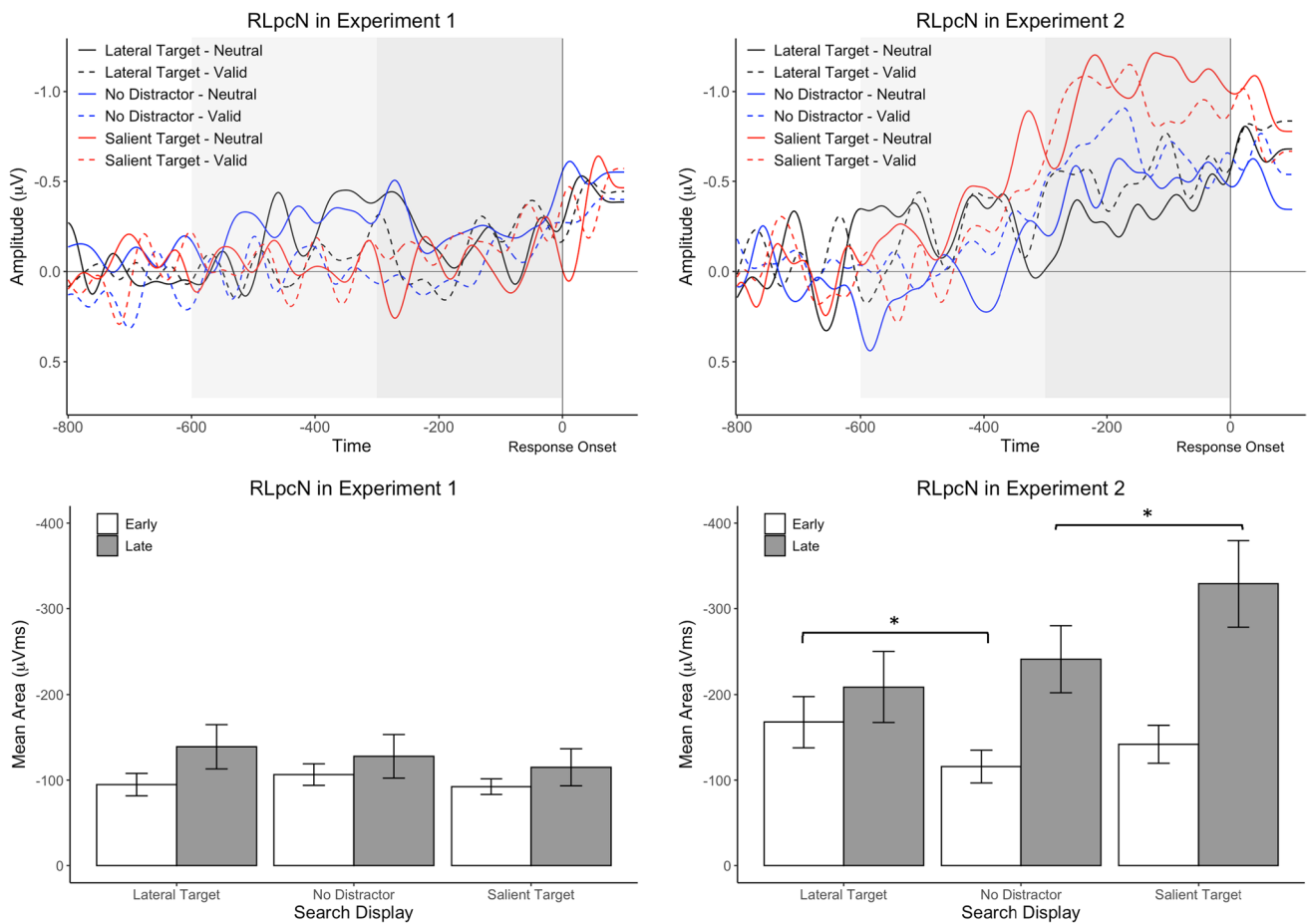


Fig. 3 Top: RLpcN difference waves from electrode sites PO7/PO8 for the different cue and search display conditions with lateralized targets in Experiments 1 and 2. Shaded areas represent the time windows in which the RLpcN area was quantified (light gray for the early segment of the RLpcN, and dark gray for the later segment). Note that the signal was baseline corrected to the 200 ms prior to array onset and then aligned with the onset of the

response (time-point zero). A low-pass filter of 15 Hz was used for visualization purposes. Bottom: Mean RLpcN area in the two experiments separated into early and late segments (collapsed across cueing conditions; early segment from 600 ms to 300 ms before response onset, and late segment from 300 ms to response onset (0 ms). Error bars indicate standard errors of condition means. * $p < .05$. (Color figure online)

= 0.44. The main effects of search display and cue conditions were not significant ($ps > .28$), and cue condition did not interact with segment or the other factors ($ps > .14$), suggesting that cueing generally had little or no effect on the RLpcN in the present study. The two-way interaction between experiment and segment, in turn, was significant, $F(1, 36) = 10.14, p = .003, \eta_p^2 = 0.22$. Planned comparisons showed that the RLpcN area was larger in Experiment 2 compared with Experiment 1, marginally for the first segment, $t(22.22) = 1.88, p = .07, d = 0.63$, and significantly for the second segment, $t(25.95) = 3.02, p = .006, d = 1.01$, of the component, suggesting that the interaction between experiment and segment was due to a larger difference between the experiments for the second segment (133 $\mu\text{V}\cdot\text{ms}$), compared with the first (44 $\mu\text{V}\cdot\text{ms}$). The interactions between experiment and search display, $F(2, 72) = 3.55, p = .04, \eta_p^2 = 0.09$, segment and search display, $F(2,$

72) = 8.58, $p = .0005, \eta_p^2 = 0.19$, as well as the three-way interaction between experiment, segment, and search display condition were significant as well, $F(2, 72) = 15.90, p < .0001, \eta_p^2 = 0.31$.

To trace the source of these significant interactions, separate rm-ANOVAs were performed on the data from each experiment, with search display conditions (lateral-target, no-distractor, salient target), and segment (first, second) as within-subject factors. The analysis of the data from Experiment 1 revealed that the effect of segment did not reach significance, $F(1, 20) = 3.11, p = .09, \eta_p^2 = 0.13$, although a slightly larger negativity was observed in the second ($M = -64, SD = 50 \mu\text{V}\cdot\text{ms}$) compared with the first ($M = -49, SD = 22 \mu\text{V}\cdot\text{ms}$) segment of the RLpcN. The main effect of search display and the interaction between search display and segment were not significant ($F < 1$), $F(2, 40) = 1.44, p = .25, \eta_p^2 = 0.07$, respectively. This generally suggests that

in Experiment 1, the data is relatively homogeneous across conditions and segments.

The analysis of the data from Experiment 2, on the other hand, revealed a significant main effect of segment, $F(1, 16) = 25.75, p = .0001, \eta_p^2 = 0.62$, no significant effect of search display, $F(1, 16) = 2.54, p = .10, \eta_p^2 = 0.14$, and a significant interaction between the two factors, $F(2, 32) = 13.87, p < .0001, \eta_p^2 = 0.46$. To trace the source of this interaction and to test specifically for the hypothesized effect of salient-distractor presence on the first segment of the RLpcN in the difficult task, planned comparisons were conducted on the data from the lateral-target and no-distractor conditions. This analysis showed a significant increase in negativity when a salient distractor was present in Experiment 2, $t(16) = 2.88, p = .01, d = 0.70$. No such effect was found in Experiment 1, $t(20) = 0.95, p = .35, d = 0.21$, and no effect was found on the second segment in both experiments—Experiment 1: $t(20) = -0.54, p = .59, d = -0.12$; Experiment 2: $t(16) = 0.99, p = .34, d = 0.24$.

To test for the hypothesized effect of target salience on the second segment of the RLpcN, we compared the negativity observed in the salient-target and no-distractor conditions in both experiments. A mixed ANOVA, with search display (no-distractor, salient-target) as a within-subject factor and experiment as a between-subjects factor, revealed significant main effects of experiment, $F(1, 36) = 13.17, p = .0009, \eta_p^2 = 0.27$, and search display, $F(1, 36) = 4.86, p = .03, \eta_p^2 = 0.19$, and their interaction, $F(1, 36) = 8.73, p = .006, \eta_p^2 = 0.20$. Planned comparisons showed significantly larger negativity for salient targets compared with nonsalient ones in Experiment 2, $t(16) = 2.71, p = .02, d = 0.66$, but no such difference in Experiment 1, $t(20) = -0.80, p = .43, d = -0.18$.

Discussion

The goal of the current study was to examine post-selection processes in visual search tasks that combined top-down and bottom-up attention-control sources through the SPCN and a recently identified component—the RLpcN. Specifically, we analyzed the negative area of posterior contralateral activity elicited by the target, time locked to either the stimulus or response onset. Moreover, for the RLpcN, we measured early and late activity, presumably related to the initial deployment of attention and to the subsequent processes at the attended location, respectively. The target could be a salient color singleton, or identical to the nontargets in color. A salient color-singleton distractor was present or absent, and the search array followed either a valid or a neutral spatial cue. To sum up our results: We found clear effects of experiment on the SPCN and the later segment of the RLpcN, indicating a stronger role of post-selection processes in the

compound task of Experiment 2. Additionally, we observed an effect of salient distractor presence on the early segment of the RLpcN, and target salience was found to affect the later segment of the RLpcN, indicating different roles for salience in our paradigm. Finally, no effect of cueing the target location was found, suggesting that our manipulation of top-down guidance of attention was not relevant for the processes captured by the components measured here.

Task difficulty affects post-selection processes

Our main hypothesis concerned the sensitivity of the SPCN and RLpcN to task difficulty as manipulated across our two experiments. Furthermore, we were interested in disentangling the effects of search difficulty and task difficulty in our experiments by examining early and late activity within the RLpcN. Specifically, while the search in Experiment 1 was relatively easy, as the target was a salient orientation singleton, in Experiment 2 the search was made more difficult by tilting the nontargets, making them more similar to the target (Barras & Kerzel, 2017). Additionally, in Experiment 1, the task was to discriminate the target according to its orientation; hence, the response alternatives were mapped to the feature of the target that guided the search. In Experiment 2, the search was still guided by the orientation feature, but the task pertained a second step of locating a small gap within the target. Since previous studies found an increase in SPCN (CDA) amplitudes for a difficult target identification (Töllner et al., 2013), and the later segment of the RLpcN was previously found to correlate with the SPCN latency and to reflect response selection (Drisdelle & Jolicœur, 2019, 2020), we hypothesized that a larger RLpcN area would be observed in the later segment of the component for the compound task in Experiment 2, compared with the simple discrimination task in Experiment 1. The results supported our hypothesis, as both the SPCN and the later segment of the RLpcN were found to be larger in Experiment 2.

Top-down guidance of attention to the target location and distractor filtering

Our next hypothesis regarded the effect of precueing the target location. As top-down guidance of attention to the target location should facilitate the initial deployment of attention, an effect could have emerged for the different cue conditions on the early segment of the RLpcN. However, no effect of cueing condition, or an interaction with segment was observed. This somewhat contrasts with the effect of cue we observed on the N2pc in our previous study (Rashal et al., 2022). We suspect that the activity related to the N2pc was smeared or otherwise obscured by noise that was measured in the RLpcN time window, and thus, pointing out the importance of incorporating both stimulus-locked

and response-locked measures, rather than just one of these directions, for a comprehensive interpretation.

Our results further substantiate the advantage of a response-locked analysis in recovering signals obscured by temporal smearing in a stimulus-locked analysis. Specifically, in Experiment 2 of our previous study, task difficulty resulted in the absence of a N2pc for non-salient targets following a neutral cue. We suspected that this was the result of a switch in strategy, where the participants engaged in a serial search, and thus, the N2pc elicited by the target was temporally smeared since the analysis was stimulus locked, and the latency of this component would have varied across trials. In the current study, response-locking the signal and using signed-area rather than average amplitude allowed us to capture the negativity related to attentional engagement onto the targets in these conditions. Evidence for this comes from the permutation tests that showed a meaningful lateralization in the early segment of the RLpcN in those conditions, which was not the case with the N2pc, and from the significant increase in negativity observed when a salient distractor was present in Experiment 2, an effect that, again, was not observed on the N2pc in our previous study (Rashal et al., 2022).

Interestingly, it has been previously reported that an informative endogenous cue could increase the SPCN amplitude (Kiss et al., 2008). However, in that study, the target appeared in one of three possible locations following an informative cue, and six possible locations in the uninformative cue. Thus, rejection of nontargets was probably simpler when an informative cue preceded the search array compared with an uninformative cue. Hence, lower SPCN amplitudes in that study could be indicative of processes related to search and rejection among nontargets in working memory. In the same line, Luria and Vogel (2011) reported an increase in CDA (SPCN) amplitudes for difficult searches in large heterogeneous arrays and proposed that working memory operations were required in their difficult search for the filtering of irrelevant information. In our study, the target was likely to appear in one of two locations (75% in the two lateralized locations); thus, following allocation of attention to the target location by the cue, search and rejection processes were not required, and would have been minimal following a neutral cue.

Importantly, no effect of salient distractor presence was found on the SPCN or the later part of the RLpcN, suggesting that irrelevant information could be filtered without the involvement of post-selection processes in our study. This result is in accord with theories of distractor suppression, postulating that suppression of a salient distractor reduces its interference with target selection (e.g., Gaspelin & Luck, 2018; Liesefeld et al., 2021). Related evidence for distractor suppression has been observed with behavior and EEG (e.g., Feldmann-Wüstefeld et al., 2021; Gaspelin & Luck, 2018;

Liesefeld et al., 2021; Wang et al., 2019), as well as eye movements (e.g., Gaspelin et al., 2017; Sauter et al., 2021). In our previous study (Rashal et al., 2022), laterally presented salient distractors indeed elicited a P_D when the target appeared on the vertical midline, indicating that suppression occurred in the search displays containing a salient distractor. Since the RLpcN reflects processing of the attended target, the lack of a salient-distractor presence effect on the later segment of the component suggests that the mechanisms responsible for the suppression of the distractor did not interact with post-selection processing of the target.

Target salience effects

No effect of search display was found on the RLpcN in Experiment 1, suggesting that our manipulations of target and distractor salience were not consequential to the processing following target selection in a simple discrimination task. However, in Experiment 2, an effect of target salience was observed on the later segment of the component, showing a larger RLpcN area for salient targets. This is in accordance with earlier studies that showed effects of stimulus-driven attention on working memory (e.g., Fine & Minnery, 2009; Santangelo & Macaluso, 2013; Wills-Conn et al., 2019), and the increase of this effect with task difficulty (Fine & Minnery, 2009). Critically, however, the little research that has been done on its neurophysiological basis associated this effect with higher-level operations. For example, Wills-Conn et al. (2019) showed a larger parietal P3 wave during the encoding of salient letters, suggesting target salience affected processes related to cognitive control such as enhanced attention to target information and the updating of working memory. An imaging study by Santangelo and Macaluso (2013) showed that the successful retrieval of objects that were positioned in salient locations during encoding was associated with encoding-related activity in the right superior parietal gyrus and the posterior parietal cortex, where the latter has been associated with different aspects of cognitive control. Some evidence of the effect of salience on working memory was observed in a study using a compound task, in which on some trials, salient distractors did not elicit a P_D but instead elicited a CDA, supposedly indicating that salient distractors that captured attention rather than being suppressed gained access into working memory (Gaspar & McDonald, 2014).

The lack of a target salience effect in Experiment 1 suggests that it is related to the processing of information related to the target rather than to the attended location, since it would have been equally easy to select the salient target in both experiments, while the information needed for making a response in Experiment 2 required detailed processing of target information. Still, only a statistical trend indicating an increase in SPCN area was found for salient targets. Thus,

it seems that the RLpcN is a better indicator of the post-selection processes required in our paradigm—for example, response selection in a compound task, where the attribute that guides the search is irrelevant to the response mapping. This is supported by essentially a lack of SPCN for the easy task in Experiment 1, where, presumably, response selection was facilitated due to the search being guided by a relevant target attribute.

Conclusions

The current study provides novel results concerning the combined effect of top-down and bottom-up attentional control sources in easy and difficult search tasks. By measuring the negative area, we demonstrated a clear effect of task difficulty on the SPCN, and effects of task difficulty and target salience on the later segment of the RLpcN, which is associated with working memory and response selection, as well as an effect of salient distractor presence on the earlier segment of the RLpcN, which is associated with initial deployment of attention to the selected item. Not only does the current study corroborate the conclusions drawn by Rashal et al. (2022) regarding the effects of search and task difficulty in the context of combined top-down and bottom-up sources of attention control, it also provides further support to the approach of conducting complementary stimulus-locked and response-locked analyses in the investigation of the neural mechanisms of attention, while adding to our understanding of this still relatively new component, the RLpcN.

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