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Attentional guidance by relative features: Behavioral and electrophysiological evidence

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Abstract

Our ability to select task-relevant information from cluttered visual environments is widely believed to be due to our ability to tune attention to the particular elementary feature values of a sought-after target (e.g., red, orange, yellow). By contrast, recent findings showed that attention is often tuned to feature relationships, that is, features that the target has relative to irrelevant features in the context (e.g., redder, yellower). However, the evidence for such a relational account is so far exclusively based on behavioral measures that do not allow a safe inference about early perceptual processes. The present study provides a critical test of the relational account, by measuring an electrophysiological marker in the EEG of participants (N2pc) in response to briefly presented distractors (cues) that could either match the physical features of the target or its relative features. In a first experiment, the target color and nontarget color were kept constant across trials. In line with a relational account, we found that only cues with the same relative color as the target were attended, regardless of whether the cues had the same physical color as the target. In a second experiment, we demonstrate that attention is biased to the exact target feature value when the target is embedded in a randomly varying context. Taken together, these results provide the first electrophysiological evidence that attention can modulate early perceptual processes differently; in a context-dependent manner versus a context-independent manner, resulting in marked differences in the range of colors that can attract attention.

Descriptors: Attention, Cognitive control, Visual processes, EEG, N2pc

Early sensory analyses usually provide more information than can be processed at once. Selective attention describes the processes applied to limit this input to a smaller subset of information. Many theories of visual attention assume that selection is determined by a priority map of activation, a topographical representation of the visual field that codes the attentional priority of each location. A standard assumption in current models of selective attention is that the item at the location with peak priority is selected first for attentional in-depth processing (e.g., Awh, Belopolsky, & Theeuwes, 2012; Itti & Koch, 2001; Müller et al., 2010; Navalpakkam & Itti, 2007; Wolfe, 2007; Zelinsky & Bisley, 2015; but see Eimer & Grubert, 2014).

Activation values in the priority map depend on two factors: bottom-up controlled factors such as feature contrast or salience (Nothdurft, 1993, 2000) resulting from hardwired properties of early sensory processing, and top-down controlled factors, reflecting observers' selection intentions and search goals. In search for a known target object (forming a task set), it is assumed that working memory representations of this object's properties are activated (attentional templates) and that these mental representations guide attention efficiently and quickly to task set matching events in the visual field (e.g., Desimone & Duncan, 1995; Folk, Remington, & Johnston, 1992; Woodman, Luck, & Schall, 2007). For instance, when observers look for red targets, attention can be limited to select red items, presumably reflecting a stronger representation of red on the level of the priority map (through tuning of attention to red, in other words, through response gain modulation of neurons responding to red). Which rules, however, govern the top-down tuning of attention to features more specifically?

The influence of top-down control on attentional priority has frequently been investigated with spatial cueing tasks (e.g., Eimer & Kiss, 2008; Folk & Remington, 1998; Jonides, 1981; Posner & Cohen, 1984). To ensure that observers initiate feature-based top-down control, they are typically asked to search for a target with a prespecified feature. Folk and Remington (1998), for example, asked participants to search for a red target among three white nontargets and to identify this target (X or =). To assess how top-down control influences attentional selection, they briefly presented

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a task-irrelevant cue prior to each search array. Across trials, this cue was either shown in the target color (e.g., red) or a distractor color (e.g., green). Importantly, cues were spatially unpredictive with respect to the target location so that observers had no incentive to attend to them. Despite the cues' spatial unpredictability, Folk and Remington observed spatial cueing effects, that is, faster reaction times (RTs) when the target was presented at the same relative to a different location than the preceding cue. However, this was only the case for cues that possessed the target (red) and not the distractor color (green), demonstrating that only cues that matched the top-down task set had attracted (captured) attention and therefore facilitated target selection in the subsequent search array. Such spatial cueing effects therefore reflect the specific properties (e.g., red) to which top-down control had been configured and serve as a measure for successful attentional top-down tuning. Generally, such findings were interpreted in the framework of a feature similarity account, claiming that attention is top-down tuned to the target's physical feature (e.g., Anderson & Folk, 2010; Folk & Remington, 1998; also see Treue & Martinez Trujillo, 1999). According to feature similarity accounts, attentional priority should be highest for items exactly matching the physical target feature and should decrease the more an item differs from the set featural target identity.

More recent findings, however, indicate that attention is not necessarily tuned to the physical target features, but can also be biased to relative target attributes in a context-dependent manner (e.g., Becker, 2010, 2014). In a series of spatial cueing experiments, attentional capture was found to depend on whether the cue's relative features (relative to the cue context; e.g., redder, larger, darker) matched the target's relative features (relative to the target context; e.g., redder, larger, darker). Becker, Folk, and Remington (2013), for example, presented observers with orange targets among yellowish-orange nontargets (relative target color: redder). RT cueing effects were observed for a red cue among orange items as well as for a yellowish-orange cue among yellow items (both relative cue colors: redder), even though neither cue matched the exact physical color of the target. Simultaneously, an orange cue surrounded by red context elements did not capture attention (relative cue color: yellower), although it matched the specific target color (orange). Such findings support a relational account of attention, suggesting that attention can be tuned to the relative, rather than physical target color (e.g., Becker, Folk, & Remington, 2010). According to the relational account, attentional priority should be highest for items that differ in the same featural direction (e.g., redder or yellower) from their context elements as the target from its nontarget elements, independently of whether or not these items match the target's exact feature value (e.g., Becker, 2010). Subsequent studies expanded on these findings (Becker, Harris, Venini, & Retell, 2014; Harris, Remington, & Becker, 2013) and showed that attention will by default be tuned to the relative (rather than the physical) target feature when both the target and the target context features remain constant.

In fact, attention was only found to be biased to the physical target feature when an orange target was presented randomly among either red or yellow nontargets. This procedure of intermixed (redder or yellower) trials rendered the relative target feature unreliable and resulted in cueing effects elicited only by physical target color matching (orange) cues, indicating that attention was biased to the specific target feature independently of the context (as predicted by feature similarity accounts).

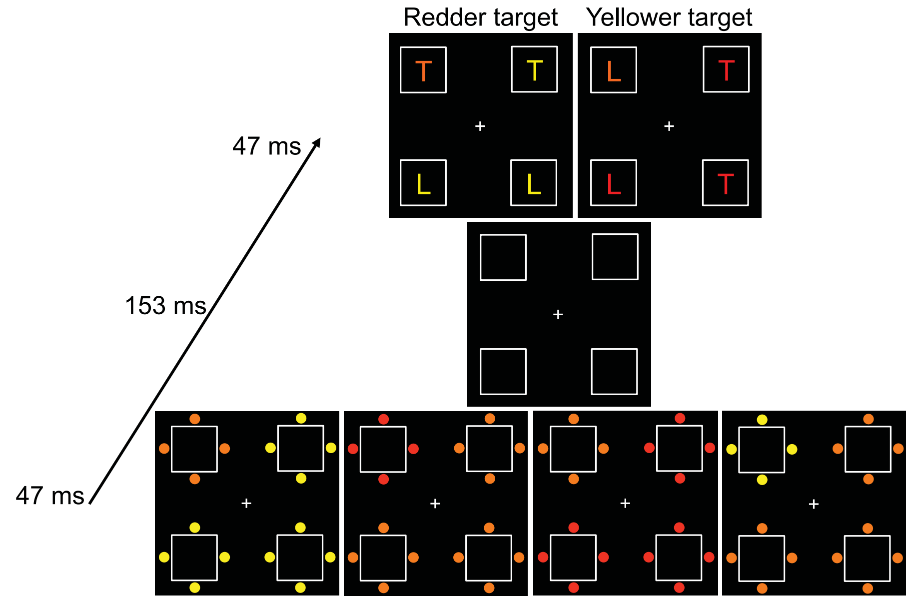
Importantly, the evidence for this relational account is yet solely based on behavioral studies that inferred attentional capture from RT spatial cueing effects. RTs, however, are recorded after response execution and constitute a measure of the sum of all processing stages from stimulus onset until response execution. They can therefore only be an indirect measure of attentional capture, as not only perceptual, but also decisional or response-related processes can in theory contribute to the measured spatial cueing effects. Furthermore, in spatial cueing tasks, RTs are measured in response to search arrays and not in response to the preceding cue arrays where attentional capture is substantiated. Transient, short-lived attentional effects of particular cues could therefore dissipate even before the target is actually presented (e.g., due to rapid disengagement of attention from the cue; Lamy & Egeth, 2003; Theeuwes, Atchley, & Kramer, 2000; see also Kiss, Grubert, & Eimer, 2013, for divergent behavioral and electrophysiological findings along these lines). Thus, previous behavioral results on relational capture cannot rule out a possible role of feature-based processes in modulating attentional capture by the cue (which dissipated before the target was presented), or ascertain that the relative features of cue and target in fact modulated early attentional processes (instead of later, decisional processes).

The present study addressed these limitations of behavioral measures by additionally using the N2pc component of the ERP as an electrophysiological marker of attentional selection. The N2pc is an enhanced negativity over lateral extrastriate visual cortex that emerges around 200 ms after stimulus onset contralateral to the side of an attended stimulus. Importantly, the N2pc can be locked to the onset of the cue arrays and therefore provide a direct measure of attentional capture by particular cues (e.g., Eimer & Kiss, 2008; Lien, Ruthruff, Goodin, & Remington, 2008; Sawaki & Luck, 2013).

In two spatial cueing experiments, we measured behavioral cueing effects and cue-locked N2pc components to task set matching and nonmatching cues in a visual search for prespecified targets. Critically, fixed-color targets (orange) were either presented in a constant context (red or yellow nontargets for different sets of observers; Experiment 1) or a variable context (red or yellow nontargets intermixed across trials; Experiment 2). According to previous studies (e.g., Becker et al., 2013; Harris et al., 2013), in Experiment 1 participants should bias attention to the relative color of the target (redder, yellower), while in Experiment 2, attention should be biased to the target's physical color (orange). In both experiments, the respective (relational or featural) task set matching cues should elicit RT cueing effects (e.g., Harris et al., 2013). If the faster RTs on trials in which the target is presented at the cued relative to the uncued location truly reflect attentional capture on a perceptual level, the same task set matching cues should also trigger reliable N2pc components. Moreover, in the absence of rapid attentional disengagement from the cue, cues that do not match the respective task set should evoke neither behavioral nor electrophysiological evidence of attentional capture (e.g., Kiss et al., 2013).

Experiment 1

In Experiment 1, we tested whether attention is biased to the physical or relative target color when the target and target context colors are fixed. To ensure a generalization of our results and to exclude potential confounds by color-specific search asymmetries (e.g., Fortier-Gauthier, Dell'Acqua, & Jolicoeur, 2013), one group of observers searched for a unique orange target (singleton target) among three yellow context items (relative task set: redder; physical task set: orange), whereas a different group of observers searched for an orange singleton among three red nontargets (relative task set: yellower; physical task set: orange; Figure 1). Search displays were



Target	Cues			
E1: Redder	PERF	RELA	FEAT	NONE
E1: Yellower	FEAT	NONE	PERF	RELA
E2: R. or Y.	FEATyel	NOred	FEATred	NOyel

Figure 1. Schematic illustration of the cue and search displays. The same four cue displays were presented in both experiments. In Experiment 1, the target and nontarget colors were fixed across the entire experiment, and half of the observers searched for an orange target among all yellow nontargets (redder target condition), and the other half searched for the same target among all red nontargets (yellower target condition). Depending on the target condition, the cue displays with the orange cue were either PERF or FEAT cues, and the cue displays with the red and yellow cue were either RELA or NONE cues (see main text for definition of these acronyms). In Experiment 2, the two target displays were presented intermixed within a block, so that the target was always orange, but randomly redder or yellower than the context. The cue displays with the orange cue were now either FEATyel or FEATred cues, whereas the cue displays with the red and yellow cue were either NOred or NOyel cues.

preceded randomly by one out of four possible types of cue arrays: (1) In perfectly matching (PERF) cue displays, the colors were identical to those of the search displays. The singleton cue possessed the physical target color (orange) and was presented among three nontarget-colored context items (i.e., yellow or red, respectively). (2) In relatively matching (RELA) cue displays, the singleton cue matched the relative (redder or yellower), rather than the physical (orange) target feature (i.e., a red or yellow singleton cue, respectively, among orange context items). (3) In feature-matching (FEAT) cue displays, the singleton cue matched the physical target feature (orange), but in contrast to PERF cue displays, the cue context items had a different color than the nontargets in the search array (i.e., red or yellow, respectively, when search array nontargets were yellow or red). (4) In nonmatching (NONE) cue displays, the singleton cue and cue context color assignment was exactly the opposite compared to the target and nontarget color assignment in the search arrays (i.e., a yellow or red singleton cue, respectively, presented among orange context items).

According to a feature-similarity account, the PERF and FEAT cues that matched the target's physical color (orange) should capture attention and elicit behavioral cueing effects and solid N2pc components. On the other hand, RELA and NONE cues (red/yellow cues among orange context items) should fail to attract attention, as they do not match the physical target color of the task set for orange.

Importantly, according to a relational account, only the PERF and RELA cues should attract attention and trigger corresponding behavioral and electrophysiological responses, because they both match the relational task set with respect to the cue's context color (e.g., red cues are redder with respect to an orange context). In turn, FEAT and NONE cues should not produce such attentional capture effects, as in these displays the cue and cue context color assignment is exactly reversed relative to the relational task set (e.g., orange cues are yellower with respect to a red context).

Method

Participants. Twenty-four participants from the University of Queensland, Australia, completed Experiment 1; 12 completed the redder target condition (nine females, mean age of 23 years) and 12 the yellower target condition (11 females, mean age of 22 years). All participants were right-handed, reported normal neurological health, color vision, and normal or corrected-to-normal visual acuity. Five participants from the original sample were replaced due to exceedingly high alpha or eye movement activity resulting in a loss of more than 25% of trials in the artifact rejection. All participants gave informed consent prior to the experiment and were compensated with AU$20 for their participation. All procedures used in Experiment 1 and 2 adhered to the ethical principles of human experimental research (Declaration of Helsinki), and were approved by the human ethics review committee of the University of Queensland.

Apparatus. Participants were seated in a dimly lit room, and viewed the stimulus display (17-inch CRT monitor, 85 Hz, 1,024 × 768 pixels) from a viewing distance of 57 cm. The display's white point was set to D65. Observers pressed one of two designated response keys on a USB number pad using their right index and middle finger. Colors were measured with a Mavolux colorimeter and are specified in CIE 1976 Lu'v' triplets with L in cd/m^2.

Stimuli. Stimuli were generated using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and were presented on a black background (0.30 cd/m^2). Three types of displays were presented in each trial: fixation, cue, and target displays (Figure 1). The fixation display consisted of a central white fixation cross (0.3° × 0.3°, line width: 0.03°) and four light gray placeholder squares (2° × 2°, line width: 0.03°), one in each quadrant of the display, positioned equidistantly on the outlines of an imaginary circle with a radius of 6° around fixation. The cue display consisted of the fixation display, with the addition of four dot cues (0.4° × 0.4°, each) positioned around each placeholder at the 12, 3, 6, and 9 o'clock locations (on an imaginary circle of 1.3° around the center of each placeholder). One of the four dot cues, the singleton cue, had a unique color. The remaining three sets of four dot cues constituted the cue context and were drawn in the same color. The possible colors in the cue display were yellow (12.0 cd/m^2, $u' = .20$, $v' = .55$), orange (12.0 cd/m^2, $u' = .29$, $v' = .54$), or red (12.0 cd/m^2, $u' = .37$, $v' = .53$). These colors were combined to four possible cue arrays: (1) an orange cue among yellow context items, (2) a red cue among orange context items, (3) an orange cue among red context items, and (4) a yellow cue among orange context items. Depending on the target condition (redder, yellower target), the cue displays with the orange cue were either PERF or FEAT cues, and the cue displays with the red and yellow cue were either RELA or NONE cues (see Figure 1).

The target display consisted of the fixation display and four letters (Ls or Ts; 1.0° × 1.4°, line width: 0.2°), which were centered inside the four placeholders. Each target display always contained two Ls and two Ts. Target letters were orange singletons among three yellow nontargets in the redder target condition and among three red nontargets in the yellower target condition.

Design. The color of the target and nontargets was held constant throughout the experiment, whereas the cue displays varied across trials. To ensure that the cue was always nonpredictive of the target location and that the response (T, L) was independent of the cue and target position, the cue type (PERF, RELA, FEAT, and NONE), cue position (position 1 to 4), target position (position 1 to 4), and target identity (L, T) were fully counterbalanced across trials, resulting in 128 trials that were presented in random order. Each participant completed eight blocks of 128 trials, for a total of 1,024 experimental trials.

Procedure. Prior to the experiment, participants were instructed to report the identity of the orange target letter in the search display (L or T) by pressing the corresponding left or right response key with their middle or index finger, respectively (the key-to-response assignment was counterbalanced across participants). Participants were instructed to maintain central fixation throughout each experimental block and to respond as fast and accurately as possible.

Each trial started with the presentation of a fixation display, randomly presented between 700 and 1,100 ms. Fixation was followed by the cue, another fixation, and then the search display, presented sequentially for 47 ms, 153 ms, and 47 ms, respectively (Figure 1). After the search array, a fixation display was presented until a response was given and an additional 500 ms. After each response, participants received an auditory feedback of a high pitched tone for correct (1050 Hz, 100 ms), and a low pitched tone (750 Hz, 100 ms) for incorrect, anticipatory, and delayed responses ($\mathrm{RT} < 200$ or $> 2{,}000$ ms). Before the start of a new trial, the fixation cross was removed for 100 ms to remind participants to fixate for the next trial. Participants had breaks after 64 trials, during which they received feedback about their accuracy rate in the preceding block.

EEG recording and analysis. EEG was recorded using active Ag/AgCl electrodes of a 64-channel BioSemi ActiveTwo EEG system (Biosemi Instrumentations, Amsterdam, The Netherlands), digitized at 1,024 Hz. The electrooculogam (EOG) was recorded from electrodes placed at the outer canthus of each eye, and above and below the left eye. Data were analyzed using the ERPLAB Toolbox (Lopez-Calderon & Luck, 2014) and EEGLAB Toolbox (Delorme & Makeig, 2004). Offline, the raw EEG was rereferenced to the average of the left and right mastoids, 30 Hz low-pass filtered (12 dB Butterworth), and downsampled to 256 Hz.

The EEG was segmented from 100 ms prior to 400 ms after cue onset and baseline corrected with respect to the prestimulus interval (−100 to 0 ms). Trials were excluded from analysis if they contained a fast, slow, or incorrect response, if RT exceeded the individual cell mean RT by more than 3.5 standard deviations, or if they were contaminated with artifacts (horizontal EOG [HEOG] exceeding 80 μV or 16 μV in a step function with a 200-ms window width and a 10-ms window step, Luck, 2014; vertical EOG [VEOG] exceeding 80 μV; all other channels exceeding 100 μV). These criteria led to the exclusion of 12.1% of all trials in the redder target condition (ranging from 1.1 to 24.9%) and 12.1% in the yellower target condition (ranging from 3.7 to 23.4%). To assess residual eye movements, we computed individual HEOG waveforms for left- and right-cue trials. For all participants, the averaged HEOG did not exceed 3.2 μV, which suggests that residual eye movements were less than 0.2° in size (Lins, Picton, Berg, & Scherg, 1993; see also McDonald & Ward, 1999, for a similar HEOG calibration).

For both target conditions, ERPs were averaged separately for each combination of cue type (PERF, RELA, FEAT, NONE) and cue side (left, right). N2pc components in response to cue arrays were quantified on the basis of mean amplitudes obtained in the 210–290 ms time window after cue onset at lateral posterior electrode sites PO7 and PO8 (similar time windows to substantiate N2pc components at these standard electrode sites were, for example, used by Grubert & Eimer, 2015; Kiss et al., 2013; Kiss, Grubert, Petersen, & Eimer, 2012; Lien et al., 2008).

Results

An alpha level of .05 (two-tailed) was used to determine statistical significance. The *p* values were adjusted using the Greenhouse-Geisser epsilon correction for nonsphericity when necessary.

Mean RT and errors. A 4 × 2 × 2 mixed measures analysis of variance (ANOVA) with the factors cue type (PERF, RELA, FEAT, NONE), cue validity (valid [target at cued location], invalid [target not at cued location]), and the between-subjects factor target condition (redder, yellower) showed no significant interactions involving the factor target condition, either on mean correct RTs, all $F\mathrm{s} < 2.53$, $p\mathrm{s} > .10$, or on error rates, all $F\mathrm{s} < 1$ (or on N2pc amplitudes, all $F\mathrm{s} < 1$). Therefore, for all further analyses, data were pooled across the two target conditions. Average mean RTs as a function of cue type and cue validity are shown in Figure 2.

The results of a 4 × 2 repeated measures ANOVA with the factors cue type (PERF, RELA, FEAT, NONE) and cue validity

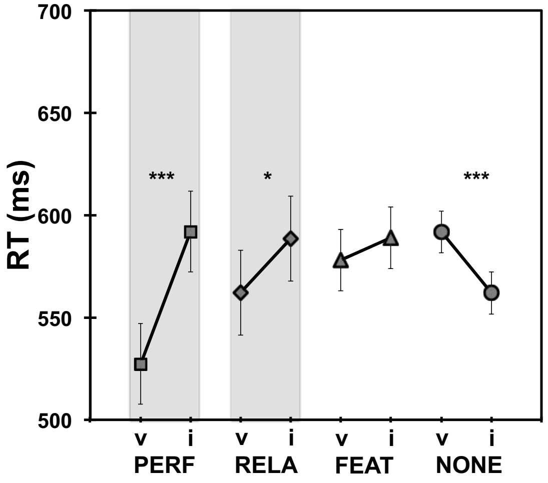


Figure 2. Average mean RTs on valid (v) and invalid cue trials (i) from Experiment 1. The gray columns highlight the conditions for which relative tuning predicted attentional capture (indicated by a positive slope of a linegraph). Error bars show within-subject 95% CIs for the respective difference between the valid and invalid cue condition (Franz & Loftus, 2012). $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$.

(valid, invalid) computed over the mean correct RTs showed significant main effects of cue type, $F(3,69) = 16.98$, $p < .001$, $\eta_p^2 = 0.43$, and cue validity, $F(1,23) = 47.35$, $p < .001$, $\eta_p^2 = 0.67$, as well as a significant interaction, $F(3,69) = 17.62$, $p < .001$, $\eta_p^2 = 0.43$, indicating that cueing effects differed between the cues. Pairwise comparisons showed a significant cueing effect for PERF cues that were identical to the target (65 ms), $t(23) = 8.62$, $p < .001$. In line with the prediction of the relational account, RELA cues that matched the relative target color elicited significant cueing effects (26 ms), $t(23) = 2.68$, $p = .010$, whereas FEAT cues that matched the physical target color failed to elicit significant cueing effects (11 ms), $t(23) = 1.04$, $p = .310$. NONE cues that matched neither the relative nor the physical target color showed a significantly reversed cueing effect (-30 ms), $t(23) = 5.79$, $p < .001$.

The mean error proportions as a function of cue type and cue validity are displayed in Table 1. The same 4 × 2 ANOVA computed over the mean error rates showed similar results, with significant main effects of cue type, $F(3,69) = 4.02$, $p = .010$, $\eta_p^2 = 0.15$, cue validity, $F(1,23) = 20.91$, $p < .001$, $\eta_p^2 = 0.48$, and a significant interaction, $F(3,69) = 7.13$, $p < .001$, $\eta_p^2 = 0.24$. Pairwise comparisons showed significant cueing effects for PERF cues (3.5%), $t(23) = 4.57$, $p < .001$, and RELA cues (3.6%), $t(23) = 3.79$, $p < .001$. FEAT and NONE cues that did not match the relative color of the target did not elicit significant cueing effects, all ts < 1.

Table 1. *Mean Error Proportions (%) on Valid and Invalid Trials and Cue Validity Effects as a Function of Cue Type*

Experiment 1				Experiment 2			
	Cue validity				Cue validity		
Cue type	Valid	Invalid	Effect	Cue type	Valid	Invalid	Effect
PERF	4.7	8.2	3.5***	FEATyel	5.2	7.7	2.5*
RELA	3.6	7.2	3.6**	NOred	7.5	6.1	−1.4
FEAT	7.2	6.7	−0.5	FEATred	4.5	9.5	5.0*
NONE	7.0	6.5	−0.5	NOyel	7.9	6.1	−1.8*

$^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

N2pc. Figure 3 (left panel) depicts ERPs at posterior electrode sites PO7/8 contra- and ipsilateral to the cue side and the corresponding topographical scalp maps, separately for each cue type. The bottom panel shows the respective difference waveforms obtained by subtracting ipsi- from contralateral ERPs. As shown in Figure 3, a significant N2pc (increased contra- relative to ipsilateral activity in the 210–290 ms time window postcue) was observed only for PERF and RELA cues, but not for FEAT or NONE cues. This observation was confirmed by a 4 × 2 repeated measures ANOVA on mean N2pc amplitudes with the factors cue type and laterality (contralateral, ipsilateral). The ANOVA revealed a main effect of laterality, $F(1,23) = 15.75$, $p < .001$, $\eta_p^2 = 0.41$, and a significant interaction, $F(3,69) = 16.81$, $p < .001$, $\eta_p^2 = 0.42$, indicating that N2pc amplitudes differed between cue conditions. In line with the behavioral findings, pairwise comparisons revealed a significant N2pc for PERF cues (mean amplitude: -0.96 μV), $t(23) = 4.69$, $p < .001$, and RELA cues (-0.65 μV), $t(23) = 3.92$, $p < .001$). No reliable N2pc was obtained for FEAT cues that matched the physical, but not the relative target feature (-0.04 μV), $t < 1$. NONE cues that matched neither the target's physical nor relative feature triggered a small, but significant contralateral positivity (0.29 μV), $t(23) = 3.24$, $p < .01$.

Discussion

The results of Experiment 1 demonstrate that attention was tuned to the relative target color (redder or yellower, depending on the nontarget context). In line with the assumptions of a relational account (Becker, 2010), only those cues that matched the relative target color (PERF and RELA cues) elicited RT cueing effects and reliable N2pc components, indicative of attention capture. Cues that did not match the target's relative color (FEAT and NONE cues) failed to produce reliable cueing effects or N2pc components, despite the fact that some of these cues shared the target's physical color (FEAT cues). These results validate that attention to the cues depended on a relational task set, which shows that attention was top-down tuned to the relative color of the target, not its physical color. Notably, the cues that failed to match either the target's physical or relative color (NONE cues) triggered inverse RT cueing effects and a positive deflection contralateral to the cue during the N2pc time window. This positive deflection might be interpreted as a P_D component (distractor positivity), which has been previously linked to active distractor suppression (e.g., Gaspar & McDonald, 2014; Hickey, Di Lollo, & McDonald, 2009; Jannati, Gaspar, & McDonald, 2013; Sawaki & Luck, 2010, 2013). Cues in a different relative color than the target might have received additional suppression when they also had a different physical color. An alternative explanation could be that the inverted RT cueing effects and the positivity in ERPs reflect attentional "misguidance" toward the cue context items, as those shared the target-matching relative (as well as the target's physical) color (Harris et al., 2013). Since only one cue context item of this sort appeared at the side of the cue, but appeared twice at the opposite side of the cue, the positivity contralateral to the cue might reflect a small, but reliable N2pc to the two opposite side cue context items (Lien, Ruthruff, & Cornett, 2010). However, our stimulus setup does not allow deciding whether these inverse cueing effects were caused by cue suppression (distractor cue

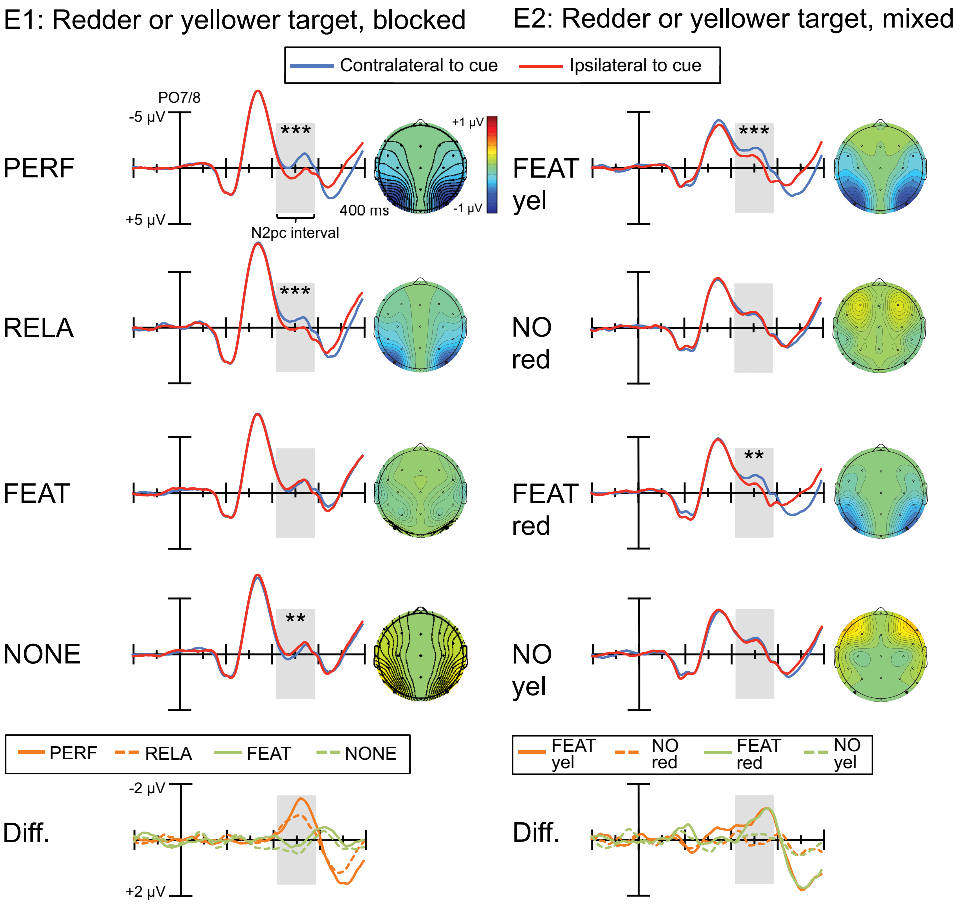


Figure 3. Contra- and ipsilateral grand-averaged ERPs at electrode sites PO7 and PO8 and corresponding topographical scalp maps for each cue type (four top rows), depicted separately for Experiment 1 (left) and Experiment 2 (right). The two bottom panels show the difference waves (Diff), which were obtained by subtracting ipsi- from contralateral ERPs. The gray shaded areas highlight activity in the N2pc time interval (210–290 ms postcue onset). Scalp maps plot negative activity in blue and positive activity in red.

P_D) or attentional processing of the cue context (target-matching context N2pc).[1]

A second noteworthy aspect of the results was that the relatively and physically matching (PERF) cues elicited larger RT cueing effects than relatively, but not physically matching cues (RELA; 65 ms vs. 26 ms), $t(23) = 3.91$, $p < .001$. Similar trends were also found in the N2pc, though the corresponding difference failed to reach significance (-0.95 μV vs. -0.65 μV), $t(23) = 1.74$, $p = .10$. This feature-specific modulation was not predicted by the relational account. However, it is also rather unlikely to reflect a feature-specific bias that coexisted with an attentional bias for the relative features because, in this case, the FEAT cue should also have attracted attention, contrary to the results. Instead, weaker validity effects for the relatively matching cue could be due to faster disengagement of attention from cues and/or faster rejection of these cues that commenced after the cue was selected (e.g., Becker et al., 2014). According to this view, only the initial transient attention shift would be determined by the relative features of target and cue, with subsequent identification processes relying also on feature-specific information. This explanation is in line with the observation that feature-specific processes affected the later RT measure more strongly than the earlier N2pc, and with the observation that a featural match modulated performance only when the cue already matched the relative feature of the target (i.e., had the propensity to attract attention), which would otherwise be difficult to explain.

The finding that all relatively matching cues but not all physically matching cues elicited a significant N2pc provides converging behavioral and electrophysiological evidence for attentional tuning to the relative target color, rather than the physically exact target color value. Critically, in Experiment 1, both the relative and the physical target color remained constant throughout the experiment, principally allowing biasing attention to the relative or physical target feature. The fact that solid N2pc components were found only in response to cues that matched the observers' relative task set provides further (and for the first time electrophysiological) evidence that attention is preferentially biased to the relative target

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[1] Note that all N2pc components were followed by large positive deflections. In a recent spatial cueing experiment, such positive deflections following N2pc components were interpreted as P_D components indexing active suppression of the previously selected cues (i.e., active termination of perceptual processing of task-set matching cues to enable subsequent attentional reorienting to the target; Sawaki, Geng, & Luck, 2012, Experiment 2). However, in their experiment Sawaki et al. used a cue-search array stimulus onset asynchrony (SOA) of 1,600–1,800 ms allowing for all cue-locked N2pc and P_D components to be elicited without being overridden by any perceptual components triggered by the onset of the subsequent search array. Due to the short SOA of 200 ms used in our study, any deflections following the N2pc are highly likely confounded by such early search array-elicited ERPs and were therefore not analyzed.

properties when the conditions allow successful localization of the target by either its relative or physical features (i.e., when the relative and physical feature of the target remains constant; see Becker et al., 2014; Harris et al., 2013).

It could be argued, however, that the attentional bias observed in Experiment 1 was not due to a preference, but a necessity. That is, top-down tuning could be rather coarse-grained and might not allow top-down selection of all possible individual feature values. For example, a possible top-down tuning mechanism described in the Guided Search model (Wolfe, 1994, 2007) allows top-down tuning to color via four broad, categorical channels that are centered on yellow, blue, green, and red. Correspondingly, in search for an orange target among yellow or red nontargets, attention could only be tuned to red or yellow, but not orange, because there is no orange channel. Furthermore, the target and nontarget colors were quite similar to each other, which could have rendered selection of the target in virtue of its physical color very difficult or even impossible (see also Bauer, Jolicoeur, & Cowan, 1998; D'Zmura, 1991; Hodsoll & Humphreys, 2001). If it is correct that attention cannot be successfully top-down biased to a target feature value such as orange in Experiment 1, it would be wrong to claim that the results exemplify a relational top-down tuning mechanism that is inconsistent with the feature similarity view.

Experiment 2 was designed to test whether the stimulus conditions of Experiment 1 indeed did not allow effective top-down tuning to the target feature value, by encouraging observers to bias attention to the physical color of the target in Experiment 2.

Experiment 2

In Experiment 2, we tested whether attention can be tuned to a specific target feature such as orange. Physical stimulation in both cue and search arrays was identical to Experiment 1, but in Experiment 2 we encouraged observers to adopt a task set for the physical target color by rendering the use of a relational task set impossible. This was achieved by varying the target's relative features between redder and yellower randomly across trials (we presented the two possible target displays from Experiment 1 in an intermixed fashion). In Experiment 2, the target color was kept fixed to orange, but the nontargets were randomly red or yellow, rendering the target's relational identity unpredictable (yellower or redder) across trials. With this manipulation, top-down tuning to a relative target color would not allow efficient target detection, thus encouraging observers to bias attention to the physical target feature in a context-independent manner (Harris et al., 2013).

To probe whether attention was tuned to the specific target color, the same four cue displays were presented as in Experiment 1 (Figure 1). Given that the nontargets varied randomly across trials, none of the cues matched the relative features of the target anymore. Orange cues that were embedded in a red or yellow context were now both feature-matching cues, and were labeled FEATred and FEATyel, to indicate the different cue contexts. Red and yellow cues that were presented in an orange context were now labeled NOred and NOyel, respectively, to indicate the cue colors for these nonmatching cues.

If attention can be successfully biased to an intermediate target color value with the stimuli used in Experiment 1, only the physically matching, orange cues should capture attention. All other cues should fail to attract attention. Conversely, if attention cannot be top-down biased to the physical target feature (orange), or if such a top-down bias does not result in successful selection of the target (e.g., because the nontarget colors are too similar to orange to allow discriminating the target from the nontargets), search for the target should be inefficient and none of the cues should attract attention.

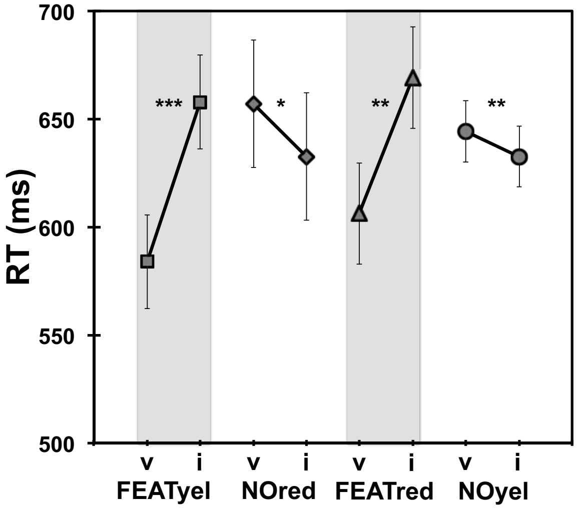

Figure 4. Average mean RTs on valid and invalid cue trials from Experiment 2, in which the target always had a constant feature value (orange), but was randomly presented in a context of all red or all yellow nontargets. The gray columns highlight the conditions for which attentional capture is predicted, provided that attention can be tuned exclusively to the intermediate feature value of orange.

Method

Participants. Twelve new participants completed Experiment 2 (10 females, mean age of 24 years). Three participants from the original sample were replaced due to exceedingly high overall error rates (> 15%).

Apparatus, stimuli, design, and procedure. The apparatus, stimuli, design, and procedure were identical to Experiment 1 (Figure 1), except that the orange targets were randomly embedded in the context of yellow or red nontargets. Trials were excluded based on the same criteria as in Experiment 1 (on average 8.3% of all trials, ranging from 3.9 to 18.8%).

Results

Mean RT and errors. Mean RTs on correct trials are presented in Figure 4, and mean proportions of errors are summarized in Table 1. A 4 × 2 ANOVA comprising the variables cue type (FEATred, FEATyel, NOred, NOyel) and cue validity (valid, invalid) revealed main effects of cue type, $F(3,33) = 5.11$, $p = .005$, $\eta_p^2 = 0.32$; cue validity, $F(1,11) = 29.91$, $p < .001$, $\eta_p^2 = 0.73$, and a significant two-way interaction, $F(3,33) = 18.97$, $p < .001$, $\eta_p^2 = 0.63$. Pairwise comparisons revealed significant cueing effects for both physically matching, orange cues, FEATyel: 74 ms, $t(11) = 6.28$, $p < .001$; FEATred: 63 ms, $t(11) = 4.26$, $p = .001$. The two nonmatching cues in turn showed reverse cueing effects, with faster RTs on invalid compared to valid trials, NOred: −24 ms, $t(11) = 2.26$, $p = .045$; NOyel: −12 ms, $t(11) = 3.30$, $p = .007$.

The same ANOVA computed over the mean error rates showed only a significant Cue Type × Cue Validity interaction, $F(3,33) = 5.51$, $p = .004$, $\eta_p^2 = 0.33$. Pairwise comparisons revealed significant cueing effects for both target color matching cues, FEATred: 5.0%, $t(11) = 3.13$, $p = .010$; FEATyel: 2.5%, $t(11) = 2.84$, $p = .016$. The physically nonmatching red cue produced no effect, NOred: −1.4%, $t(11) = 0.75$, $p = .47$. The yellow cue showed an inverse cueing effect, NOyel: −1.8%, $t(11) = 2.86$, $p = .016$.

N2pc. Figure 3 (right panel) shows the grand average of contra- and ipsilateral waveforms, and the respective difference waveforms (contra- minus ipsilateral ERPs) elicited by the four different cue types. A 4 × 2 ANOVA showed a significant main effect of laterality, $F(1,11) = 17.83$, $p = .001$, $\eta_p^2 = 0.62$, and a significant interaction between cue type and laterality, $F(3,33) = 8.49$, $p < .001$, $\eta_p^2 = 0.44$. Pairwise comparisons revealed that both target color-matching, orange cues elicited significant N2pc components, FEATred: −0.69 μV, $t(11) = 5.71$, $p < .001$; FEATyel: −0.76 μV, $t(11) = 4.15$, $p = .002$. However, there was no substantial difference between ipsi- and contralateral waveforms for cues that did not match the physical target color, NOred: 0.03 μV, $t(11) = 0.29$, $p = .778$; NOyel: −0.12 μV, $t(11) = 0.69$, $p = .502$.

Discussion

The results indicate that attention was tuned to the specific target color in Experiment 2. Only cues that matched the physical target color triggered behavioral cueing effects and N2pc components, indicative of attentional capture. Cues with target nonmatching colors (red, yellow) did not produce any behavioral or electrophysiological evidence of attentional processing. From these results of Experiment 2, it can be concluded that attention could have been biased to the physical target feature in the stimulus conditions of Experiment 1. In other words, the results of Experiment 1 were truly due to a strategic task set adaptation rather than hardwired limitations in top-down tuning of attentional selection.

As in Experiment 1, we obtained inverse RT cueing effects to cues that did not match the physical target color. Similar to Experiment 1, these inverted cueing effects might reflect the suppression of the target-dissimilar cue color (red, yellow), or the selection of the context cues that matched the target color (orange). However, in Experiment 2 the inverse cueing effects were not accompanied by a reliable distractor positivity (P_D). It might be that two colors had to be suppressed in Experiment 2. However, this requirement evidently did not result in early distractor suppression (P_D), but can still apparently result in inverse cueing effects (which have to be attributed to postselective processes).

General Discussion

Taken together, we measured behavioral and electrophysiological markers of attentional capture in two spatial cueing experiments. In search for a fixed target color among a constant target context (fixed nontarget colors), observers used a relational task set to guide attentional object selection (Experiment 1). Only cues that matched the relative (redder or yellower) target color elicited RT cueing effects and N2pc components, indicating that only these cues (RELA cues) captured attention. Cues that did not match the relative target color did not trigger any behavioral or electrophysiological evidence for attentional processing. Importantly, this was even the case for cues that matched the target's physical color value (FEAT cue) and only failed to match the target's relative color. This pattern of results is in line with the relational account (Becker, 2010) but not with feature similarity accounts (e.g., Anderson & Folk, 2010; Folk & Remington, 1998; Folk et al., 1992), which would have predicted attentional capture only by cues that matched the target's physical color.

Along similar lines, our findings are also not in line with the display-wide orienting hypothesis (Gibson & Kelsey, 1998; see Burnham, 2007, for an extensive overview), which predicts attentional capture for cueing displays that match the appearance of the target display. For instance, Gibson and Kelsey (1998; Experiment 2) demonstrated that display properties such as abrupt onsets can mediate attentional capture for abrupt onset cues even when the target is not singled out by an onset and the onset is only a display-wide property of the entire target display. By contrast, cues containing an irrelevant feature not present in the search display (e.g., red, when the search display consisted only of white letters) did not attract attention. Although this account also proposes that attentional capture depends on target as well as target context features, it cannot explain the observed results pattern. For example, in the redder target condition (orange target, yellow nontargets), a set for display-wide features would result in capture by any cue display containing the colors orange and yellow, which applies both to the relatively and physically matching cue displays (PERF; orange cue among yellow items) and the cue displays matching neither the relational nor physical target feature (NONE; yellow cue among orange items), which however failed to modulate attention. Furthermore, attentional orienting to display-wide features seems inconsistent with the observed capture effects for relationally, but not physically matching cues (RELA; red cue among orange items), which included features not contained in the target display (e.g., red).

In sum, the present results favor a relational account over a feature similarity and display-wide features account. However, one alternative account that could potentially provide an alternative explanation for our results is the optimal tuning account (e.g., Navalpakkam and Itti, 2007). According to this account, attention can be top-down biased to an "exaggerated" target feature (exaggerated in the opposite direction of the nontarget feature value distribution), to increase the signal-to-noise ratio when the target is difficult to discriminate from the nontargets. For example, in search for an orange target among yellow nontargets (the redder target in Experiment 1), attention might be top-down biased to red or an intermediate color value between red and orange. This might explain attentional capture by relationally matching (RELA) cues, as these cues indeed matched the exaggerated target feature (e.g., red). Similarly to the relational account, optimal tuning assumes that target and target context features jointly determine the mode of attentional control. However, unlike the relational account, optimal tuning assumes that attention is tuned to a specific feature value and that stimuli only attract attention when they are similar to the exaggerated feature value (in line with feature similarity accounts).

The relational account and optimal tuning account will often make the same predictions and are thus difficult to distinguish from one another. Previous studies, however, showed that cues possessing the nontarget feature can still attract attention to the same extent as cues with an exaggerated target feature (Becker et al., 2013), which argues against an optimal tuning account and supports a relational account.[2]

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[2] We did not provide a critical test of the optimal tuning account in the present study because designs that include a nontarget-colored cue require using four different colors (red, reddish orange, yellowish orange, and yellow; see, e.g., Becker et al., 2013). With the present equipment, it was not possible to render four different colors easily discriminable while maintaining equiluminance for the purpose of EEG measurements (e.g., Woodman, 2010).

In this respect, it is important to note that the relational account can accommodate many previous behavioral and electrophysiological findings that were interpreted in favor of feature-specific accounts, including feature similarity accounts and the optimal tuning account. This holds because most studies varied not only the feature of the cue (target-matching vs. nonmatching feature value) but also the relative feature of the cue (target-matching vs. nonmatching relative feature), and thus cannot distinguish between the different views (e.g., Folk & Remington, 1998; Gaspelin, Margett-Jordan, & Ruthruff, 2015; Lien et al., 2008; Lien, Ruthruff, & Johnston, 2010). For example, in search for a red target among white nontargets, observing attentional capture by a red cue but not a green cue (e.g., Folk & Remington, 1998) is consistent both with a relational account and a feature-specific account, as the red cue matches both the target feature (red) and the target's relative feature (redder), whereas the green cue matches neither the target feature (red) nor its relative feature (redder). To distinguish the relational account from feature-specific accounts, it is necessary to vary the contextual properties of the target and cue independently of their specific feature values.

Previous studies measuring RT validity effects in the spatial cueing paradigm (or eye movements in visual search) demonstrated that observers by default mode engage in a relational search strategy, and only switch to a feature-specific selection strategy when the target cannot be localized in virtue of a stable relative feature (e.g., when the nontargets randomly vary; Becker et al., 2013, 2014; Harris et al., 2013). The present results support these findings and provide additional electrophysiological evidence for them, by showing that the exact same stimuli elicit a relational search strategy when the nontarget context is constant (Experiment 1) and a feature-specific search strategy when the relative features of the target randomly vary (redder/yellower; Experiment 2).

Critically, when the relationship between target and nontarget colors was made unpredictable across trials, the use of a relational task set became impossible, and participants swapped their search strategy and based attentional guidance on a task set defining the exact physical target color (Experiment 2). As predicted by feature similarity accounts, in Experiment 2, only cues that matched the exact featural search template attracted attention, as measured by RT cueing effects and solid N2pc components; target dissimilar cues, which did not share the target color, did not attract attention. This finding is theoretically important as it shows that attentional tuning to the relative target color in Experiment 1 was due to a search mode preference and not some hardwired limitations in attentional control or effects of discriminability between target and nontarget features (e.g., Navalpakkam & Itti, 2007; Wolfe, 1994, 2007).

Moreover, the EEG results confirmed that these changes in search strategy affect processing at an early, perceptual stage (not only later stages concerned with stimulus identification or response selection). It can therefore be concluded that previously observed relational cueing effects on the behavioral level were not (only) substantiated on postselective processing stages. With this, the present results allow ruling out the possibility that feature-matching cues would always attract attention (i.e., feature similarity view), but that these effects were not detectable in behavioral responses because attention could be rapidly disengaged from target-matching cues or distractors (e.g., Theeuwes, 2010; Theeuwes et al., 2000).

To sum up, the present results provide the most direct evidence for a context-dependent mechanism of attentional control, in which the target context determines how attention is deployed. Importantly, this is not only behavioral, but also electrophysiological support, as RT cueing effects were found to converge with N2pc components that measure attentional capture by the cue more directly. Our results therefore show that attentional capture strongly depends on the target's relative stimulus properties and that capture by cues that match the relative but not the physical target feature occurs at an early, perceptual stage of visual processing.

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