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Electrophysiological evidence for the optimal tuning of attention

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Optimal tuning of attention refers to shifts in goal-driven attention that increase the difference between the representation of the target and nontarget features. Evidence for optimal tuning comes from studies measuring the memory representation of the target and, to a lesser degree, from studies measuring attentional selectivity. In one study on attentional selectivity, cueing effects were found to be greater for cue colors deviating away from the nontarget color compared to cue colors deviating toward the nontarget color, suggesting that participants' search goal was optimally tuned. To address alternative accounts, we measured event-related potentials (ERPs) elicited by different cue colors at posterior electrodes PO7/PO8. We found that ERPs associated with attentional orienting (N1pc) or selection (N2pc) were larger for cue colors deviating away from the nontarget color, which is consistent with the optimal tuning of attention. In contrast, the results are difficult to reconcile with alternative accounts such as rapid disengagement or object updating. Further, we aimed to evaluate contributions from sensory adaptation by analyzing the Ppc component, a lateralized ERP in the P1 time range. Two control conditions, however, suggested that the Ppc was more likely driven by imbalanced saliency than sensory adaptation.

Keywords Visual search, Attentional capture, Optimal tuning, Sensory adaptation

Visual search for an object starts with a memory representation of the target features, which is referred to as attentional template[1]. Subsequently, the neural response to visual features corresponding to the attentional template is enhanced, which guides attention toward candidate target objects[2,3]. Navalpakkam and Itti[4] suggested that the attentional template may be adjusted in some situations to reduce the overlap between target and nontarget features (see also[5]). For instance, to find an orange-yellow tiger in yellow-green grass, it may be better to search for orange instead of orange-yellow because the difference between target and nontarget colors is greater. In Navalpakkam and Itti's experiments, participants searched for a target in a color that was very close to the color of the nontargets. On some trials, the search task was replaced by a memory task and participants had to indicate the color of the target. Consistent with optimal tuning of attention, participants' memory representation of the target was systematically biased away from the nontarget color. For instance, instead of correctly remembering that the tiger was orange-yellow, participants would indicate that the tiger was orange. The memory bias away from the nontarget color is a robust phenomenon that has been observed in several studies[6–12].

Despite the ample evidence for a memory bias, there is less evidence that the biased memory representation is used to guide attention. For instance, Scolari and Serences[7] failed to observe higher sensitivity for stimuli deviating away from the nontargets. Higher sensitivity is expected if there was neural enhancement of stimuli corresponding to the memory representation. Some support for attentional guidance by the biased attentional template was provided by Kerzel[8] who observed that cueing effects were largest for colors biased away from nontarget colors (see Fig. 1). In general, cueing effects are largest for colors that match the attentional template[13]. For instance, cueing effects occur for a green cue when observers search for a green target, but not when they search for a red target. Kerzel[8] observed that cue colors deviating by – 15° away from the nontarget color elicited larger cueing effects than colors deviating by + 15° towards the nontarget color, which is consistent with the optimal tuning of attention.

Alternative accounts

However, there are alternative interpretations of cueing effects in terms of rapid disengagement, object updating, and sensory adaptation, which we will evaluate by measuring event-related potentials. Theeuwes[14] suggested that the initial saliency-driven allocation of attention is the same for matching and non-matching cues, but the withdrawal of attention occurs earlier for non-matching than matching cues. The rapid disengagement from non-matching cues may reduce cueing effects. However, electrophysiological studies using the N2pc[15,16] as a

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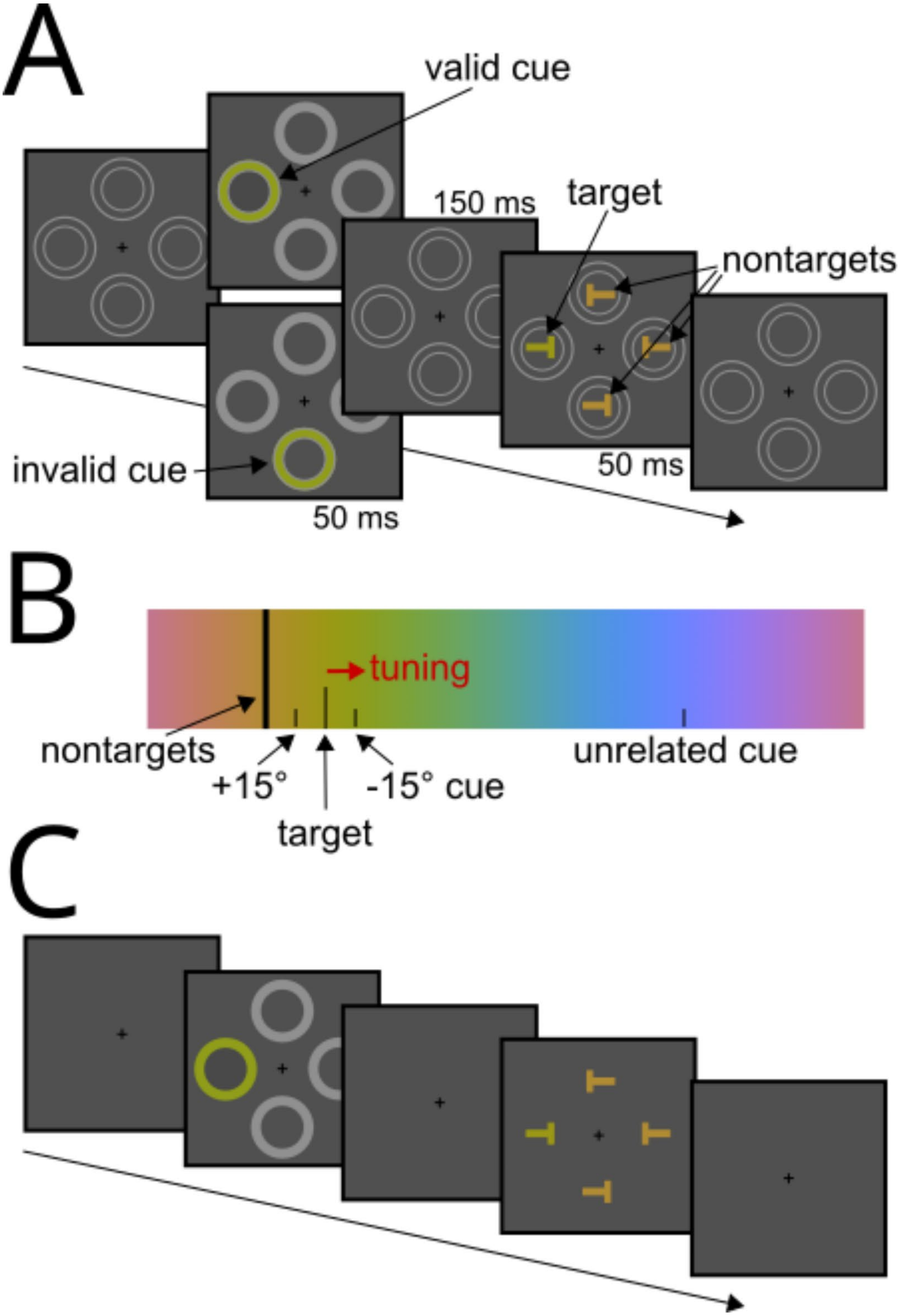

Fig. 1. Illustration of experimental stimuli. (**A**) Illustrates the time course of a trial in Experiment 1. Valid cues appeared at the target location and invalid cues at a nontarget location. (**B**) Shows possible cue, target, and nontarget colors in a CIELAB-based color space. The cue color deviated either toward (+ 15°) or away (– 15°) from the nontarget color. The unrelated cue color was 180° from the target color. According to optimal tuning, attention is tuned away from the nontarget color. (**C**) Illustrates stimuli from Experiment 2 where the placeholders were not shown.

marker of attentional allocation were inconsistent with rapid disengagement. Eimer and Kiss[17] showed that the N2pc was not elicited by non-matching cues, suggesting that non-matching cues were never attended, not even initially (see also[18,19]). Despite the well-documented differences between matching and non-matching cues, it is not entirely clear what to expect for the critical cue colors in the study on the optimal tuning of attention. The critical cue colors were target-similar but deviated either toward or away from the nontarget color. Therefore, they were neither entirely matching nor entirely non-matching and we cannot rule out the rapid-disengagement account. That is, the initial allocation of attention may have been equal for the two cue colors, but attention was more rapidly disengaged from cue colors deviating toward the nontarget color.

Further, Carmel and Lamy[20,21] suggested that object updating may modulate the beneficial effects of valid cues. On valid trials, cue and target appear successively at the same location and may therefore be integrated into a single object. With matching cues, cue and target features are the same, promoting object continuity, whereas with mismatching cues, they change, requiring object updating. The time to update the object may offset the RT gains typically conveyed by valid cues, explaining the smaller cueing effects with non-matching cues. The object updating account may apply to cueing studies on optimal tuning. That is, valid trials with cues deviating away from the nontargets may require less object updating because the cue color is a better match to the shifted representation of the target.

Another problem is that in studies on the optimal tuning of attention, target and nontarget colors were mostly fixed. That is, participants were exposed to the same nontarget color on hundreds of trials. As a result, there may have been sensory adaptation to the nontarget and nearby colors, which may have reduced the ability of cue colors close to the nontarget color to attract attention. To avoid sensory adaptation, Scolari and Serences[7] changed the target-nontarget relation randomly on each trial. As mentioned above, they failed to observe evidence for optimal tuning with this design. Further, Kerzel and Huynh Cong[22] observed that the difference between cue colors deviating away and towards the nontarget color was attenuated when two target-nontarget relations alternated randomly. Random variation of the colors is likely to reduce sensory adaptation, but detailed analysis of effects of inter-trial transition suggested that there may not be a single mechanism explaining the attenuation of optimal tuning with two target-nontarget relations.

Predictions of optimal tuning, rapid disengagement, object updating and sensory adaptation

To test the predictions of optimal tuning, rapid disengagement, object updating, and sensory adaptation, we measured cue-elicited ERPs at posterior electrodes PO7/PO8. Previous research has shown that cues matching the target color elicit a contralateral negativity (the N2pc) at these electrodes around 200 ms after cue onset. In contrast, cues not matching the target color do not elicit the N2pc[17–19]. The three accounts make different predictions concerning the cue-elicited N2pc. The optimal tuning account predicts a larger cue-elicited N2pc for cue colors deviating away from the nontarget color than for cue colors deviating towards, showing that more attention was allocated to colors corresponding to the optimally tuned attentional template. Rapid disengagement predicts that the cue-elicited N2pc is initially the same for both cue colors, before it rapidly decreases for cue colors deviating towards the nontarget color. Object updating predicts no difference in the cue-elicited N2pc components because the differences in cueing effects are attributed to differences in object updating, which are unrelated to attention.

While optimal tuning, rapid disengagement and object updating make predictions concerning the cue-elicited N2pc, sensory adaptation predicts changes in an earlier time interval. Luck and Hillyard[23] observed that ERPs at posterior electrodes were more positive contralateral to a color singleton around 100 ms after stimulus onset. They suggested that neurons responding to the nontarget color were repeatedly stimulated, which resulted in sensory adaptation. In contrast, there was less sensory adaptation for the color of the singleton, which elicited a more positive P1-component in the contralateral hemisphere. This positivity is referred to as Ppc[24,25]. If sensory adaptation to the nontarget color accounted for the smaller cueing effects with cues deviating toward the nontarget color, we would expect a smaller Ppc component with these cues. Further, sensory adaptation does not preclude attentional effects on the N1pc and N2pc components. That is, sensory adaptation may co-occur with optimal tuning or rapid disengagement. To evaluate whether the Ppc reflects sensory adaptation at all, we included an unrelated cue color. The Ppc is expected to be larger for an unrelated cue color because it was never shown in the search display and appeared only on 1/3 of trials in the cue displays, which should lead to less sensory adaptation.

Experiment 1

To test the accounts presented above, we recorded ERPs in the cueing paradigm that has previously provided evidence for optimal tuning of attention[8]. In this paradigm, cue colors deviating away from the nontarget color were found to result in larger cueing effects than cue colors deviating toward the nontarget color (see Fig. 1). Cueing effects are calculated by subtracting mean RTs on trials where the cue appeared at the target location (valid trials) from mean RTs on trials where it appeared at a nontarget location (invalid trials). Further, we calculated lateralized ERPs at posterior electrodes PO7/PO8 in three intervals. The intervals around peaks of the N1 and N2 components are related to attentional processing, whereas an earlier interval around the peak of the P1 component is related to sensory processing. Separating the intervals around the N1 and N2 components allows us to distinguish between the early and late deployment of attention. A contralateral negativity in the N1 time range is referred to as N1pc and is considered a reflection of an initial orienting response to salient items in the display[26–30]. A contralateral negativity in the N2 time range is referred to as N2pc and is associated with attentional selection[3,15]. A contralateral positivity in the P1 time range is referred to as Ppc and has been associated with sensory adaptation[23], but also with imbalanced saliency[31–33]. The cue-elicited N1pc, N2pc, and Ppc components were calculated by subtracting mean voltages ipsilateral to the cue from mean voltages contralateral to the cue.

Methods

Transparency and openness promotion

The number of participants was partially determined by the counterbalancing of colors. There were 10 different combinations of target and nontarget colors, requiring multiples of 10. We therefore collected data until we had 30 valid datasets. Undergraduate students in psychology at the University of Geneva participated in the experiment (3 male; age: $M = 21.4$ years, $SD = 3.5$). Four datasets were replaced because of excessive data loss (see below). In a related study by Kerzel and Huynh Cong[34], the effect of cue color on the N2pc was large with $\eta_p^2 = 0.413$, which would require only 4 participants. Because a null result was possible for the ERP components and we did not want to miss the effect if it existed, we increased the sample size to 30. G*Power 3.1[35] indicated that we could detect effect sizes as small as $d_z = 0.53$ in two-tailed t-tests (alpha = 0.050, power = 0.80). The experiments in this article were not formally preregistered. Data management, aggregation and plots were performed with MATLAB 2022a (The Mathworks, Natick, MA), and IBM SPSS 27 (IBM, Armonk, NY) was used for inferential statistics. The author declares that he has no conflict of interest. Students participated for class credit and reported normal or corrected-to-normal vision. The study was approved by the ethics committee of the University of Geneva (authorization number CUREG-2022-02-23) and was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Informed written consent was given before the experiment started. Data were collected in 2024.

Apparatus

The stimuli were presented on a 22.5-inch LCD monitor (100 Hz, 1,920 × 1,200 pixels, standard backlight; VPixx Technologies Inc., Saint-Bruno, Canada). An i1Display Pro (VPixx Edition) colorimeter by X-Rite (Grand Rapids, Michigan, United States) was used to measure the stimulus colors. Head position was stabilized with a chin/forehead rest at a viewing distance of 66 cm. Responses were collected on a RESPONSEPixx handheld 5-button response box (VPixx Technologies Inc., Saint-Bruno, Canada) with left, right, top, bottom and center button. A desktop-mounted EyeLink1000 (SR Research, Ontario, Canada) recorded eye-movements at a sampling rate of 1000 Hz. For clarity, degrees of visual angle are abbreviated as dva to avoid confusion with degrees of rotation (°), which are used to characterize the colors. To detect saccades, we set the EyeLink1000 to the standard saccade criteria for cognitive research (i.e., velocity of 30 dva/s and acceleration of 8000 dva/sec^2). MATLAB 2022a (The Mathworks, Natick, MA) with the Psychtoolbox[36,37] and Eyelink Toolbox[38] was used to run the experiment.

Stimuli

There were three different displays: a placeholder, a cue, and a target display (see Fig. 1A). The central fixation cross (diameter of 0.4 dva, 0.07 dva linewidth) was always visible. The placeholders were four outline rings shown to the left, right, above and below the fixation cross. The distance between the fixation cross and the center of the rings was 3 dva. The outline rings were made up of two circles with diameters of 2.8 dva and 2.4 dva and a linewidth of 1 pixel or 0.02 dva. In the cue display, the outline rings were filled. The cue was the ring filled with color. The remaining rings were filled with the same light gray as the placeholders. The target display consisted of the placeholder display and the letter T oriented 90° to the left or right (1 dva length, 0.2 dva linewidth). One T was shown inside each placeholder and all Ts were colored. The target T was a color singleton. That is, its color was different from the nontarget Ts and all nontarget Ts shared the same color.

The background was medium gray, xyY = (0.312, 0.332, 24.3 cd/m^2), while the placeholders and the gray cues were light gray, xyY = (0.312, 0.332, 48.8 cd/m^2). The cue, target and nontarget colors were selected on an isoluminant color wheel in a CIELAB-based color space (see Fig. 1B) where distances between colors were proportional to perceived color differences[39]. The lightness of the color wheel was L* = 59 (corresponding to 48.8 cd/m^2) and its chroma (saturation) was 64.

Design

There were 48 combinations resulting from crossing three cue colors (− 15°, + 15°, 180°), four cue positions (left, right, top, bottom), and four target positions (left, right, top, bottom). Thus, the cue was spatially non-predictive. The 48 combinations were shown once in each block and there were 18 blocks for a total of 864 trials. The target color was fixed for each participant. The possible target colors were at a rotation of 0°, 45°, 90°, 135°, and 315° on the color wheel. Figure 1B shows the colors from 0° to 360° from left to right. The nontarget color was at either − 30° or + 30° from the target color and fixed for each participant. The five target colors and two possible deviations of the nontarget color yielded ten different combinations. Three participants were assigned to each combination.

Procedure

The placeholder display was shown unless the cue or target displays appeared. During the intertrial-interval of 400 ms, the fixation cross turned dark gray (18.9 cd/m^2) to indicate that it was admissible to blink. Then, the eyetracker waited for participants to look at the central fixation cross. If central fixation was detected for 300 ms, the trial was started. If no central fixation was detected for 5000 ms, recalibration was initiated. A trial started with the presentation of the placeholder display for randomly between 300 and 600 ms. Then, the cue display was shown for 50 ms, followed by the placeholder display for 150 ms and the target display for 50 ms. That is, the onset of the target was 200 ms after the onset of the cue. Participants responded to the letter T oriented to the left or right by pressing a spatially corresponding button. They were instructed to respond as rapidly and accurately as possible while ignoring the cue display. Trials with breaks of fixation, choice errors, anticipations (RTs < 200 ms) and late responses (RTs > 1,500 ms) were followed by visual feedback. Every 48 trials, the percentage of fixation and choice errors, and the median RTs in the preceding trial block were displayed for at least 3,000 ms during a self-terminated pause.

Electrophysiological recording and initial data processing

We recorded electrophysiological signals from active Ag/AgCl electrodes (ActiCap Slim) converted by an actiCHamp amplifier at 1,000 Hz using the BrainVision Recorder software (version 1.25.0001). The recording software, devices and conductive gel used to connect the electrodes were produced by Brain Products (Gilching, Germany). We deactivated cutoffs and notchfilters in the filter settings of the BrainVision Recorder software. Twenty-six electrodes were placed on the scalp (Fp1, Fp2, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8, PO9, PO10) and six electrodes on the outer canthi of each eye, above and below the right eye, and on each earlobe. Cz was the online reference and AFz the ground site. EEG data were processed using MATLAB 2022a (The Mathworks, Natick, MA) with the EEGLAB[40] and ERPLAB[41] extensions. Before analysis, the EEG was re-referenced to the average earlobes and filtered between 0.1 and 30 Hz with a bandpass second-order Butterworth filter (roll-off 12db/octave, command "pop_basicfilter" in ERP-lab). The HEOG channel was the difference between left and right eye electrodes, and the VEOG was the difference between upper and lower eye electrodes. The EEG was segmented into 400 ms epochs from 100 ms before to 300 ms after onset of probe or target displays. The first 100 ms served as baseline.

Trial and dataset rejection (ERPs)

In the analysis of ERPs, trials were rejected when the peak-to-peak activity at any electrode exceeded ± 80 µV between 100 before to 300 ms after cue onset. This threshold was lowered to ± 50 µV for the HEOG and VEOG channels. Similarly, trials where the eyetracker detected blinks or saccades larger than 1 dva, or trials where a behavioral error occurred were rejected. Datasets were discarded if more than 30% of the data were missing. This was the case for four datasets where only 7%, 19%, 56%, and 66% of trials were retained.

Results

We conducted ANOVAs on mean individual RTs and voltage differences. *t*-tests were conducted to follow up on significant effects. We controlled for false discovery rate according to Benjamini and Hochberg[42], but we report uncorrected *p*-values for clarity. On valid trials, the cue appeared at the target location. On invalid trials, it appeared at a nontarget location. The difference between valid and invalid trials is referred to as cueing effect (invalid–valid).

Reaction time results

In the analysis of RTs, we successively excluded trials with RTs longer than 1,500 ms (0.1%), choice errors (4.6%), and trials with RTs deviating by more than 2.5 *SD*s from the respective condition mean (2.1%). Mean RTs are shown as a function of cue validity and cue color in Fig. 2. We entered individual mean RTs in a repeated-measures 2 (cue color: away, toward, unrelated) × 2 (cue validity: valid, invalid) ANOVA. The main effects of cue color, $F(2, 58) = 9.60$, $p < .001$, $\eta_p^2 = 0.249$, and cue validity, $F(1, 29) = 34.58$, $p < .001$, $\eta_p^2 = 0.544$, entered a significant interaction, $F(2, 58) = 47.10$, $p < .001$, $\eta_p^2 = 0.619$. To follow up on this interaction, we calculated cueing effects for

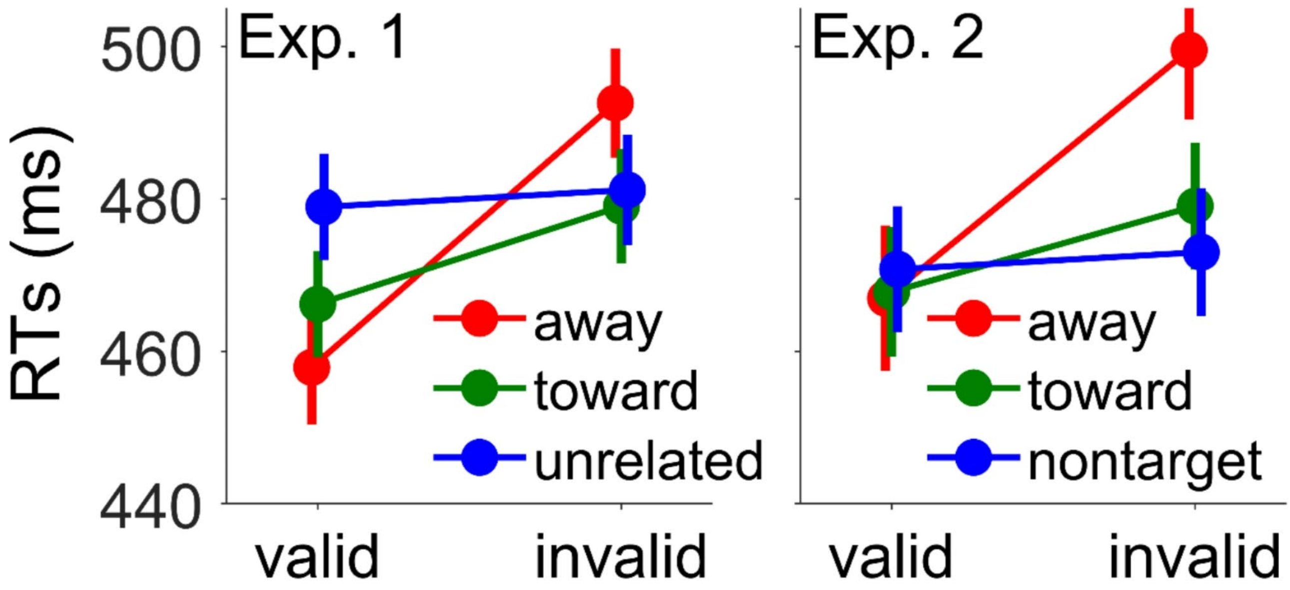

Fig. 2. Reaction time (RT) results from Experiments 1 and 2. RTs in milliseconds are shown as a function of cue validity (valid, invalid) and cue color (away, toward, unrelated or nontarget). Error bars show the between-subject standard error.

each cue color. Table 1 reports the means and results of t-tests against zero. Further, we compared cueing effects between cue colors according to our experimental hypotheses. Cueing effects with a cue color deviating away from the nontarget color were larger than cueing effects with a cue color deviating towards the nontarget color (35 vs. 12 ms), $t(29) = 7.43$, $p < .001$, Cohen's $d_z = 1.36$, which is consistent with the optimal tuning of attention. In addition, cueing effects with a cue color deviating toward the nontarget color were larger than cueing effects with an unrelated color (12 vs. 1 ms), $t(29) = 3.60$, $p = .001$, Cohen's $d_z = 0.66$, showing that cue colors resembling the target attracted attention more strongly than cues in an unrelated color. Running the same ANOVA on the percentages of choice errors revealed a significant interaction, $F(2, 58) = 5.96$, $p = .006$, $\eta_p^2 = 0.162$. However, none of the one-sample t-tests comparing cueing effects to zero were significant after controlling for the false discovery rate (see Table 1).

Electrophysiological results

Trials with cues on vertical locations (432 trials per participant) were discarded because lateralized ERPs to the cue could not be calculated. There were 144 trials per cue color and participant where the cue was on a horizontal location. For each cue color and participant, the range of retained trials was 111–138 ($M = 127$, $SD = 7$). Based on our experimental questions, we were interested in lateralized potentials in the P1, N1, and N2 time ranges. To select the analysis windows, we calculated the grand average ERPs across all conditions and searched for the peak in the respective time ranges. Instead of using the N2 peak, however, we used the peak of the positive-going deflection between the N1 and N2, which was a better fit for the N2pc in our dataset. The respective peaks were at 90, 169, and 230 ms after onset of the cue, which correspond to the analysis intervals for the Ppc, N1pc and N2pc components. We calculated the difference between voltages at electrodes PO7 and PO8 contra- and ipsilateral to the cue in a 50 ms time window centered on each peak. Figure 3 shows the three time-windows for the ipsi- and contralateral voltages (top panels) and the difference waves (bottom panel).

We evaluated predictions of the optimal-tuning, rapid-disengagement and object-updating accounts in a 2 (cue color: toward, away) × 2 (interval: N1, N2) ANOVA. The effect of cue color was significant, $F(2, 58) = 11.04$, $p < .001$, $\eta_p^2 = 0.276$. Follow-up t-tests showed that the contralateral negativity averaged across the N1 and N2 intervals was larger for cue colors deviating away from the nontarget color than for cue colors deviating toward the nontarget color (− 0.97 vs. − 0.53 µV), $t(29) = 3.95$, $p < .001$, Cohen's $d_z = 0.72$, which is consistent with the optimal-tuning account, but inconsistent with the object-updating account. The mean N1pc and N2pc to cue colors deviating toward the nontarget color did not reliably differ from unrelated cues (− 0.53 vs. − 0.35 µV), $t(29) = 1.40$, $p = .172$, Cohen's $d_z = 0.25$. Further, the interaction between cue color and interval was not significant, $F(2, 58) = 0.67$, $p = .513$, $\eta_p^2 = 0.023$, providing no evidence for the idea that the contralateral negativity decreased from the N1 to the N2 interval for cue colors deviating toward the nontarget colors, as suggested by the rapid-disengagement account. Table 2 shows that only components elicited by the cue color deviating away from the nontarget color were reliably different from zero.

To evaluate effects of sensory adaptation, we conducted a repeated-measures ANOVA on the Ppc. The effect of cue color was non-significant, $F(2, 58) = 1.04$, $p = .362$, $\eta_p^2 = 0.034$, providing no support for contributions of sensory adaptations. In particular, the difference between cue colors deviating away and toward the nontarget color was not significant (0.65 vs. 0.68 µV), $t(29) = 0.30$, $p = .767$, Cohen's $d_z = 0.05$. The Ppc components in the selected time window were reliable for each cue color (see Table 2). However, Fig. 3 suggests that the time window was not well-centered on the peak of the difference waves. To make sure that we did not miss an effect, we calculated contra-ipsi differences in the 50 ms-interval centered on the peak of the difference waves, which occurred after 116 ms (i.e., 26 ms later than the peak of the P1). The respective interval is indicated by an outline rectangle in the lower panel of Fig. 3. We confirmed the absence of a main effect of cue color, $F(2, 58) = 0.16$, $p = .851$, $\eta_p^2 = 0.006$. The means were 1.12, 1.20, and 1.17 for away, toward, and unrelated. Again, the difference between cue colors deviating away and toward the nontarget color was not significant (1.12 vs. 1.20 µV), $t(29) = 0.51$, $p = .615$, Cohen's $d_z = 0.09$.

	Valid	Invalid	CE	t(29)	d_z	*p*	BH
RTs (ms)							
Away	457	492	35	9.92	1.81	< 0.001	y
Toward	465	478	12	3.75	0.69	0.001	y
Unrelated	478	479	1	0.33	0.06	0.744	n
Choice errors (%)							
Away	3.7	5.5	1.7	2.25	0.41	0.032	n
Toward	3.6	4.4	0.8	1.24	0.23	0.225	n
Unrelated	5.2	4.2	− 1.1	− 2.18	− 0.40	0.037	n

Table 1. Reaction time results from experiment 1. Mean reaction times (RTs) and choice errors as a function of cue validity and cue color, and results from one-sample t-tests comparing the cueing effect (CE) to zero. CEs were obtained by subtracting the valid from the invalid condition. The column BH indicates whether CEs were significantly different from zero after controlling for false discovery rate with six tests according to Benjamini and Hochberg[42].

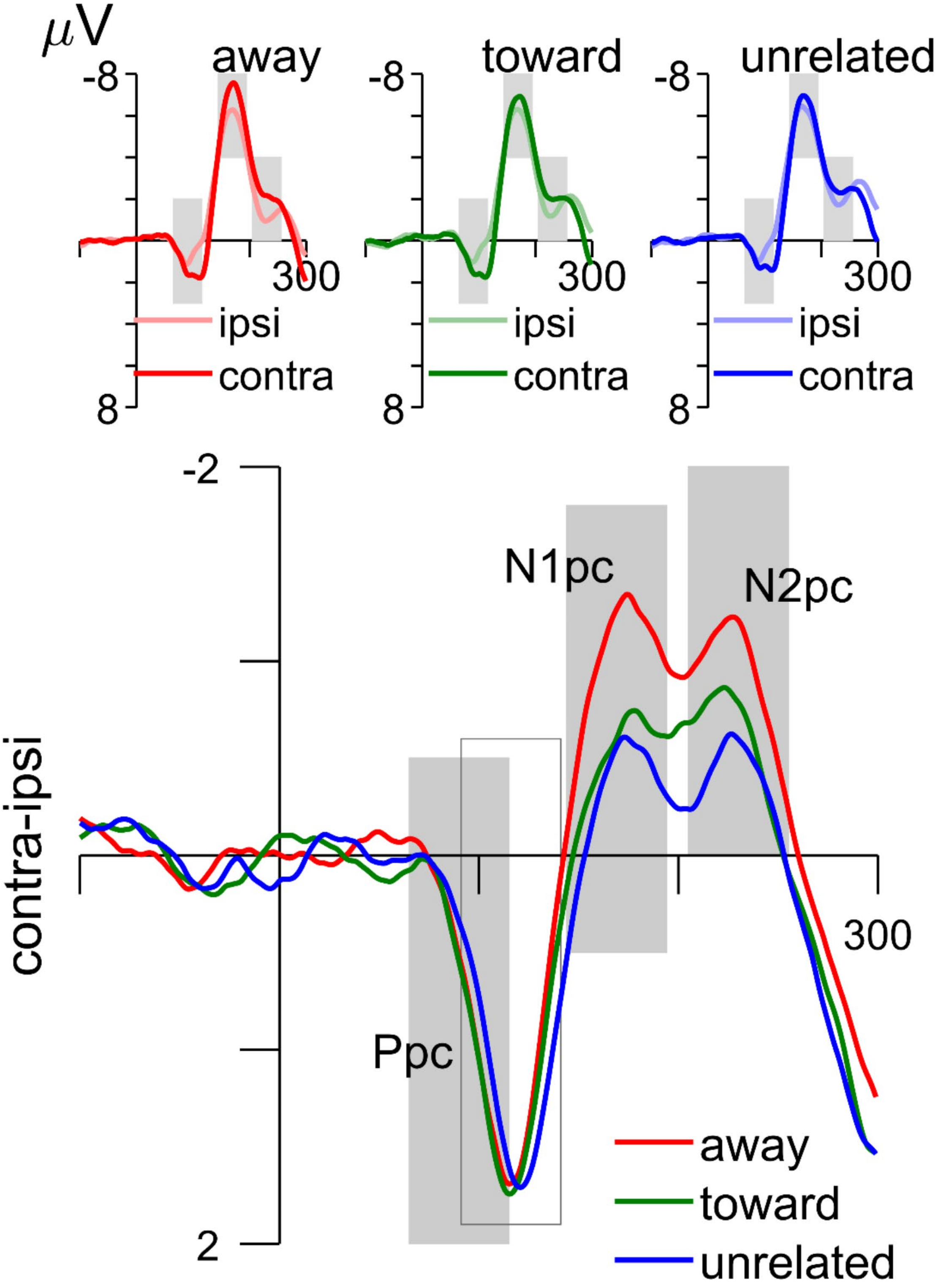

Fig. 3. Electrophysiological results from Experiment 1. The upper panels show the mean ipsi- and contralateral voltages at electrodes PO7/PO8 in response to the three different cue colors. The lower panel shows the difference waves (contra-ipsi). Epochs were 400 ms long, from – 100 ms before cue onset to 300 ms after. The target appeared 200 ms after cue onset.

Discussion

We replicated larger cueing effects for cue colors deviating away from the nontarget color. In addition, the electrophysiological results allow for conclusions regarding the optimal-tuning, rapid-disengagement, object-updating and sensory-adaptation accounts. As predicted by optimal tuning, the N1pc and N2pc components

	M	t(29)	d_z	*p*	BH
Ppc (μV)					
Away	0.65	5.41	0.99	< 0.001	y
Toward	0.69	5.33	0.97	< 0.001	y
Unrelated	0.51	4.22	0.77	< 0.001	y
N1pc (μV)					
Away	− 1.00	− 4.89	− 0.89	< 0.001	y
Toward	− 0.48	− 2.19	− 0.40	0.037	n
Unrelated	− 0.30	− 1.42	− 0.26	0.167	n
N2pc (μV)					
Away	− 0.93	− 2.73	− 0.50	0.011	y
Toward	− 0.58	− 1.69	− 0.31	0.101	n
Unrelated	− 0.39	− 1.18	− 0.22	0.248	n

Table 2. Electrophysiological results from experiment 1. Mean voltage differences in the Ppc, N1pc and N2pc time windows for each cue color, and results from one sample t-tests against zero. The column BH indicates whether the mean was significantly different from zero after controlling for false discovery rate with nine tests according to Benjamini and Hochberg[42].

were larger to cues deviating away from the nontarget color. Differences between cue colors were the same in the early and late intervals (i.e., N1pc and N2pc), which is inconsistent with the rapid-disengagement account. Further, differences in ERPs associated with the allocation of attention rule out non-attentional explanations such as object updating.

Finally, the Ppc component did not differ between cue colors, providing no evidence for sensory adaptation. However, this conclusion is compromised by the results from the unrelated cue color. Because this color was less frequent than the target color, we expected less sensory adaptation and a larger Ppc component, but the Ppc was the same. Therefore, it is possible that the Ppc component is not sufficiently sensitive to reveal effects of sensory adaptation in the current paradigm. Besides reflecting sensory adaptation[23], the Ppc is thought to reflect imbalanced saliency of otherwise equiluminant stimuli[24,31–34,43]. For instance, in previous studies on cueing effects, there was a cue-elicited Ppc in the P1 time range from 75 to 125 ms, which did not depend on the match between cue color and attentional template[34,43].

However, this cue-elicited Ppc was not reported in studies by Eimer et al.[17–19]. A possible explanation for the discrepancy is the presence of placeholders. In the current study, placeholders were presented to mark the stimulus locations, whereas no placeholders were presented in the studies by Eimer and colleagues. The presence of placeholders in the current study may have led to sensory adaptation to light gray. This adaptation could have diminished the P1 contralateral to the gray ring compared to the colored cue on the other side of fixation. This imbalance would then manifest as a Ppc. However, there is no systematic comparison between displays with and without placeholders. In addition, the presence of the Ppc was not formally tested in studies by Eimer and colleagues[17–19], but inspection of their figures suggests that it was absent.

Experiment 2

The aim of Experiment 2 was to further examine the effects of sensory adaptation. First, we removed the placeholder displays from Experiment 1 to reduce sensory adaptation to light gray. Consequently, the P1 contralateral to the gray ring in the cue display should be equal to the P1 contralateral to the colored cue on the other side of fixation. This implies a reduction or elimination of the Ppc to the cue. Second, we replaced the unrelated cue color by the nontarget color. Given that the nontarget color was presented most frequently throughout the experiment, we would expect the strongest sensory adaptation to occur for this color. If the Ppc to this color does not show a decrease, the Ppc may not be sensitive to sensory adaptation at all. Finally, Experiment 2 also served to replicate the major results from Experiment 1, notably larger N1pc and N2pc components elicited by cues deviating away from the nontargets relative to cues deviating toward the nontargets.

Methods

The methods were as in Experiment 1 except that the placeholders were omitted (see Fig. 1C). In addition, the unrelated cue color was replaced by the nontarget color. Three datasets with less than 70% retained trials (41%, 47%, 56%) were discarded. As in Experiment 1, three participants were assigned to each color combination for a sample size of 30 participants.

Results

Reaction time results

In the analysis of RTs, we successively excluded trials with RTs longer than 1,500 ms (0.1%), choice errors (3.7%), and trials with RTs deviating more than 2.5 *SD*s from the respective condition mean (2.1%). Mean RTs are shown as a function of cue validity and cue color in Fig. 2. We entered individual mean RTs in a repeated-measures 2 (cue color: away, toward, nontarget) × 2 (cue validity: valid, invalid) ANOVA. The main effect of cue color, $F(2, 58) = 18.70$, $p < .001$, $\eta_p^2 = 0.392$, and cue validity, $F(1, 29) = 26.78$, $p < .001$, $\eta_p^2 = 0.480$, entered a significant interaction, *F*(2, 58) = 31.07, *p* < .001, η_p^2 = 0.517. To follow up on this interaction, we calculated cueing effects for each cue color. Table 3 reports the means and results of t-tests against zero. Further, we compared cueing effects between cue colors according to our experimental hypotheses. Cueing effects with a cue color deviating away from the nontarget color were larger than cueing effects with a cue color deviating towards the nontarget color (33 vs. 11 ms), *t*(29) = 5.79, *p* < .001, Cohen's d_z = 1.06, which is consistent with the optimal tuning of attention. In addition, cueing effects with a cue color deviating toward the nontarget color were larger than cueing effects with the nontarget color (11 vs. 2 ms), *t*(29) = 2.37, *p* = .025, Cohen's d_z = 0.43, showing that cue colors resembling the target attracted more attention. Running the same ANOVA on the percentages of choice errors revealed a significant effect of validity, *F*(1, 29) = 5.89, *p* = .022, η_p^2 = 0.169, and a significant interaction, *F*(2, 58) = 4.92, *p* = .011, η_p^2 = 0.145. Only the cueing effect with a cue color deviating away from the nontarget color was significant (see Table 3).

Electrophysiological results

Data processing was as in Experiment 1. For each cue color and participant, the range of retained trials was 81–142 (*M* = 126, *SD* = 12) for cue colors deviating away from the nontarget color, 111–142 (*M* = 128, *SD* = 9) for cue colors deviating toward the nontarget color, and 111–144 (*M* = 130, *SD* = 7) for cues in the nontarget color. The peaks of the P1, N1, and N2 components were at 91, 156, and 223 ms after onset of the cue. Figure 4 shows the resulting time-windows for the ipsi- and contralateral voltages (top panels) and the difference waves (bottom panel). Table 4 reports the means and t-tests against zero.

We ran a 2 (cue color: toward, away) × 2 (interval: N1, N2) ANOVA on the difference between ipsi- and contralateral voltages. Unlike in Experiment 1, voltage differences increased from the N1pc to the N2pc interval (− 0.22 vs. − 0.87 µV), *F*(2, 58) = 9.13, *p* = .005, η_p^2 = 0.239, suggesting that the N1pc component was less pronounced than in Experiment 1. The voltage difference depended on the cue color, *F*(2, 58) = 5.71, *p* = .005, η_p^2 = 0.164, but there was no interaction with interval, *F*(2, 58) = 1.58, *p* = .214, η_p^2 = 0.052. Follow-up t-tests showed that the contralateral negativity averaged across N1 and N2 intervals was larger for cue colors deviating away from the nontarget color than for cue colors deviating toward the nontarget color (− 0.79 vs. − 0.49 µV), *t*(29) = 2.21, *p* = .035, Cohen's d_z = 0.40. The mean N1pc and N2pc to cue colors deviating toward the nontarget color did not reliably differ from cues in the nontarget color (− 0.49 vs. − 0.36 µV), *t*(29) = 0.99, *p* = .332, Cohen's d_z = 0.18.

To evaluate the effects of sensory adaptation, we conducted a repeated-measures ANOVA on the Ppc in the interval centered on the peak of the P1 (at 91 ms). The effect of cue color was non-significant, *F*(2, 58) = 0.22, *p* = .806, η_p^2 = 0.007, providing no support for contributions of sensory adaptation. In particular, the difference between cue colors deviating away and toward the nontarget color was not significant (0.65 vs. 0.68 µV), *t*(29) = 0.61, *p* = .547, Cohen's d_z = 0.11. However, the Ppc components in the selected time window were reliable for each cue color (see Table 4). We conducted the same ANOVA on the Ppc in the interval centered on the peak of the Ppc, which occurred at 112 ms (see outline rectangle in Fig. 4). We confirmed the absence of a main effect of cue color, *F*(2, 58) = 0.17, *p* = .841, η_p^2 = 0.006. The means were 0.95, 0.88, and 0.89 for cue colors deviating away and toward the nontarget color, and for cues in the nontarget color.

Discussion

We evaluated whether the cue-elicited Ppc was sensitive to sensory adaptation in the current paradigm. To this end, we removed the placeholder circles and replaced the unrelated cue color by the nontarget color. As in Experiment 1, we observed no effects of cue color on the Ppc, suggesting that it did not reflect sensory adaptation. If the Ppc was influenced by sensory adaptation, we would expect a reduced Ppc to cues in the nontarget color, as this color was presented most frequently. Further, the cue-elicited Ppc persisted although sensory adaptation to light gray was avoided by removing the placeholder circles. Therefore, the cue-elicited Ppc is unlikely to reflect sensory adaptation at all. Our findings are more in line with the hypothesis that the Ppc reflects imbalanced saliency[24,31–34,43]. Further, it is not entirely clear why previous studies did not observe a Ppc to their cue displays[17–19]. Possibly, differences in stimulus size explain the discrepancy. In previous studies by Eimer and colleagues, a single cue was composed of a set of four closely aligned dots subtending only 0.8 dva, but we used a ring with a diameter of 2.8 dva. Maybe larger cues amplify the imbalanced saliency and promote the occurrence of a Ppc, but more research is needed to clarify this issue. Further, Experiment 2 replicates the major findings from Experiment 1. The N1pc and N2pc components were larger for cue colors deviating

	Valid	Invalid	CE	t(29)	d_z	*p*	BH
RTs (ms)							
Away	467	500	33	6.95	1.27	< 0.001	y
Toward	468	479	11	3.02	0.55	0.005	y
Nontarget	471	473	2	0.89	0.16	0.378	n
Choice errors (%)							
Away	2.6	4.5	1.9	3.88	0.71	0.001	y
Toward	3.5	3.9	0.4	0.72	0.13	0.478	n
Nontarget	3.2	3.2	0.0	− 0.03	0.01	0.975	n

Table 3. Reaction time results from experiment 2.

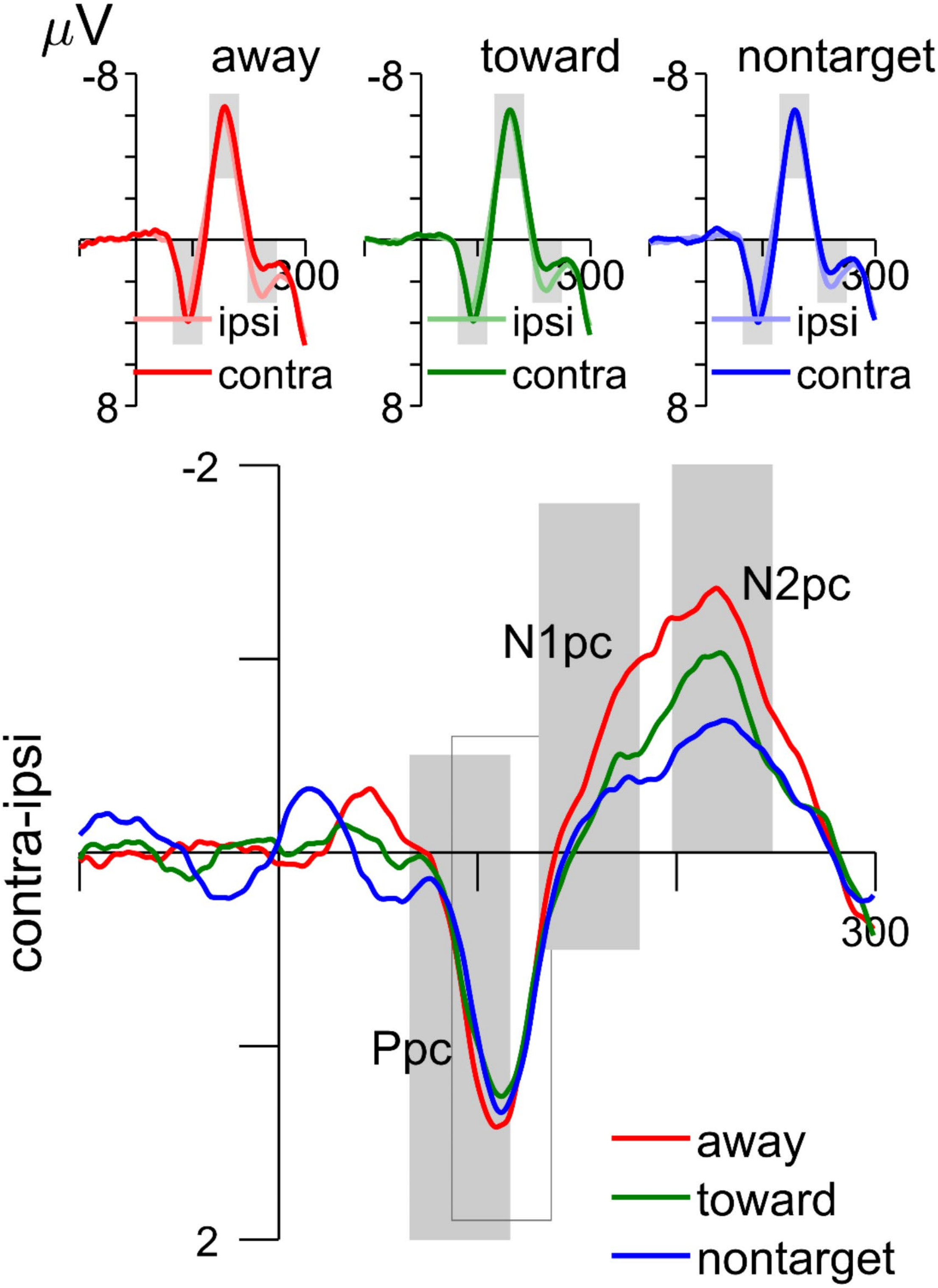

Fig. 4. Electrophysiological results from Experiment 2.

away from the nontarget color, which supports optimal tuning. As in Experiment 1, the time course of the contralateral negativity was inconsistent with rapid disengagement and finally, the occurrence of N1pc and N2pc components was inconsistent with the object-updating account. Further, the N1pc appeared less pronounced than in Experiment 1, which may be related to the absence of placeholders, but more research is needed to clarify this issue.

	M	t(29)	d_z	*p*	BH
Ppc (μV)					
Away	0.69	8.17	1.49	< 0.001	y
Toward	0.61	5.05	0.92	< 0.001	y
Nontarget	0.63	6.30	1.15	< 0.001	y
N1pc (μV)					
Away	− 0.42	− 3.10	− 0.57	0.004	y
Toward	− 0.13	− 0.77	− 0.14	0.447	n
Nontarget	− 0.11	− 0.86	− 0.16	0.398	n
N2pc (μV)					
Away	− 1.17	− 3.83	− 0.70	< 0.001	y
Toward	− 0.84	− 2.74	− 0.50	0.010	y
Nontarget	− 0.60	− 2.38	− 0.43	0.024	y

Table 4. Electrophysiological results from experiment 2.

General discussion

We investigated behavioral and electrophysiological responses in a cueing experiment with cue colors that deviated either toward or away from the nontarget color. Behaviorally, we replicated results showing that cueing effects elicited by cue colors deviating away from the nontarget color were larger than cueing effects elicited by cue colors deviating toward the nontarget color[8,22]. Because cueing effects are largest for cue colors corresponding to the attentional template[13], the results suggest that observers' search goal was a color deviating away from the nontarget color. This result dovetails with previous reports of a shift in the memory representation away from the nontarget color[6–12]. Taken together, the shift in cueing effects and memory judgments support the idea of optimal tuning of attention[4,5].

Rapid disengagement and object updating

The primary objective of this study was to evaluate alternative explanations of cueing effects. We addressed the rapid-disengagement, object-updating and sensory-adaptation accounts. According to the rapid disengagement account[14], the initial allocation of attention is saliency-driven, but the subsequent withdrawal of attention occurs earlier for colors that do not match participants' search goals. Consistent with previous studies[17–19], we found no evidence for rapid disengagement because the differences in the cue-elicited negativities were the same in the early and late intervals (N1pc vs. N2pc). The object updating account[20,21] claims that less object updating is needed for cue colors deviating away from the nontarget color because they match the biased target representation. This account does not involve attention. However, we found that components associated with attention were larger for cue colors deviating away from the nontarget color, which is inconsistent with any non-attentional account.

Sensory adaptation

Finally, we tried to evaluate the contributions of sensory adaptation. Because the majority color in the search displays was the nontarget color, there may have been sensory adaptation to the nontarget and neighboring colors. As a result, cue colors shifted toward the nontarget color may have undergone more sensory adaptation than cue colors shifted away from the nontarget color (see p. 11941 in[7]). We focused on the Ppc component, an early positivity at electrodes PO7/PO8, to index sensory adaptation[23], but found no difference between cue colors deviating toward and away from the nontarget color. However, results from two control conditions cast doubts on our assumption that the Ppc was influenced by sensory adaptation. The unrelated cue color in Experiment 1 should have been less affected by sensory adaptation because it was less frequently presented. In contrast, the nontarget color in Experiment 2 should have been more affected because it was more frequently presented. However, the Ppc was unchanged. This lack of differentiation across cue colors suggests that the Ppc reflects imbalanced saliency rather than sensory adaptation[24,31–34,43].

Further, we would like to clarify the relation between the Ppc in the current study and similar positivities in other studies. Here, we refer to the early positivity in the time range of the P1 (75–125 ms) as Ppc. It may be more precise to refer to it as P1pc[26] because positivities in later time intervals were also referred to as Ppc. For instance, Leblanc, Prime[44] coined the term Ppc, but referred to a positivity in the N1 range (140–190 ms). Similarly, Sawaki and Luck[45] observed a positivity in the N1 range (125–225 ms) but called it P_D because it was associated with distractor suppression (for review, see[46]). Other positivities after the N1 range were also labelled P_D, but were related to the disengagement and suppression after attentional capture[47] or they were labelled CP and related to the enhancement at the cued location when the search display appeared[34,48]. Therefore, it is important to note that we focused on the earliest occurrence of the Ppc to isolate processes related to sensory adaptation, consistent with Luck and Hillyard[23].

Reliability of ERPs and cueing effects

We observed no significant differences in the N1pc or N2pc between cue colors deviating toward the nontarget color and cue colors used as controls (unrelated color in Experiment 1, nontarget color in Experiment 2).

Descriptively, the N1pc and N2pc were larger for cue colors deviating toward the nontarget color. However, this difference did not reach significance, which is unexpected because the color deviating toward the nontarget color was more like the target color than the control colors and, therefore, more attention-grabbing. While lateralized ERPs did not reveal the expected difference, cueing effects did. Cueing effects for cue colors deviating toward the nontarget color were small (11–12 ms), but significantly different from cueing effects in the control conditions (1–2 ms). Thus, it appears that cueing effects were more sensitive to small differences in attentional orienting or selection than electrophysiological measures. In general, cueing effects are very robust and require only a few observations. For instance, in the classical study by Folk and Remington[13], there were only 8 and 24 observations for valid and invalid trials, respectively. In contrast, measurements of the N2pc require many more observations to yield robust results. In the current study, mean voltage differences were based on more than 100 trials. While this number is typical for work on lateralized ERPs, it results in more trials than necessary for the calculation of cueing effects. As a result, the cueing effects were less contaminated by noise and small differences between cue colors reached significance.

Conclusions

In summary, we evaluated whether prior evidence for the optimal tuning of attention could be accounted for by rapid disengagement, object updating, or sensory adaptation. Consistent with optimal tuning away from the nontarget color, cueing effects were larger for cue colors that deviated away from the nontarget color. In addition, electrophysiological recordings revealed larger N1pc and N2pc components elicited by cues deviating away from the nontarget color. Given the established link between the N1pc and N2pc components and attention, our findings provide support for optimal tuning while contradicting non-attentional accounts of cueing effects, such as object updating. Further, our results do not support the rapid disengagement account, as the difference in the contralateral negativity between cues remained stable across the early and late intervals. Finally, a thorough evaluation of the sensory adaptation account may not have been feasible because results from control conditions point towards imbalanced saliency as the primary driver of the Ppc component. Nonetheless, the current results support the view that optimal tuning of attention affects all stages of the search process, from establishing a biased memory representation to attentional orienting and selection of stimuli matching this representation.

Data availability

The data are available at https://osf.io/u5v7f/ and the program code will be made available upon request. Please send an email to dirk.kerzel@unige.ch.

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Author contributions

The author planned the experiments, carried them out, analyzed them and wrote the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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