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Article

2021

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How to cite

KERZEL, Dirk, HUYNH CONG, Stanislas. Attentional templates are sharpened through differential signal enhancement, not differential allocation of attention. In: Journal of Cognitive Neuroscience, 2021, vol. 33, n° 4, p. 594–610. doi: 10.1162/jocn_a_01677

This publication URL: <https://archive-ouverte.unige.ch//unige:152154>

Publication DOI: [10.1162/jocn_a_01677](https://doi.org/10.1162/jocn_a_01677)



Attentional Templates Are Sharpened through Differential Signal Enhancement, Not Differential Allocation of Attention

Dirk Kerzel and Stanislas Huynh Cong

Abstract

■ In visual search, the internal representation of the target feature is referred to as the attentional template. The attentional template can be broad or precise depending on the task requirements. In singleton search, the attentional template is broad because the target is the only colored element in the display. In feature search, a precise attentional template is required because the target is in a specific color in an array of varied colors. To measure the precision of the attentional template, we used a cue-target paradigm where cueing benefits decrease when the cue color differs from the target color. Consistent with broad and precise attentional templates, the decrease of cueing effects was stronger in feature than in singleton search. Measurements of ERPs showed that the N2pc elicited by the cue decreased with increasing color difference,

suggesting that attention was more strongly captured by cues that were similar to the target. However, the cue-elicited N2pc did not differ between feature and singleton search, making it unlikely to reflect the mechanism underlying attentional template precision. Furthermore, there was no evidence for attentional suppression as there was no cue-elicited P_D, even in conditions where the cueing benefit turned into a same-location cost. However, an index of signal enhancement, the contralateral positivity, reflected attention template precision. In general, there was sensory enhancement of the stimulus appearing at the cued location in the search display. With broad attentional templates, any stimulus at the cued location was enhanced, whereas enhancement was restricted to target-matching colors with precise attentional templates. ■

INTRODUCTION

Visual search is partly guided by an internal representation of the target stimulus, which is referred to as *attentional template* (Duncan & Humphreys, 1989) or target template (Vickery, King, & Jiang, 2005). The attentional template is stored in visual working memory (Geng & Witkowski, 2019; Hout & Goldinger, 2015; Schneider, 2013; Carlisle, Arita, Pardo, & Woodman, 2011; Olivers, Peters, Houtkamp, & Roelfsema, 2011; Bundesen, 1990; Duncan & Humphreys, 1989) and is matched to incoming visual signals for in-depth processing. Top-down guidance by the attentional template contrasts with bottom-up guidance by the saliency of stimuli. In various search tasks, it has been shown that stimuli standing out from the visual scene interfere with the current search goals, although they may be completely irrelevant (Liesefeld & Müller, 2019; Theeuwes, 2018, 2019; Büsel, Voracek, & Ansorge, 2018; Gaspelin & Luck, 2018; Awh, Belopolsky, & Theeuwes, 2012; Lamy, Leber, & Egeth, 2012).

Bottom-up and top-down factors guiding search are not always independent. A well-known example of the interaction between top-down and bottom-up factors is the distinction between search for a target with a unique feature among otherwise equal stimuli (singleton search) and search for a target with a specific feature among varied stimuli (feature search). The search strategies may differ

between singleton and feature search. For instance, when participants search for a shape singleton, the attentional template does not have to include precise target features because the saliency of the target allows for its localization. Instead of searching for a specific target feature, participants may look for a stimulus that is different from the others. As a consequence, attention may be erroneously shifted to other salient stimuli, such as a color singleton, resulting in increased RTs on distractor-present compared to distractor-absent trials (Theeuwes, 1991, 2018, 2019). However, distraction by an irrelevant color singleton disappears when the relevant shape of the target is made inconspicuous by showing it together with various other shapes. In this case, search cannot rely on bottom-up saliency and must be guided by the stored representation of the target features in a top-down manner (Barras & Kerzel, 2016; Leber & Egeth, 2006; Lamy, Leber, & Egeth, 2004; Bacon & Egeth, 1994). While search for singleton and feature targets are often opposed as categorical differences, it may be better to consider them as two extreme forms of attentional template precision. On a continuum, the attentional template is broad in singleton search, whereas it is precise in feature search. However, the exact precision of the attentional template may vary as a function of task requirements.

To illustrate differences between precise and broad attentional templates, we refer to the modified spatial cueing paradigm by Folk, Remington, and Johnston (1992), where a cue and search display are shown in rapid succession.

Attentional capture by the cue is evidenced by shorter RTs when the cue appears at the same location as the target in the search display (valid cue trials) compared to when it appears elsewhere (invalid cue trials). The difference in RTs is commonly referred to as the *cueing effect*. One example for broad attentional templates is Experiment 3 of Anderson and Folk (2012), where participants searched for a color singleton whose color varied unpredictably between two different colors. As a result, the attentional template was broad and cues in dissimilar nontarget colors captured attention (see also Experiment 1 in Irons, Folk, & Remington, 2012). Whereas the experiment of Anderson and Folk (2012) provides evidence for broad attentional templates, other studies suggested that singleton targets do not necessarily result in broad attentional templates. For instance, participants in Folk and Remington (1998) searched for a color singleton, but unlike in Anderson and Folk (2012), only a single target color was shown. With fixed target color, only cues in the target color captured attention, whereas unrelated cue colors did not. Thus, the precision of the attentional template was better than expected on the basis of singleton search alone (see also Harris, Jacoby, Remington, Travis, & Mattingley, 2019; Mertes & Schneider, 2018; Harris, Becker, & Remington, 2015; Eimer & Kiss, 2010). In contrast, precise attentional templates are required when the target is shown with a nontarget in a different color and it is no longer possible to search for a singleton (Kerzel & Witzel, 2019; Grubert & Eimer, 2016; Irons et al., 2012; Ansorge, Horstmann, & Carbone, 2005). Thus, attentional templates are necessarily precise in feature search, but may vary between broad and precise in singleton search (see also Becker, Martin, & Hamblin-Frohman, 2019).

To measure the precision of attentional templates more directly, Kerzel (2019) manipulated the difference between cue and target color in degrees of rotation in CIELAB color space. CIELAB is a model of color appearance where distances approximate perceived color differences (Witzel & Gegenfurtner, 2015, 2018). Previous research had mostly distinguished between target-matching cues and target-nonmatching cues. However, nonmatching cues may approach the target color to various degrees. For instance, a cue color that differs from the target color by $\pm 60^\circ$ is dissimilar, whereas a cue that differs by $\pm 30^\circ$ from the target color is more similar, but both would be categorized as target-nonmatching. Measuring cueing effects for cue colors between the dissimilar $\pm 60^\circ$ cue color and the target-matching 0° color allows for a description of the precision of attentional templates. In general, cueing effects were largest for the target-matching cue color and decreased with increasing difference between cue and target color. This decrease was observed for feature search, but more surprisingly, it was also observed for singleton search, suggesting that the attentional template was more precise than pure singleton search would predict. However, the cueing effects decreased more strongly for feature than singleton search, indicating that the precision

of the attentional template was better in feature than in singleton search. Furthermore, opposite results were observed for large color differences ($\pm 60^\circ$). In singleton search, a cueing benefit was observed with shorter RTs for targets at the cued location. In contrast, there were same-location costs in feature search, with longer RTs at the cued than at uncued locations.

In the current study, we measured ERPs to investigate the mechanisms underlying the sharpening of the attentional template. There are at least two nonexclusive mechanisms that may serve this purpose. The first possibility to achieve precise attentional templates is to restrict attentional selection to the template-matching colors. Improvements in attentional selectivity should be evident in an electrophysiological marker of attentional selectivity, the N2pc. Broad attentional templates should result in attentional selection of cues in colors different from the target, whereas precise attentional templates should restrict attentional selection to cues in target-similar colors. The N2pc is a more negative voltage contralateral than ipsilateral to candidate target objects (Zivony, Allon, Luria, & Lamy, 2018; Eimer, 1996; Luck & Hillyard, 1994; also referred to as PCN, Töllner, Müller, & Zehetleitner, 2012). The N2pc occurs at posterior electrodes PO7/8, from about 180–300 msec after stimulus onset. Electrophysiological results obtained in the modified spatial cueing paradigm suggests that attentional selectivity for target features is reflected in the cue-elicited N2pc because the cue-elicited N2pc was larger for target-matching cue colors (Mertes & Schneider, 2018; Grubert & Eimer, 2016; Mertes, Wascher, & Schneider, 2016; Eimer & Kiss, 2008; Lien, Ruthruff, Goodin, & Remington, 2008). Furthermore, Yeh, Yeh, and Kuo (2019) have already established that the N2pc is sensitive to the similarity between target and distractors in the shape dimension.

In the context of the differential allocation of attention, it may also be possible that dissimilar colors are attentionally suppressed, which may explain why cueing benefits with dissimilar colors turn into same-location costs. Attentional suppression of the cue has been invoked to account for same-location costs with dissimilar cue colors in feature search (Eimer, Kiss, Press, & Sauter, 2009; Lamy & Egeth, 2003), but nonattentional explanations have also been put forth (Schoeberl, Ditye, & Ansorge, 2018; Carmel & Lamy, 2014, 2015). Under the suppression hypothesis, we expect cues with dissimilar colors in feature search to elicit an ERP linked to attentional suppression, the P_D . The P_D is a positivity contralateral to the suppressed stimulus at posterior electrodes PO7/8 (Liesefeld, Liesefeld, Töllner, & Müller, 2017; Burra & Kerzel, 2013; Feldmann-Wüstefeld & Schubö, 2013; Sawaki & Luck, 2013; Hickey, Di Lollo, & McDonald, 2009; see reviews in Gaspelin & Luck, 2018; Geng, 2014). However, the literature is inconsistent regarding the precise temporal interval of the P_D . The P_D has been reported in early intervals from 150 to 200 msec (e.g., Weaver, van Zoest, & Hickey, 2017; Sawaki & Luck, 2010) but also in late intervals from 300 to 400 msec (e.g., Liesefeld et al., 2017; Sawaki, Geng, & Luck, 2012). The early

P_D may be related to sensory imbalance (Barras & Kerzel, 2017; Schönhammer, Grubert, Kerzel, & Becker, 2016; Jannati, Gaspar, & McDonald, 2013; Leblanc, Prime, & Jolicoeur, 2008; Luck & Hillyard, 1994), and the late P_D may be related to the termination of an attention shift (Sawaki et al., 2012; Hilimire, Mounts, Parks, & Corballis, 2011). Therefore, we focused on the P_D in the same time interval as the N2pc (see also Schönhammer, Becker, & Kerzel, 2020; Barras & Kerzel, 2016; Gaspar & McDonald, 2014; Jannati et al., 2013) where it may reflect the flip side of attentional selection.

The second possible mechanism to achieve precise attentional templates may be to modulate cue-induced signal enhancement of the subsequent search display. Livingstone, Christie, Wright, and McDonald (2017) observed that the N2pc to target-matching cues was followed by a contralateral positivity (CP) to the search display. The CP occurred at the same posterior electrodes as the N2pc, but, in the time range of the P1, about 100–150 msec after onset of the search display (Livingstone et al., 2017). It is likely that the CP results from an increase of the contralateral P1 to the stimulus appearing at the same location as the cue. Previous research has established that an increased P1 to cued targets reflects attentional enhancement of perceptual processing (Allon & Luria, 2019; Fukuda & Vogel, 2009; Störmer, McDonald, & Hillyard, 2009; Hopfinger & Ries, 2005; McDonald, Teder-Salejarvi, Di Russo, & Hillyard, 2005; Heinze, Luck, Mangun, & Hillyard, 1990; Luck, Heinze, Mangun, & Hillyard, 1990). Although the CP is induced by the lateralized cue, it is triggered by the search display. Consequently, later presentation of the search display delays the CP. Livingstone et al. (2017) suggested that the CP reflects signal enhancement of any stimulus in the search display appearing at the previously cued location. Thereby, the target stimulus is enhanced on valid cue trials, which reduces RTs. In contrast, a nontarget stimulus is enhanced on invalid cue trials, which increases RTs because resources are diverted from the target location. To account for changes in the precision of the attentional template, we suggest that the CP may vary little as a function of cue color when the attentional template is broad, whereas the CP closely follows the cue color when the attentional template is precise.

EXPERIMENTS 1 AND 2

We employed the modified spatial cueing paradigm to investigate the neural basis of attentional template precision. To induce broad attentional templates, participants in Experiment 1 searched for a color singleton among gray nontargets. As the target was the only colored item, it was not necessary to search for a specific color. In contrast, participants in Experiment 2 performed feature search for a specific color in a multicolored search display, which required a precise attentional template. We varied the difference between cue and target color in CIELAB-space (see Figure 1). The cue color matched the target color (i.e., 0° cue color) or it differed

by $\pm 30^\circ$ or $\pm 60^\circ$. The dissimilar $\pm 60^\circ$ cue color is expected to result in cueing benefits in singleton search and cueing costs in feature search (Kerzel, 2019).

We measured ERPs and analyzed the difference between contra- and ipsilateral voltages at posterior electrodes PO7/8. To account for changes in cueing effects between singleton and feature search, we proposed two mechanisms, each of which is associated with a distinct electrophysiological signature. According to the hypothesis of differential allocation of attention, we expect small differences in the cue-elicited N2pc between similar and dissimilar cue colors in singleton search, but large differences in feature search. If there was attentional suppression of dissimilar cue colors in feature search, the N2pc may turn into a P_D for the $\pm 60^\circ$ cue color. According to the hypothesis of differential signal enhancement, we expect small differences in the CP between similar and dissimilar cue colors in singleton search, but large differences in feature search. Because our paradigm was similar to Livingstone et al. (2017), we can be sure that the N2pc/ P_D and the CP components occur in distinct time windows at posterior electrodes PO7/8. Statistical support for either of the two hypotheses would be an interaction between search task and cue color.

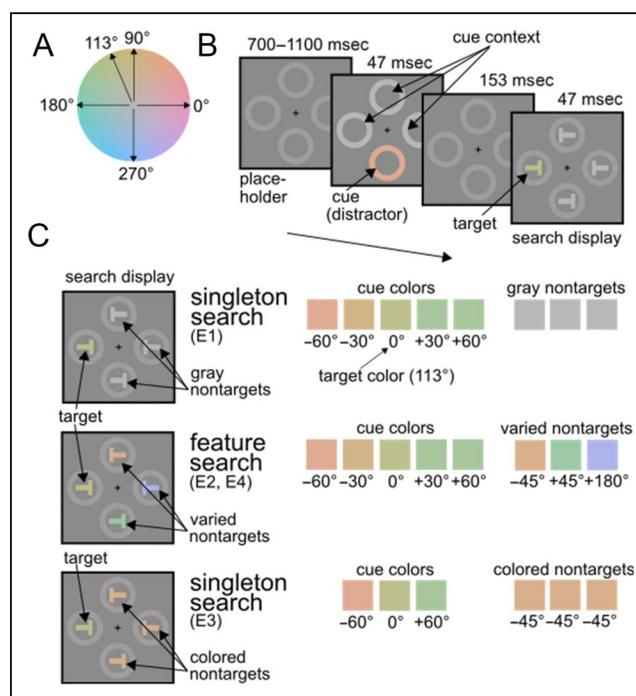


Figure 1. Illustration of experimental stimuli. (A) illustrates the experimental colors. We used colors from CIELAB-space that were at the same distance (radius) from gray and therefore had the same saturation. The hue of the colors corresponds to the rotation of the color around gray. (B) shows the time course of a trial. In the experiments, the placeholders were outline rings and not filled rings as in the illustration. (C) shows the different search displays, cue colors, and nontarget colors in Experiments 1–4 (E1–E4). The degree of rotation from the target color is indicated for the cue and nontarget colors.

Methods

Participants

Sample size was based on the study by Livingstone et al. (2017), which had 20 participants per experimental condition. We had 24 data sets in the singleton group (4 men, age: $M = 22$ years, $SD = 6$ years) and 24 in the feature group (6 men, age: $M = 21$ years, $SD = 3$ years) after replacing two data sets because of missing trials (see below). The study was approved by the ethics committee of the Faculty of Psychology and Educational Sciences of the University of Geneva and was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Informed consent was given before the experiment.

Apparatus and Stimuli

Stimuli were displayed on a 21-in. cathode ray tube (CRT) monitor with a refresh rate of 85 Hz and a pixel resolution of 1280×1024 (horizontal \times vertical), viewed at 80 cm. The Psychtoolbox (Kleiner, Brainard, & Pelli, 2007; Brainard, 1997) was used to run the experiment.

A central fixation cross with a diameter of 0.5° was shown throughout. There was a placeholder, a cue, and a search display. The placeholder display contained four outline rings. Displays with four possible positions have been shown to reliably elicit the pattern of contingent attentional capture (Yeh & Liao, 2008, 2010). The distance from the center of the fixation cross to the center of the outline rings was 3° . The inner and outer circle making up the outline rings had a radius of 1.2° and 1.4° , respectively. The line-width of the circles was 1 pixel or 0.02° . In the cue display, the outline rings were filled. Three rings were filled with the same light gray as the outline rings and one ring with a color. The colored ring was the cue. In the search display, a T rotated by 90° clockwise or counterclockwise was shown inside each placeholder. The bars making up the rotated T were 1° long and 0.2° thick. In each display, two Ts were rotated clockwise and two counterclockwise.

The color differences were quantified in CIELAB-space. The white-point of CIELAB was $xyY = (0.29, 0.30, 89.27)$. Stimuli were presented on a gray background with the chromaticities of the white-point and a lightness of $L^* = 55$, which corresponds to a luminance of 20.5 cd/m^2 . In the context of this study, "color" is synonymous with "hue" because neither saturation nor lightness varied. The fixation cross, the placeholders, the achromatic cues, and the achromatic Ts were light gray ($L^* = 73$ or 40.3 cd/m^2). The colors that served as cue, target, and nontarget colors were sampled along a hue circle at a lightness of $L^* = 73$ and a saturation (chroma) of 34. The color of the target was fixed for each participant.

Procedure

A trial started with the presentation of the fixation cross for a randomly selected duration between 0.7 and 1.1 sec. Then,

the cue display was shown for 47 msec followed by a placeholder display for 153 msec. Finally, the search display was shown for 47 msec. Thus, the cue-target SOA was 200 msec and the total sequence lasted 247 msec. Participants were asked to report the orientation of the target T by mouse click. Participants pressed the left mouse button for a T rotated counterclockwise and the right mouse button for a T rotated clockwise. Choice errors and late trials (RTs > 2 sec) were reported to the participant by visual feedback. Participants were asked to maintain fixation on the central fixation cross, to ignore the cue, and to respond as rapidly as possible while keeping the error rate below 10%. After blocks of 96 trials, mean RT and the error rate were shown during a self-determined break of at least 5 sec. At the beginning of the experiment, participants practiced the experimental task until they felt comfortable with it. Practice trials were not recorded, but participants completed at least 30 trials.

Design

In singleton search (Experiment 1), the nontargets were gray. In feature search (Experiment 2), the nontargets deviated by -45° , $+45^\circ$, and $+180^\circ$ from the target color and were randomly placed on each trial. The 96 combinations of cue position (left, right, top, bottom), target position (left, right, top, bottom), cue color (0° , $\pm 30^\circ$, $\pm 60^\circ$), and response (left, right) were presented once in a block of trials. Participants worked through nine trial blocks for 864 trials. The cue appeared at the target location on 25% of trials (valid cue trials) and on a different location on 75% of trials (invalid cue trials). Thus, the cue position did not predict the target position. The target color was balanced between participants. Initially, we had a set of eight colors, from 22.5° of rotation in CIELAB-space to 337.5° in steps of 45° . However, we found the bluish colors (202.5° and 247.5°) to be harder to discriminate than the others (see also Bae, Olkkonen, Allred, & Flombaum, 2015), which may be because of the relatively low saturation allowed for by the CRT display. Therefore, these colors were removed from the set of colors. Four participants in each group received one of the remaining six target colors.

Electrophysiological Recording and Initial Data Processing

An actiCHamp amplifier (Brain Products) with active Ag/AgCl electrodes was used. Data were recorded using the PyCorder software by Brain Products. In the filter settings of the PyCorder software, we deactivated cutoffs and the notchfilter. Continuous EEG was sampled at 1000 Hz from 26 scalp electrodes and six additional electrodes placed on the outer canthi of each eye, above and below the right eye, and on each earlobe. Cz served as online reference and AFz as ground site. The data were analyzed using ERPLAB (Lopez-Calderon & Luck, 2014), an extension of EEGLAB (Delorme & Makeig, 2004). Raw EEG was

rereferenced to the average earlobes and filtered between 0.1 and 30 Hz with a bandpass second-order Butterworth filter (roll-off 12 db/octave, command *pop_basicfilter* in ERP-lab). The difference between left and right eye electrode constituted the HEOG channel, and the difference between upper and lower eye electrode constituted the VEOG channel. The EEG was segmented into 500-msec epochs extending from 100 msec before to 400 msec after stimulus onset. The first 100 msec served as the baseline.

Results

Data from all experiments are available on the page <https://osf.io/ez3td/> in the Open Science Framework.

Exclusion of Trials and Data Sets

Trials with behavioral errors and RTs slower than 2 sec were excluded from analysis for both behavioral and ERP analysis. Furthermore, individual trials in the ERP analysis were rejected when blinks and vertical eye movements (difference in VEOG channel exceeding $\pm 50 \mu\text{V}$), horizontal eye movements (steps in HEOG channel exceeding $\pm 16 \mu\text{V}$), and muscular or other artifacts (any electrode exceeding $\pm 80 \mu\text{V}$) occurred between 100 msec before to 400 msec after stimulus onset. Two data sets in the feature group were replaced because more than 25% of the trials were lost (39% and 37% lost trials, respectively). The 25% criterion is consistently applied in our laboratory and is frequently used in the literature on the N2pc (Luck, 2014).

Statistical Corrections

For the ANOVAs, Greenhouse–Geisser correction of the degrees of freedom was applied when the assumption of sphericity was violated. For the independent-samples *t* tests, the degrees of freedom were corrected when variances were unequal. For multiple-paired *t* tests, the critical *p* value was adjusted to control the FDR (Benjamini & Hochberg, 1995), but the uncorrected *p* values are reported for clarity.

Behavior

Forty-eight data sets were analyzed. Trials with RTs slower than 2 sec were excluded (0.01%). Subsequently, data were trimmed for each participant and condition by removing trials with RTs that were more than 2.5 *SDs* above the respective condition mean. This resulted in the exclusion of additional 2% of the trials for the behavioral analysis. Mean RTs are shown in Figure 2. Mean cueing effects (invalid–valid) for RTs and percentage of choice errors are shown in Table 1. In addition, Table 1 reports whether cueing effects were significantly different from zero. Individual mean RTs of correct responses for each experiment were

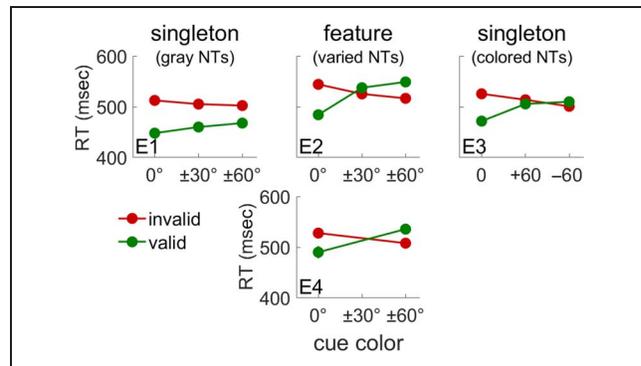


Figure 2. RTs in invalid and valid cue trials as a function of cue color and experiment (E1–E4). Error bars show the *SEM* (between-participants), but are mostly smaller than the symbols. NT = nontarget.

subjected to a 3 (Cue Color: 0° , $\pm 30^\circ$ and $\pm 60^\circ$) \times 2 (Cue Validity: valid, invalid) repeated-measures ANOVA.

In singleton search (Experiment 1), there was a main effect of Cue Color, $F(2, 46) = 3.92, p = .027, \eta_p^2 = .146$, and a main effect of Cue Validity, $F(1, 23) = 134.06, p < .001, \eta_p^2 = .854$, but more importantly, there was an interaction of Cue Color and Cue Validity, $F(1.6, 36.5) = 18.04, p < .001, \eta_p^2 = .44$. The interaction showed that the cueing effect was largest when the cue was in the target color (65 msec for 0° cue color) and decreased with increasing color difference (45 and 35 msec for $\pm 30^\circ$ and $\pm 60^\circ$ cue colors, respectively).

In feature search (Experiment 2), there was also a main effect of Cue Color, $F(2, 46) = 43.41, p < .001, \eta_p^2 = .654$, and a significant interaction of Cue Color and Cue Validity was observed, $F(2, 46) = 137.54, p < .001, \eta_p^2 = .857$. As for singleton search, the interaction showed that the cueing effect was largest when the cue was in the target color (60 msec for 0° cue color) and decreased with increasing color difference (-12 and -32 msec for $\pm 30^\circ$ and $\pm 60^\circ$ cue colors, respectively). However, the decrease of the cueing effect was stronger in feature search than in singleton search.

As can be seen in Figure 2, cueing effects in Experiment 1 decreased only moderately and were always cueing benefits, whereas cueing effects turned into same-location costs in Experiment 2. The larger decrease of cueing effects with feature search was confirmed by adding search task (i.e., experiment) as a between-participant factor to the ANOVA. The three-way interaction between Search Task, Cue Color, and Cue Validity was significant, $F(2, 92) = 37.55, p < .001, \eta_p^2 = .449$, confirming that the decrease of cueing effects was stronger with feature than with singleton search.

Next, we ran the same mixed three-way ANOVA (Search Task \times Cue Color \times Cue Validity) on percentage of choice errors. The main effect of Cue Validity and all two-way interactions were significant, $F_s > 3.77, p_s < .027, \eta_p^2 > .076$. More importantly, we found that the three-way ANOVA approached significance, $F(2, 92) = 3.04, p = .053, \eta_p^2 = .317$. Inspection of Table 1 shows that the pattern of choice

Table 1. Mean Cueing Effects (Invalid–Valid) in RTs (msec) and Choice Errors (%) for Experiments 1–4

	<i>Cue Color</i>	<i>E1</i>	<i>E2</i>	<i>E4</i>	<i>Cue Color</i>	<i>E3</i>
RTs						
	0°	65* (23)	60* (32)	38* (30)	0°	54* (30)
	±30°	45* (24)	–12 (28)		+60°	8 (29)
	±60°	35* (27)	–32* (19)	–28* (14)	–60°	–9 (20)
Errors						
	0°	3* (2.6)	1.4* (2.3)	2* (2.8)	0°	2.5* (3.1)
	±30°	2.8* (2.7)	–1.1 (2.6)		+60°	0.9 (2.6)
	±60°	0.7 (2.3)	–2.4* (2.9)	–2.7* (2.6)	–60°	–0.7 (2.4)

The standard deviation of the mean (between-participants) is indicated in parenthesis. Means that were significantly different from zero are indicated by an asterisk. FDR was controlled using the method of Benjamini and Hochberg (1995). Because Experiments 1 and 2 were analyzed together, we corrected for six tests in Experiments 1–2, but only for three in Experiment 3 and two in Experiment 4. Note that the order of Experiments 3 and 4 in the table was turned around for ease of exposition.

errors resembled the pattern of RTs. There were positive cueing effects in the singleton group that decreased with increasing difference between cue and target color. In the feature group, the decrease was stronger and there were same-location costs with the ±60° cue color. The overall percentage of choice errors was 3.1%.

Electrophysiology

After rejecting trials with electrophysiological artifacts, behavioral errors, or RTs longer than 2 sec, 90% of the trials of interest remained for analysis. We analyzed trials where the cue was presented on a lateral position, separately for each cue color, which resulted in 144 trials per bin. On average, 129 trials (range: 104–142) were retained for the 0° cue color, 130 trials (range: 102–142) for the ±30° cue color, and 130 trials (range: 109–141) for the ±60° cue color. The ipsi- and contralateral potentials at electrodes PO7/8 are shown in the three upper rows of Figure 3, and the respective difference waves (obtained by subtracting ipsi- from contralateral activity) are shown in the bottom row of Figure 3.

Analysis intervals for the N2pc and CP were selected according to previous studies (Livingstone et al., 2017; Sawaki & Luck, 2013). The cue-elicited N2pc was measured between 175 and 225 msec after cue onset. The CP was measured between 300 and 350 msec after cue onset, which corresponds to 100–150 msec after target onset because the target was presented 200 msec after the cue. In addition, we observed an early positivity that occurred about 110 msec after cue onset. The positivity is referred to as Ppc, and one (but not the only) interpretation is that it reflects imbalanced sensory stimulation (Barras & Kerzel, 2017; Schönhammer et al., 2016; Jannati et al., 2013; Leblanc et al., 2008; Luck & Hillyard, 1994). For the Ppc, we placed

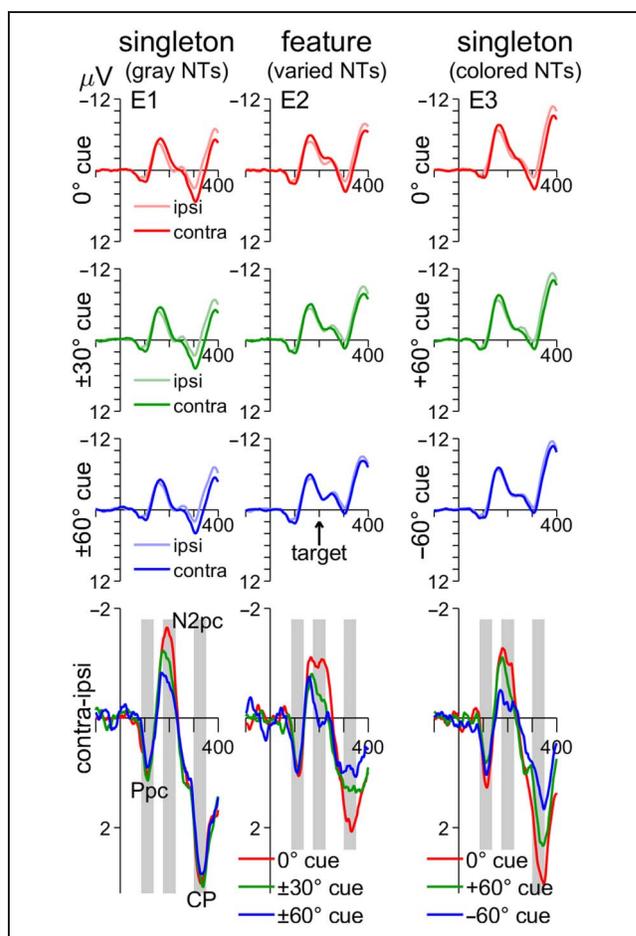


Figure 3. Electrophysiological results from Experiments 1–3 as a function of cue color. The three upper rows show the ERPs to lateral cues at ipsi- and contralateral electrodes PO7/8. The bottom row shows the difference waves between contra- and ipsilateral electrodes. The shaded areas indicate the averaging intervals corresponding to the Ppc, N2pc, and CP. Target onset was 200 msec after cue onset.

the analysis interval on the maximum deflection, from 86 to 136 msec after cue onset.

N2pc

We subjected average voltage differences in the 50-msec interval from 175–225 msec after cue onset to a 2 (Search Task: singleton, feature) \times 3 (Cue Color: 0°, \pm 30° and \pm 60°) mixed ANOVA. The cue-elicited N2pc decreased with increasing difference between cue and target color, $F(1.5, 69.2) = 32.34, p < .001, \eta_p^2 = .413$. The magnitude of the cue-elicited N2pc was $-1.2, -0.7,$ and $-0.3 \mu\text{V}$ for the 0°, \pm 30°, and \pm 60° cue color, respectively. The N2pc tended to be larger in singleton than in feature search (-1 vs. $-0.5 \mu\text{V}$), $F(1, 46) = 2.94, p = .093, \eta_p^2 = .06$. The suppression hypothesis predicts the occurrence of a P_D with dissimilar cue colors in feature search. However, there was no significant P_D for the \pm 60° cue color ($0.002 \mu\text{V}$), $p = .991$. All the remaining conditions showed significant N2pcs, $ts(23) > 2.99, ps < .006$, Cohen's $d_z > 0.61$, except for the \pm 30° cue color in feature search ($-0.5 \mu\text{V}$), $t(23) = 1.94, p = .065$. Furthermore, the hypothesis of differential allocation of attention predicts an interaction of search task and cue color. However, this interaction was far from significance, $p = .692$, showing that the effect of Cue Color was similar in both tasks.

CP

We subjected average voltage differences in the 50-msec interval from 300–350 msec after cue onset to the same mixed 2 \times 3 ANOVA as above. There was a main effect of Cue Color, $F(1.7, 77.8) = 7.67, p = .001, \eta_p^2 = .143$. More importantly, there was a significant interaction between Cue Color and Search Task, $F(2, 92) = 4.05, p = .021, \eta_p^2 = .081$, as predicted by the hypothesis of differential signal enhancement. We followed up on the significant interaction by running separate one-way ANOVAs on each search task. In singleton search (Experiment 1), the effect of Cue Color was not significant, $p = .643$. The average CP across the three cue colors was $2.7 \mu\text{V}$. In contrast, there was a significant effect of Cue Color in feature search (Experiment 2), $F(2, 46) = 11.23, p < .001, \eta_p^2 = .328$. The CP decreased with increasing color difference between cue and target. The CP was $1.9, 1.3,$ and $1 \mu\text{V}$ for the 0°, \pm 30°, and \pm 60° cue colors, respectively. One-sample t tests showed that the CP was significantly different from zero in all conditions, $ts(23) > 6.58, ps < .001$, Cohen's $d_z > 1.33$.

Ppc

We analyzed the Ppc interval to rule out that the early sensory imbalance contributed to the later differences in the ERPs. We subjected average voltage differences in the 50-msec interval from 86–136 msec after cue onset to the same mixed 2 \times 3 ANOVA as above. There were no

significant effects, $ps > .588$. One-sample t tests showed that the Ppc was significantly different from zero in each condition, $ts(23) > 3.32, ps < .003$, Cohen's $d_z > 0.68$. The mean voltage difference of the Ppc was $0.7 \mu\text{V}$.

HEOG

We analyzed the voltages at the lateral eye electrodes to rule out potential contamination of ERPs by eye movements. Therefore, the voltage at the eye electrode ipsilateral to the cue was subtracted from the voltage at the eye electrode contralateral to the cue. We conducted the same mixed 2 \times 3 ANOVA on the mean lateralized HEOG in the same time intervals as above (Ppc, N2pc, CP). Neither of the three ANOVAs yielded a significant effect, $ps > .174$, suggesting that effects at electrodes PO7/8 were not contaminated by eye movements.

Discussion

We assessed the neural correlates of attentional template precision in the contingent capture paradigm. The precision of the attentional template was manipulated by requirements of the search task. In singleton search, a broad attentional template was sufficient because the target was the only colored item in the display. In feature search, a precise attentional template was necessary because the target had to be located amidst varied nontarget colors. We measured cueing effects to describe the precision of the attentional template. Compared to singleton search, cueing effects decreased more strongly with increasing color difference in feature search. Furthermore, precise attentional templates in feature search resulted in same-location costs for 60° cue colors. We evaluated two hypotheses regarding the mechanisms underlying attentional template precision: differential allocation of attention and differential signal enhancement.

The hypothesis of differential allocation of attention holds that attention is allocated to any cue color in singleton search, whereas it is allocated according to the match between cue and target color in feature search. The hypothesis predicts a stronger effect of cue color on the N2pc in feature than in singleton search. However, we observed no two-way interaction between search task and cue color, which is at odds with the hypothesis of differential allocation of attention. Rather, the cue-elicited N2pc decreased with cue color in both feature and singleton search. Previous research has already established that the N2pc is larger for target-matching than target-nonmatching cue colors (Grubert & Eimer, 2016; Lien et al., 2008). However, the cue and target colors were vastly different in these studies (e.g., green and red). Here, we show that the cue-elicited N2pc follows the similarity between cue and target colors in a continuous manner. Thus, the N2pc may account for the general decrease of cueing effects with increasing difference between cue and

target color. However, the N2pc does not reflect the more precise attentional template in feature compared to singleton search. Furthermore, it was previously suggested that same-location costs with dissimilar cue colors in feature search result from attentional suppression of nonmatching features (Eimer et al., 2009; Lamy & Egeth, 2003). If same-location costs resulted from attentional suppression, the N2pc component was expected to turn into a P_D component. However, there was no significant lateralized component (neither P_D nor N2pc) in the respective condition.

Finally, we evaluated the hypothesis of differential signal enhancement, which predicts larger changes of the CP with precise than broad attentional templates. Consistent with differential signal enhancement, we observed changes of the CP with increasing color difference in feature search, but not in singleton search. These results suggest that enhancement of the stimulus at the cued location was contingent on the match between cue and target color in feature search, but not in singleton search. In singleton search, signal enhancement was similar for all cue colors. In feature search, signal enhancement was stronger for target-similar than target-dissimilar cue colors. Thus, differential signal enhancement may underlie differences in attentional template precision between singleton and feature search.

EXPERIMENT 3

One objection to the conclusions from Experiments 1 and 2 is that the search displays in singleton and feature search differed strongly. Because the CP was triggered by the search display, spurious effects may have resulted from individual nontarget stimuli in feature search (e.g., the 180° nontarget color). To rule out confounding effects, we replaced the gray nontargets by nontargets of the same color (see Figure 1C). With gray nontargets in Experiment 1, it was sufficient to search for any color, whereas the colored nontargets in the current experiment required search for a different color, which implies a more precise attentional template. The color difference between target and colored nontargets was -45° , which is less than the color difference between target and the dissimilar cue colors ($\pm 60^\circ$). Because the precision had to be at least 45° to find the target, we do not expect the $\pm 60^\circ$ cue colors to result in strong cueing benefits. However, cueing effects may differ between the $+60^\circ$ and -60° cue colors because of the similarity with respect to the nontarget color. The $+60^\circ$ cue color was rotated away from the nontarget colors, resulting in a color difference of 105° between the -45° nontarget and $+60^\circ$ cue color. Thus, the difference between nontarget and $+60^\circ$ cue color was larger than the difference between nontarget and target color (i.e., 105° vs. 45°), which may cause the $+60^\circ$ cue to be more salient than the target. In contrast, the -60° cue color was rotated toward the nontarget color, so that the -60° cue color was more similar to the -45° nontarget

than to the target color. If there was attentional suppression of distracting stimuli, it would be useful to apply it to the -60° cue color because this would also facilitate rejection of the -45° nontarget color.

Methods

The methods were as in Experiment 1 with the following exceptions. Instead of gray nontargets, we presented nontargets with a color that was rotated by -45° from the target color. The cue colors were rotated by 0° , $+60^\circ$, and -60° from the target. The 96 combinations of cue position, target position, response, and cue color (0° , $+60^\circ$, -60°) were presented once in a block of trials. Participants worked through 10 trial blocks for 960 trials. The target color remained fixed for each participant, but the rotation of the nontargets colors was flipped after half of the trials. As in Experiment 1, the six possible target colors were initially counterbalanced across participants. We collected data until we had 24 valid data sets (5 men, age: $M = 21.2$ years, $SD = 4$ years). Eight data sets were discarded. The reason were problems at electrodes PO7/8 in one case, excessive choice errors in two cases (12% and 33%), and data loss exceeding 25% in six cases (between 34% and 60% rejected trials).

Behavior

Trials with slow responses (0.2%) and outliers (2.3%) were excluded from analysis. Mean RTs are shown in Figure 2, and mean cueing effects are shown in Table 1.

Individual mean RTs of correct responses were subjected to a 3 (Cue Color: 0° , $+60^\circ$ and -60°) \times 2 (Cue Validity: valid, invalid) repeated-measures ANOVA. There was a main effect of Cue Color, $F(2, 46) = 11.09, p < .001, \eta_p^2 = .325$, and Cue Validity, $F(1, 23) = 28.03, p < .001, \eta_p^2 = .549$, but more importantly, a significant interaction, $F(2, 46) = 37.6, p < .001, \eta_p^2 = .62$. The interaction showed that the cueing effect was largest when the cue was in the target color (54 msec for 0° cue color), and strongly reduced with the $+60^\circ$ and -60° cue colors (8 and -9 msec, respectively). Because the cueing effect was close to zero with the $+60^\circ$ and -60° cue colors, but differed in opposite directions from zero, we conducted a follow-up 2 (Cue Color: $+60^\circ$, -60°) \times 2 (Cue Validity: valid, invalid) ANOVA. There was a significant interaction, $F(2, 23) = 8.27, p = .009, \eta_p^2 = .265$, showing that the cueing effects differed significantly from each other. Table 1 shows, however, that neither cueing effect differed significantly from zero.

Percentage of choice errors were subjected to the same 3 \times 2 repeated-measures ANOVA as RTs. The main effect of Cue Validity was significant, $F(1, 23) = 12.5, p = .002, \eta_p^2 = .352$, indicating that more errors occurred on invalid than valid trials (3.4% vs. 2.5%). More importantly, the crucial two-way ANOVA was significant, $F(2, 46) = 7.32, p = .002, \eta_p^2 = .241$. Inspection of Table 1 shows that cueing effects in choice errors resembled the cueing effects in RTs.

Electrophysiology

After rejecting trials with electrophysiological artifacts, behavioral errors, or RTs longer than 2 sec, 89% of the trials of interest remained for analysis. There were 160 trials per bin. On average, 141 trials (range: 116–156) were retained for the 0° cue color, 141 trials (range: 113–154) for the +60° cue color, and 145 trials (range: 130–155) for the –60° cue color.

N2pc

We subjected average voltage differences in the 50-msec interval from 175–225 msec after cue onset to a one-way (cue color: 0°, +60° and –60°) repeated-measures ANOVA. The main effect of Cue Color was significant, $F(1.5, 34.5) = 6.69, p = .003, \eta_p^2 = .225$. The magnitude of the cue-elicited N2pc was –1, –0.7, and –0.3 μV for the 0°, +60° and –60° cue color, respectively. The N2pc was significant for the 0° and +60° cue colors, $t(23) > 3.32, ps < .003$, Cohen's $d_z > 0.67$, but not for the –60° cue color, $t(23) = 1.67, p = .108$, Cohen's $d_z = 0.34$. Surprisingly, the N2pc elicited by the 0° and +60° cue colors did not differ significantly (–1 vs. –0.7 μV), $t(23) = 1.63, p = .117$, Cohen's $d_z = 0.33$, although behavioral cueing effects were only observed for the 0° cue color. In contrast, the N2pc elicited by the +60° and –60° cue colors differed significantly (–0.7 vs. –0.3 μV), $t(23) = 2.87, p = .009$, Cohen's $d_z = 0.59$, which reflects the difference in behavioral cueing effects.

CP

We subjected average voltage differences in the 50-msec interval from 300–350 msec after cue onset to the same one-way ANOVA as above. There was a main effect of Cue Color, $F(2, 46) = 20.22, p = .001, \eta_p^2 = .468$. The CP was 2.6, 1.9, and 1.2 μV for the 0°, +60°, and –60° cue colors. The CP differed significantly between the 0° and +60° cue colors, $t(23) = 6.46, p < .001$, Cohen's $d_z = 1.32$, and also between the +60° and –60°, $t(23) = 2.78, p = .011$, Cohen's $d_z = 0.57$. The decrease of the CP corresponds to the decrease of the behavioral cueing effects, although the quantitative fit is poor. Furthermore, one-sample t tests showed that the CP for each cue color was significantly different from zero, $ts(23) > 5.98, ps < .001$, Cohen's $d_z > 1.22$.

Ppc

We subjected average voltage differences in the 50-msec interval from 89–139 msec after cue onset to the same one-way ANOVA as above. The main effect of Cue Color did not reach significance, $F(2, 46) = 2.5, p = .09, \eta_p^2 = .098$. One-sample t tests showed that the Ppc for each cue color and search group was significantly different from zero, $ts(23) > 4.36, ps < .001$, Cohen's $d_z > 0.89$. The mean voltage difference of the Ppc was 0.7 μV .

HEOG

We conducted the same one-way ANOVA on the mean lateralized HEOG in the same time intervals as above (Ppc, N2pc, CP). Neither of the three ANOVAs yielded a significant effect, $ps > .07$, suggesting that effects at electrodes PO7/8 were not contaminated by eye movements.

Discussion

We used homogeneously colored nontargets in Experiment 3 to avoid the pitfalls of heterogeneous colors in feature search of Experiment 2. Although the target was a singleton, the similarity of the nontarget color (–45°) required a precise attentional template. Similar to feature search in Experiment 1, we observed that the CP followed the cueing effects. The CP was largest for the 0° cue color and decreased for the +60° and –60° cue colors. However, it should be noted that the quantitative fit between the CP and the cueing effects was poor. Cueing effects dropped strongly from the 0° to the +60° cue color (54 vs. 8 msec), but only slightly from +60° and –60° (8 vs. –9 msec). In contrast, the CP showed an almost linear decrease. Nonetheless, the hypothesis of signal enhancement is well-supported by the present data. In contrast, we found no evidence for the differential allocation of attention. The N2pc did not differ between the 0° and +60° cue colors, although there was a cueing effect of 54 msec with the 0° cue and only a nonsignificant 8-msec difference with the +60° cue. Furthermore, we did not observe a P_D, although suppression of the –60° cue color was promoted by its similarity to the nontarget color.

EXPERIMENT 4

To confirm that the CP was a response to the search display reflecting signal enhancement, and not a response to the cue, we introduced a condition with a longer delay between cue and target (see Livingstone et al., 2017). If the CP component was related to the search display, the CP is expected to disappear in the current analysis interval. However, if the CP persists even with delayed onset of the search display, it is probably elicited by the cue and may be a late positivity related to cue suppression, as suggested by some authors (Mertes et al., 2016; Sawaki & Luck, 2013). We randomly mixed two SOAs between cue and target. The first SOA was the same as in Experiment 1, the second was about 100 msec longer. With the longer SOA, we expect the CP to disappear in the 300- to 350-msec analysis interval locked to cue onset (i.e., it should occur between 400 and 450 msec after cue onset, outside the analysis interval).

Methods

The methods were as in Experiment 2 with the following exceptions. Only two cue colors (0°, ±60°) were presented instead of three. In addition, we manipulated the SOA between cue and target onset. In the SOA 200 condition, the

timing of cue and search displays was as in Experiment 2. In the SOA 300 condition, the presentation of the placeholder display between cue and search displays was increased from 153 to 247 msec, resulting in an effective SOA of 294 msec. The 128 combinations of cue position, target position, response, cue color (0° , $\pm 60^\circ$), and SOA (200, 300) were presented once in a block of trials. Participants worked through nine trial blocks for 1152 trials. We collected data until we had 24 data sets meeting our selection criteria. However, because of an error in the initial analysis, we lost one more data set, leaving 23 of 26 participants in the final sample (8 men, age: $M = 20.5$ years, $SD = 2$ years). The reasons for the exclusion of data sets were excessive choice errors in two cases (21% and 44%) and data loss exceeding 25% in one case (33% rejected trials).

Results

Behavior

Trials with slow responses (less than 0.01%) and outliers (2.3%) were excluded from analysis. Mean RTs are shown in Figure 2 (bottom), and mean cueing effects are shown in Table 1.

Individual mean RTs of correct responses were subjected to a 2 (SOA: 200, 300) \times 2 (Cue Color: 0° , $\pm 60^\circ$) \times 2 (Cue Validity: valid, invalid) repeated-measures ANOVA. Importantly, we found an interaction of Cue Color and Cue Validity, $F(1, 22) = 119.68$, $p < .001$, $\eta_p^2 = .845$. With the 0° cue color, there was a cueing benefit of 38 msec, whereas there were same-location costs of -28 msec with the $\pm 60^\circ$ cue color. The interaction of Cue Validity and Cue Color replicates Experiment 2 and was not modulated by SOA, $p = .386$. Furthermore, the ANOVA yielded some unpredicted results. The main effects of SOA, $F(1, 22) = 20.06$, $p < .001$, $\eta_p^2 = .477$, and Cue Color, $F(1, 22) = 51.91$, $p < .001$, $\eta_p^2 = .702$, were modulated by a significant interaction of these factors, $F(1, 22) = 10.76$, $p = .003$, $\eta_p^2 = .328$. The increase of RTs from the 0° to the $\pm 60^\circ$ cue color was stronger in the SOA 200 condition (512 vs. 528 msec) than in the SOA 300 condition (506 vs. 516 msec). Finally, there was an interaction of SOA and Cue Validity, $F(1, 22) = 4.46$, $p = .045$, $\eta_p^2 = .168$, showing that RTs were about equal for valid and invalid cues in the SOA 200 condition (520 vs. 519 msec), whereas RTs were shorter for valid than invalid cues in the SOA 300 condition (507 vs. 515 msec).

We ran the same two-way, repeated-measures ANOVA on percentage of choice errors. Importantly, we found the same two-way interaction between Cue Color and Cue Validity as for RTs, $F(1, 22) = 31.98$, $p < .001$, $\eta_p^2 = .592$. There was a cueing benefit with the 0° cue color (2%), whereas there were same-location costs with the $\pm 60^\circ$ cue color (-2.7%). Furthermore, the ANOVA yielded some unpredicted results. The percentage of errors was higher for the $\pm 60^\circ$ than the 0° cue color (4.2% vs. 3.1%), $F(1, 22) = 10.33$, $p = .004$, $\eta_p^2 = .32$, and the three-way interaction of SOA, Cue Color, and Cue Validity approached significance, $F(1, 22) = 3.19$, $p = .088$, $\eta_p^2 = .127$. For the

SOA 200 condition, the switch from cueing benefit to same-location costs tended to be more pronounced (2.5% vs. -3.2%) than for the SOA 300 condition (1.4% vs. -2.1%).

Electrophysiology

After rejecting trials with electrophysiological artifacts, behavioral errors, or RTs longer than 2 sec, 91% of the trials of interest remained for analysis. There were 144 trials per bin. On average, 130 trials (range: 106–142) were retained for the SOA 200/ 0° cue color, 132 trials (range: 117–143) for the SOA 200/ $\pm 60^\circ$ cue color, 128 trials (range: 103–143) for the SOA 300/ 0° Cue Color, and 131 trials (range: 108–144) for the SOA 300/ $\pm 60^\circ$ cue color. Data processing was as in Experiment 1. The mean ERPs are presented in Figure 4.

N2pc

We subjected average voltage differences in the 50-msec interval from 175–225 msec after cue onset to a 2 (SOA: 200, 300) \times 2 (Cue Color: 0° , $\pm 60^\circ$) repeated-measures ANOVA. The cue-elicited N2pc decreased from the 0° to the $\pm 60^\circ$ Cue Color (-0.9 vs. $-0.1 \mu\text{V}$), $F(1, 22) = 14.06$, $p = .001$, $\eta_p^2 = .39$, which replicates the results from Experiment 2. Unexpectedly, there was an interaction of SOA and Cue Color, $F(1, 22) = 11.64$, $p = .003$, $\eta_p^2 = .346$.

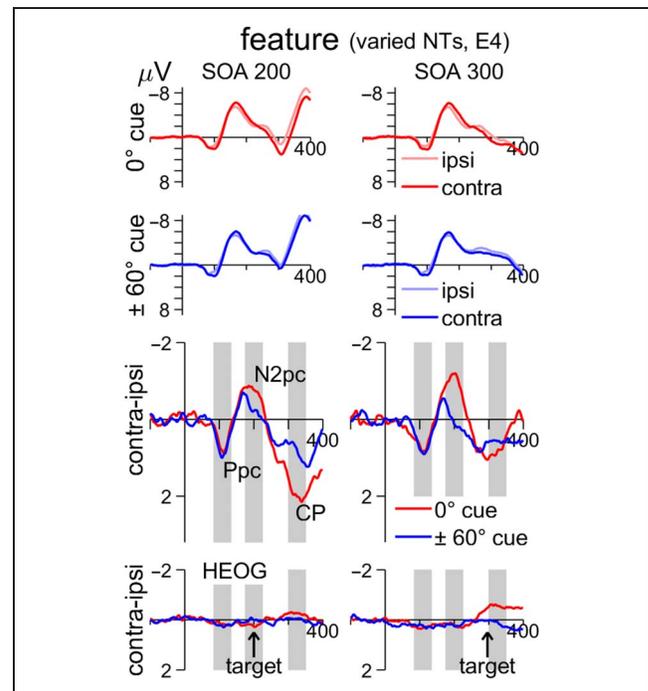


Figure 4. Electrophysiological results from Experiment 4 as a function of SOA (200, 300) and cue color (0° , $\pm 60^\circ$). The two upper rows show the ERPs to lateral cues at ipsi- and contralateral electrodes PO7/8. The third row shows the difference waves between contra- and ipsilateral electrodes PO7/8. The shaded areas indicate the averaging intervals corresponding to the Ppc, N2pc, and CP. The bottom row shows the HEOG difference waves where a negative deflection indicates an eye movement toward the cue.

The decrease from the 0° to the $\pm 60^\circ$ cue color was smaller in the SOA 200 condition (-0.7 vs. $-0.3 \mu\text{V}$) than in the SOA 300 condition (-1 vs. $0.03 \mu\text{V}$).

CP

We subjected average voltage differences in the 50-msec interval from 300–350 msec after cue onset to the same 2×2 ANOVA as above. There was a main effect of Cue Color, $F(1, 22) = 10.51, p = .004, \eta_p^2 = .325$. More importantly, there was a significant interaction between Cue Color and SOA, $F(1, 22) = 18.02, p < .001, \eta_p^2 = .45$. In the SOA 200 condition, the CP to the 0° cue color was larger than the CP to the $\pm 60^\circ$ cue color (2 vs. $0.8 \mu\text{V}$), $t(22) = 4.61, p < .001$, Cohen's $d_z = 0.96$, replicating the results from Experiment 2. In the SOA 300 condition, however, the CP did not differ between the 0° and $\pm 60^\circ$ cue color (0.8 vs. $0.6 \mu\text{V}$), $t(22) = 1.09, p = .29$, Cohen's $d_z = 0.23$, showing that the modulation of the CP was locked to the search display, which was delayed in the SOA 300 condition. One-sample t tests showed that the CP for each cue color and SOA was significantly different from zero, $t_s(22) > 2.42, p_s < .024$, Cohen's $d_z > 0.51$.

Ppc

We subjected average voltage difference in the 50-msec interval from 80–130 msec after cue onset to the same 2×2 ANOVA as above. There were no significant effects, $p_s > .208$. One-sample t tests showed that the Ppc for each cue color and search group was significantly different from zero, $t_s(23) > 3.63, p_s < .001$, Cohen's $d_z > 0.76$. The mean voltage difference of the Ppc was $0.63 \mu\text{V}$.

HEOG

We conducted the same 2×2 ANOVA on the mean HEOG in the same time intervals as above (Ppc, N2pc, CP). There was no effect in the Ppc and N2pc intervals, $p_s > .404$. However, for the CP interval, there was a significant effect of Cue Color, $F(1, 22) = 14.17, p = .001, \eta_p^2 = .392$, and the interaction between SOA and Cue Color approached significance, $F(1, 22) = 3.29, p = .083, \eta_p^2 = .13$. Paired t tests revealed a significance difference between the 0° and $\pm 60^\circ$ Cue Colors in the SOA 300 condition (-0.5 vs. $0.1 \mu\text{V}$), $t(22) = 3.85, p = .001$, Cohen's $d_z = 0.8$, but not in the SOA 200 condition (-0.3 vs. $-0.02 \mu\text{V}$), $p = .208$. However, the difference in HEOG occurred in the SOA 300 condition where no voltage difference at posterior electrodes was noted. Therefore, it seems unlikely that the HEOG contributed to the ERP results.

Discussion

By varying the SOA between cue and target onset, we tested whether the modulation of the CP component by cue color

was locked to the onset of the search display. To this end, we delayed the onset of the search display in the SOA 300 condition. As predicted, the modulation of the CP by cue color disappeared in the analysis interval from 300 to 350 msec in the SOA 300 condition, suggesting that it occurred outside the analysis interval. These results confirm the idea that the CP component reflects modulations of signal enhancement in the processing of the search display.

GENERAL DISCUSSION

We investigated the electrophysiological correlates of attentional template precision in the modified spatial cueing paradigm. To induce precise and broad attentional templates, participants performed feature or singleton search in Experiments 1 and 2, respectively. In Experiment 3, precise attentional templates were promoted in singleton search by using colored nontargets. To measure the precision of attentional templates, we manipulated the color difference between cue and target. Cueing effects decreased more strongly with increasing color difference when attentional templates were precise. We tested two hypotheses concerning the mechanisms underlying the precision of attentional templates.

Differential Signal Enhancement

One hypothesis concerning the electrophysiological correlates of precise attentional templates is that signal enhancement at the cued location varies more strongly with precise than broad attentional templates. According to Livingstone et al. (2017), signal enhancement follows the contingent capture of attention by the cue. That is, the N2pc to the cue is followed by a positivity to the stimulus appearing at the cued location. This interpretation is consistent with classical findings of enhanced P1 components to stimuli in the attended visual hemifield (Heinze et al., 1990; Luck et al., 1990) or with research demonstrating an enhanced P1 when a target stimulus appears at the location of auditory (Störmer et al., 2009; McDonald et al., 2005) or visual cues (Allon & Luria, 2019; Hopfinger & Ries, 2005). In the current set of experiments, the target position was balanced with respect to the cue position. The target appeared at the cued location in 25% of the trials and opposite the cue in another 25% of the trials. Therefore, lateralized components resulting from target processing should cancel out. In another 50% of trials, the target appeared on the vertical midline, where its processing is not expected to affect lateralized components (Woodman & Luck, 2003). Thus, the CP reflects signal enhancement of any stimulus appearing at the previously cued location. Thereby, the target stimulus was enhanced on valid trials, whereas a nontarget stimulus was enhanced on invalid trials, which results in decreased RTs for cued targets and increased RTs for uncued targets. With precise attentional templates, we observed a strong decrease in cueing effects when the cue color was dissimilar. The decreasing cueing effect was

matched by a decreasing CP component, suggesting that there was less signal enhancement at the cued location. For the $\pm 60^\circ$ cue color in Experiment 2, cueing effects were not only reduced, but inverted. Same location costs are difficult to explain by a reduction of signal enhancement. Even if there was no enhancement at the cued location, performance is not expected to be worse at the cued location. Thus, reductions of the CP do not only reflect changes of the magnitude of signal enhancement but may be associated with a switch from signal enhancement to signal suppression. It is not entirely clear how this switch fits in with the general boost of sensory processing that is associated with the underlying P1 component. However, the data strongly suggest that reduced CPs do not always lead to enhanced processing at the cued location.

Relation to Previous Interpretations of the CP

Our results shed some new light on previous interpretations of the CP. On the one hand, our conclusion that the CP changes as a function of search task is consistent with some observations from previous studies. For instance, the CP was unaffected by the match between cue and target when the target was easy to find (Mertes et al., 2016), whereas the CP was larger for matching than nonmatching cues when the target was more difficult to find (Schönhammer et al., 2016, 2020; Mertes & Schneider, 2018). On the other hand, our conclusions are at odds with the previous interpretation that the CP reflects cue suppression (Harris et al., 2019; Mertes & Schneider, 2018; Mertes et al., 2016; Sawaki & Luck, 2013). If the CP reflected cue suppression, then same-location costs should be associated with a large CP. However, we observed the opposite. In feature search, the CP was small when same-location costs occurred. In singleton search with colored nontargets, the CP was also small when there was a tendency for same-location costs. This finding is inconsistent with the idea that larger CPs reflect more suppression. Rather, our results suggest that small CPs reflect decreased signal enhancement.

Differential Allocation of Attention

According to the hypothesis of differential allocation of attention, precise attentional templates are achieved by restricting the allocation of attention to target-similar cues. A core prediction of this hypothesis is an interaction between search task and cue color in the analysis of the cue-elicited N2pc, which was not observed in Experiments 1–2. However, it may be premature to reject the hypothesis of differential allocation of attention. Harris et al. (2019) ran a related experiment where feature and singleton search were compared. In contrast to our experiments, they found a larger difference in the amplitude of the cue-elicited N2pc between target-matching and target-nonmatching cue colors in feature search than in singleton search, as predicted by the differential allocation of attention. The main difference to the current study is that we manipulated display

characteristics to induce feature and singleton search, whereas Harris et al. (2019) used the same displays and changed the instructions. In Experiments 1–2, the nontarget elements were gray in singleton search, but colored in feature search. In contrast, the nontargets were gray in both feature and singleton search in Harris et al. (2019), and participants had to withhold the response to one of two possible target colors in feature search whereas both colors were responded to in singleton search. Thus, the displays were equal, but the task varied. Another difference between studies is that the current study used a single fixed target color, whereas Harris et al. (2019) had two relevant colors. Future research will have to clarify which of these differences accounts for the discrepant results. Furthermore, there is evidence from other search paradigms that is consistent with the idea that the N2pc component was larger when the attentional template was more precise. For instance, when observers searched for a specific item from a category, rather than for any item, the N2pc was larger and occurred earlier (Jenkins, Grubert, & Eimer, 2018; Nako, Wu, Smith, & Eimer, 2014). In a similar vein, the N2pc occurred earlier and had a larger amplitude when participants were cued about the nature of the upcoming target (i.e., color or shape target, Töllner, Zehetleitner, Gramann, & Müller, 2010). The enhanced and speeded N2pc may result from an improved representation of target features in VWM that results in better attentional selectivity (Salahub, Lockhart, Dube, Al-Aidroos, & Emrich, 2019).

No Evidence for Cue Suppression

Furthermore, we evaluated whether there was attentional suppression for dissimilar cue colors in feature search. Behaviorally, cueing benefits for the dissimilar $\pm 60^\circ$ cue color in singleton search of Experiment 1 turned into same-location costs in feature search of Experiment 2. However, we did not observe the electrophysiological signature of attentional suppression, the P_D component (reviews in Liesefeld & Müller, 2019; Gaspelin & Luck, 2018; Geng, 2014), which we expected to occur in the interval from 175 to 225 msec after cue onset. A similar conclusion was reached in a related study by Schönhammer et al. (2020) with inverted cue colors. Inverted cue colors refer to a situation where the color of the singleton cue in the cue display corresponds to the color of the nontargets in the search display. For instance, a green singleton cue in a context of red items may precede a red target in a context of green nontargets. With inverted cue colors, reliable same-location costs occurred. At first sight, this result suggests inhibition of the inverted singleton cue. This idea received initial support by the occurrence of the P_D to the inverted singleton cue (Schönhammer et al., 2016). However, the P_D to the inverted singleton cue could in fact be an N2pc to the cue context. To disentangle a P_D to the inverted cue from an N2pc to the cue context, neutral gray elements were displayed. With neutral gray cues as baseline, no P_D was elicited by the inverted singleton cue. However, a

reliable N2pc emerged to the cue context. Thus, the electrophysiological results suggest that RTs to targets appearing at the same location as the inverted singleton cue were longer because attention was captured by the cue context and not because stimuli at the cued location were suppressed. In summary, the current study and Schönhammer et al. (2020) demonstrate that signs of behavioral suppression do not always result from attentional suppression, despite the face value of this interpretation (see also Kerzel & Burra, 2020).

A Two-Component Model

Although we associate the different precision of the attentional template to changes in the CP, the CP alone cannot explain the full pattern of cueing effects. Notably, the CP did not change at all in singleton search of Experiment 1, but the cueing effects decreased significantly with increasing color difference between cue and target (compare Figures 2 and 3). In contrast, the decreasing cueing effects were accompanied by decreasing N2pcs to the cues. Thus, two components may be necessary to explain the full pattern of results: (1) the allocation of attention, as reflected in the cue-elicited N2pc, and (2) the modulation of signal enhancement, as reflected in the CP. Whereas changes of the N2pc occur with broad and precise attentional templates, changes of the CP are limited to precise attentional templates and underlie the difference between feature and singleton search. Taken together, only the combination of the allocation of attention and signal enhancement provides a satisfactory explanation of the data.

Previously, Carmel and Lamy (2015) had already suggested that a multiple-component model may be necessary to account for cueing effects. Similar to the current study, Carmel and Lamy (2015) suggested that the color similarity between cue and target determined attentional capture. In addition, they suggested to consider each placeholder location as an object. On valid trials, the color at the target location is the same between cue and search displays. On invalid trials, however, the color changes and results in costs related to the updating of an object file (Kahneman, Treisman, & Gibbs, 1992). Costs related to the updating of an object file depend on the temporal continuity between cue and target objects, which was not manipulated in the current study. According to Carmel and Lamy (2015), a combination of attentional capture and object updating explained cueing effects. It may be tempting to equate object updating with signal enhancement, but object updating depends crucially on the match between colors in the cue and search displays. In contrast, signal enhancement, as indexed by the CP, occurred irrespective of the specific stimulus appearing on the cued location. Thus, signal enhancement cannot be equated with object file updating. Nonetheless, there is agreement between Carmel and Lamy (2015) and this study regarding the implicating of more than a single mechanism. Finally, these mechanisms may be subject to interindividual

differences in cognitive control, a topic that has received increasing attention in the recent literature (Carolan, Gaspar, Kleffner, & Liotti, 2020; Feldmann-Wüstefeld & Vogel, 2019; Lien, Gemperle, & Ruthruff, 2011; Mertes, Wascher, & Schneider, 2017; Verleger et al., 2014).

Conclusions

In summary, we measured the electrophysiological correlates of attentional templates for color targets in the modified spatial cueing paradigm. We found the behavioral cueing effects to decrease with increasing color difference between cue and target. The decrease was stronger in feature search than in singleton search, suggesting that attentional templates were precise in feature search and broad in singleton search. We evaluated two hypotheses regarding the difference between precise and broad attentional templates. The hypothesis of differential allocation of attention holds that the allocation of attention is restricted to target-similar colors when precise search templates are required. However, the corresponding ERP, the cue-elicited N2pc, showed no difference between feature and singleton search. In addition, the cue-elicited N2pc in singleton search with colored nontargets was large to cues that produced no behavioral cueing effects. Furthermore, we found no evidence for the idea that same-location costs in some conditions were caused by attentional suppression of the cue, as indexed by the P_D component. Our results are most in line with the hypothesis of differential signal enhancement, as indexed by the CP. In feature search, there was a decrease of the CP component with increasing color difference between cue and target (Experiment 2). In singleton search with colored nontargets (Experiment 3), there was a decrease of the CP with nonmatching cue colors. In contrast, there was no modulation of the CP with broad attentional templates in singleton search with gray nontargets (Experiment 1). Thus, signal enhancement may be attenuated for dissimilar cue colors with precise, but not with broad attentional templates, which may account for differences between feature and singleton search.

Acknowledgments

D. Kerzel was supported by the Swiss National Science Foundation 100019_182146. We wish to thank Alexandre Fortuna Pacheco, Matteo Favetta, Quentin Zongo for helping with data collection.

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Funding Information

Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung (<http://dx.doi.org/10.13039/501100001711>), grant number: 100019_182146.

Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this time period were $M(\text{an})/M = .408$, $W(\text{oman})/M = .335$, $M/W = .108$, and $W/W = .149$, the comparable proportions for the articles that these authorship teams cited were $M/M = .579$, $W/M = .243$, $M/W = .102$, and $W/W = .076$ (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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