Neural correlates of goal-directed enhancement and suppression of visual stimuli in the absence of conscious perception



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Abstract

An observer's current goals can influence the processing of visual stimuli. Such influences can work to enhance goal-relevant stimuli and suppress goal-irrelevant stimuli. Here, we combined behavioral testing and electroencephalography (EEG) to examine whether such enhancement and suppression effects arise even when the stimuli are masked from awareness. We used a feature-based spatial cueing paradigm, in which participants searched four-item arrays for a target in a specific color. Immediately before the target array, a nonpredictive cue display was presented in which a cue matched or mismatched the searched-for target color, and appeared either at the target location (spatially valid) or another location (spatially invalid). Cue displays were masked using continuous flash suppression. The EEG data revealed that target-colored cues produced robust N2pc and N_T responses—both signatures of spatial orienting—and distractor-colored cues produced a robust P_D —a signature of suppression. Critically, the cueing effects occurred for both conscious and unconscious cues. The N2pc and N_T were larger in the aware versus unaware cue condition, but the P_D was roughly equivalent in magnitude across the two conditions. Our findings suggest that top-down control settings for task-relevant features elicit selective enhancement and suppression even in the absence of conscious perception. We conclude that conscious perception modulates selective enhancement of visual features, but suppression of those features is largely independent of awareness.

Keywords Attentional capture · Visual awareness · Attention: Selective

The relationship between attention and perceptual awareness has been the subject of a lengthy and intense debate (Chica & Bartolomeo, 2012; Chun & Wolfe, 2000; Cohen, Cavanagh, Chun, & Nakayama, 2012; De Brigard & Prinz, 2010; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Iwasaki, 1993; Koch & Tsuchiya, 2007, 2012; Lamme, 2003, 2006; Mole, 2008; Posner, 1994; Prinz, 2011; Tallon-Baudry,

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Campana, Park, & Babo-Rebelo, 2018; van Boxtel, 2017; van Boxtel, Tsuchiya, & Koch, 2010; Wyart & Tallon-Baudry, 2008). Many theorists have suggested that the two processes are inseparable, if not identical (Chun & Wolfe, 2000; Cohen et al., 2012; De Brigard & Prinz, 2010; Mack & Rock, 1998; Merikle & Joordens, 1997; Mole, 2008; O'Regan & Noe, 2001; Posner, 1994; Prinz, 2011; Velmans, 1996), whereas others have argued that attention and awareness are supported by distinct neural processes, and are readily dissociated from one another (Baars, 1997, 2005; Bachmann, 2006; Block, 2005; Dehaene et al., 2006; Iwasaki, 1993; Kentridge, Heywood, & Weiskrantz, 1999a; Kentridge, Heywood, & Weiskrantz, 2004; Koch, 2004; Lamme, 2003; Maier et al., 2008; Naccache, Blandin, & Dehaene, 2002; Koch & Tsuchiya, 2007; van Boxtel et al., 2010; Watanabe et al., 2011; Woodman & Luck, 2003a).

A central dilemma in the debate is that, under normal circumstances, attended stimuli tend to be consciously perceived; likewise, salient stimuli that occupy conscious perception frequently become the focus of attention. Koch and Tsuchiya (2007) have proposed that the optimal approach for investigating associations and dissociations between attention and awareness is to use a two-by-two crossed experimental design. Under this framework, participants are instructed either to attend to or ignore sensory stimuli, and these events



are presented so that they are either consciously perceived or manipulated (via masking, etc.) so that they cannot be consciously reported. Here, we addressed the question of the relationship between spatial attention and perceptual awareness using a recently developed feature-based cueing paradigm (Lamy, Alon, Carmel, & Shalev, 2015) in which cue events were masked so that they were not available for conscious report on roughly half the trials. We combined reaction time (RT) measures of performance with electroencephalography (EEG) to examine the independent effects of attention and awareness on feature-based cueing effects (e.g., Folk & Remington, 1999; Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994; Gibson & Amelio, 2000; Gibson & Kelsey, 1998; Yantis & Egeth, 1999).

As is typical in feature-based cueing experiments (e.g., Folk & Remington, 1999; Folk et al., 1992; Folk et al., 1994; Gibson & Amelio, 2000; Gibson & Kelsey, 1998; Yantis & Egeth, 1999), targets presented at the same location as a targetcolored cue (valid trials) produce faster RTs than targets presented at a different location (invalid trials). Interestingly, this feature-based cueing effect seems to occur even when cues are not consciously perceived due to masking (e.g., Ansorge & Neumann, 2005; Hsieh, Colas, & Kanwisher, 2011; Ivanoff & Klein, 2003; Lamy et al., 2015). In most previous studies, the feature-based cueing effect has been quantified by comparing differences in reaction times (RTs) between valid and invalid cue conditions (e.g., Folk & Remington, 1999; Folk et al., 1992; Folk et al., 1994; Gibson & Amelio, 2000; Gibson & Kelsey, 1998; Yantis & Egeth, 1999). However, RT measures index the end result of an accumulated sequence of processing stages between stimulus onset and motor response (Sternberg, 1969). It is thus desirable to incorporate a more continuous measure of attentional allocation to examine the time course of feature-based cueing effects in such experiments. To this end, several investigators have employed event-related potentials (ERPs), such as the N2 posterior contralateral (N2pc) component, to measure the neural dynamics of feature-based spatial cueing effects (Eimer, 1996; Eimer & Kiss, 2008; Heinze, Luck, Mangun, & Hillyard, 1990; Kiss, van Velzen, & Eimer, 2008; Luck, 2005; Luck & Hillyard, 1994; Woodman & Luck, 1999, 2003b).

Several feature-based cueing studies have found evidence for an N2pc response to target-relevant cues that were masked from awareness (e.g., Ansorge, Horstmann, & Worschech, 2010; Ansorge, Kiss, & Eimer, 2009; Woodman & Luck, 2003a). There are, however, some important limitations with the designs used in these studies that limit the extent to which clear conclusions can be drawn regarding the relationship between spatial attention and perceptual awareness. Ansorge et al. (2010) and Ansorge et al. (2009) found that masked cues captured attention when they were task relevant, but not when they were task irrelevant, suggesting that feature-based cueing effects can be elicited even when cues are not consciously

perceived. In these studies, however, spatial orienting was not measured under both aware and unaware conditions, so the independent effects of selective attention and awareness could not be assessed.

Woodman and Luck (2003a) presented search displays that contained targets and distractors that were masked using object substitution masking (OSM). They measured N2pc responses to the targets and distractors under delayed offset and cotermination masking conditions. Interestingly, the authors found an N2pc response for both delayed offset and cotermination trials, and this response did not differ in magnitude between the masking conditions, suggesting that feature-based cueing effects might be independent of awareness. Critically, however, their participants' performance on the search task was significantly above chance even in the critical delayed-mask offset condition, suggesting that their participants might have been aware of the target and distractor stimuli in the "unaware" condition.

Lamy et al. (2015) addressed some of the issues with these previous studies by using continuous flash suppression (CFS; Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006) to mask brief visual cues presented to one eye in a feature-based cueing task. In their task, a cue display containing a single colored stimulus, which either matched the target color or was a distractor color, was presented to one eye. This cue display was masked by presenting a high-contrast flickering stimulus in the other eye. Importantly, stimulus parameters were held constant for every trial throughout the experiment, and participants were asked to report their awareness of the cue on each trial. After the cue display, targets appeared at valid or invalid locations. Participants searched for a color-defined target and reported its orientation, before indicating their awareness of the preceding cue. Valid target-colored cues produced faster RTs to targets than invalid target-colored cues, as expected. Critically, however, Lamy et al. (2015) found that the validity effect was similar in magnitude for consciously perceived and unperceived cues, suggesting that the feature-based cueing effect arises even in the absence of conscious perception of the triggering cues. The authors also found that spatially valid distractor-colored cues increased RTs to the target compared with invalid distractor-colored cues, resulting in a same location cost (see also Anderson & Folk, 2012; Belopolsky, Schreij, & Theeuwes, 2010; Carmel & Lamy, 2014; Lamy et al., 2015; Eimer, Kiss, Press, & Sauter, 2009; Folk & Remington, 2008; Lamy & Egeth, 2003; Lamy, Leber, & Egeth, 2004; Schoeberl, Ditye, & Ansorge, 2018; Schönhammer & Kerzel, 2013). Interestingly, the same location cost was found for aware trials but not for unaware trials, suggesting that the same-location cost depends on awareness of relevant cue stimuli.

Here, we sought to replicate and extend the pioneering work of Lamy et al. (2015) using a feature-based cueing task combined with CFS to manipulate participants' awareness of visual cues. We combined behavioral testing and



electroencephalography (EEG) to ask whether goal-relevant stimuli in a feature-based spatial attention task produce cueing effects even when the "cueing" events are not consciously perceived. In Experiment 1 we ran a direct replication of the behavioral task developed by Lamy et al. (2015), as described in detail above, but using a larger sample of participants and more experimental trials per condition. In Experiment 2, we recorded EEG while participants performed the same behavioral task as in Experiment 1, with the aim of investigating whether the neural signatures of feature-based cueing effects are similar for aware and unaware cues. Finally, in Experiment 3, we modified the spatial cueing task to determine whether the observed effects of aware and unaware cues on RTs and ERPs reflected selective enhancement of task-relevant features and/or active suppression of task-irrelevant features.

Experiment 1

Experiment 1 was a direct replication of Experiment 1 from Lamy et al. (2015). Cues could appear at the same location as the target or at a different location, and they either matched the target color or were a different color. Cues were masked using CFS, such that participants were only aware of the cues on approximately half of the trials. Participants were asked to identify the target's orientation as quickly as possible and, following this, report their awareness of the cue. In line with the findings of Lamy et al. (2015), we predicted that valid target-colored cues would elicit faster responses to targets than would invalid target-colored cues, and the magnitude of this same location benefit would not differ between aware and unaware trials. We also hypothesized that valid distractorcolored cues would elicit slower responses to targets than would invalid distractor-colored cues, but only when the cues were consciously perceived, in line with the findings of Lamy et al. (2015).

Method

Participants

Twenty-seven individuals participated in Experiment 1 (16 females, mean age = 22.74 years, SD = 3.50). To increase statistical power and, therefore, the probability of finding potentially small effects, we increased sample size considerably compared with the original study by Lamy et al. (2015; 14 participants). All participants reported normal or corrected-to-normal vision, and all were naïve to the experimental hypotheses. Each provided informed written consent. The University of Queensland Human Research Ethics Committee approved the studies.



Participants were tested in a dimly illuminated room. Stimuli were presented on a 24-inch LCD monitor with a resolution of 1920 × 1200 and a refresh rate of 60 Hz. Stimulus delivery and response recording were controlled using a Dell PC running Cogent software (Cogent 2000 Toolbox: Functional Imaging Laboratory, Institute of Cognitive Neuroscience, and Wellcome Department of Imaging Neuroscience) using MATLAB operating under Windows XP. Participants viewed a dichoptic display through a mirror stereoscope, at a viewing distance of approximately 57 cm. To promote stable binocular fusion, the mirrors were adjusted for each individual observer at the beginning of the experimental session.

Participants performed a spatial cueing task, in which they were asked to identify the orientation of a target-colored T shape (rotated counterclockwise ("left") or clockwise ("right") by 90°; see Fig. 1). Before the target display, a cue display was presented, but masked using continuous flash suppression (CFS), such that participants were aware of the

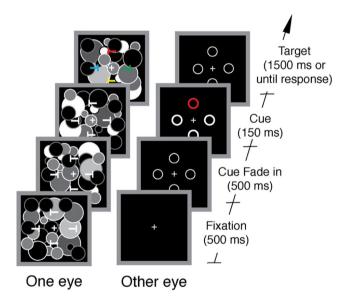


Fig. 1 Schematic of individual trial events in Experiment 1. Participants' task was to report the orientation of the target T shape and then to indicate whether they were aware of a colored cue stimulus. A flickering mask display (20 or 22 Hz) and four white T shapes (two rotated 90 degrees clockwise and two rotated 90 degrees counterclockwise) were presented to one eye throughout the experiment. Each trial began with a 500 ms fixation cross, followed by a 500 ms period in which the cue placeholders faded in to the suppressed eye. Colored cues were then presented to the suppressed eye for 150 ms. All placeholders thickened, and on cuepresent trials one of the four placeholders changed color so that it either matched the target color (target-colored cue) or was a distractor color (distractor-colored cue). In the immediately following target display, each of the four T shapes took on a unique color (red, blue, green, or yellow) for 1,500 ms or until response. Participants first indicated the orientation of the target T shape as quickly and as accurately as possible, and then reported, without time pressure, their perception of the cue on a scale from 0 (not aware of the cue) to 3 (clearly aware of the cue). (Color figure online)



cue on approximately half of the trials only (as found by Lamy et al., 2015, and confirmed in the current study following pilot testing). Cues did not predict the target location, and either matched the target color or appeared in a distractor color instead. The observers' task was to identify the orientation of the target-colored T shape (left or right) and indicate their response via a key press. Following this response, observers provided a subjective report of their perception of the cue, using a scale from 0 (not aware) to 3 (clearly visible). Observers were informed that on some trials no cue would be presented.

Stimuli were displayed against a black background (CIE: .304, .259, 1.4 cd/m²). During the entire presentation, two white (CIE: .305, .389, 214 cd/m²) fixation crosses and two gray (CIE: .305, .389, 59 cd/m²) and white (CIE: .305, .389, 214 cd/m²) striped squares $(7.3^{\circ} \times 7.3^{\circ} \times .2^{\circ}$ of visual angle) were presented on each side of the screen, such that one fixation dot and one square was visible to each eye. The task consisted of a fixation display, a cue display, and a target display.

The fixation display (500 ms) was presented to one eye (pseudorandomly to the left or right eye on each trial) and consisted of a central fixation cross (CIE: .305, .389, 214 cd/ m^2 ; $0.5^{\circ} \times 0.5^{\circ}$) surrounded by four peripheral circles (CIE: .305, .389, 214 cd/m²; 1 pixel thick; 1° radius and 2.5° from fixation). These circles were placed at the top, bottom, left, and right of the fixation cross. The peripheral circles appeared gradually from 0% contrast to 100% contrast over the 500-ms fixation display. The mask was presented to the other eye at 20 Hz. Each masking display was made of circles of various sizes (.5° to 1.5° radius) and shades of gray (light gray CIE: .299, .399, 107 cd/m²; dark gray CIE: .276, .342, .2 cd/m²; middark gray CIE: .254, .479, 6.0 cd/m²; mid-gray CIE: .277, .446, 48.3 cd/m²). Four T shapes (CIE: .305, .389, 214 cd/ m^2 ; $0.5^{\circ} \times 0.5^{\circ}$), two oriented 90° to the left and two 90° to the right, were superimposed on the masks.

In the cue display (150 ms), the peripheral circles thickened (two pixels thick). On cue-present trials, one circle changed color (red, CIE: .607, .365, 43 cd/m²; green, CIE: .294, .651,158 cd/m²; blue, CIE: .144, .083, 17 cd/m²; or yellow, CIE: .396, .561,198 cd/m²). The target color was consistent throughout the experiment. For observers searching for a red or green target, cues were either red (40% of trials), green (40% of trials), or no cue was presented (20% of trials). For observers searching for blue or yellow targets, cues were either blue (40% of trials), yellow (40% of trials), or no cue was presented (20% of trials). During the target display, T shapes changed color, such that each T was rendered in a different color (red, CIE: 607, .365, 43 cd/m²; green, CIE: .294, .651,158 cd/m²; blue, CIE: .144, .083, 17 cd/m²; or yellow, CIE: .396, .561,198 cd/m²).

On 25% of cue trials, the target-colored cue was presented in the same location as the target (valid trials), and on 75% of trials, the target-colored cue was presented in a different location (invalid trials). Thus, the cue display did not predict the location of the target. Participants performed a practice block of 32 trials. During the practice block, performance was monitored to ensure participants understood the task. If required, feedback was provided verbally. Following the practice block, participants performed 10 blocks of 64 trials (for a total of 640 experimental trials; 240 more experimental trials than in Lamy et al., 2015)

Results

Five participants were excluded from the analysis because they reported that they were consciously aware of the cue on fewer than 10% of trials. Data from the remaining 22 participants were included in the final analyses. Awareness ratings are presented in Table 1. In line with Lamy et al. (2015), we grouped cue-present trials rated 1, 2, and 3 together to form the aware trials and those rated 0 as the unaware trials. Thus, participants were aware of the cue on approximately half of cue-present trials.

Figure 2 shows mean correct RTs as a function of awareness (aware or unaware), cue type (target-colored cue or distractor-colored cue), and cue validity (valid or invalid). We conducted a 2 (awareness) × 2 (cue type) × 2 (cue validity) ANOVA on mean correct RTs. Results revealed a significant main effect of awareness, F(1, 21) = 26.294, p = .0.00004, $\eta_p^2 = .556$, BF₁₀ = 1.637e+10 (Bayesian analysis performed with JASP: Version 0.8.0.0, https://jasp-stats.org/). Mean correct RTs were faster when participants were unaware of the cue (M = 732 ms, SD = 67 ms) than when they were aware of the cue (M = 793 ms, SD = 82 ms). We ran an additional analysis that included all four awareness levels and found that RTs increased as cue awareness increased, F(3, 54) = 16.73, p < .00001.

The main effects of cue type, F(1, 21) = 3.591, p = .072, $\eta_p^2 =$.146, BF₁₀ = .371, and cue validity, F(1, 21) = .725, p = .404, η_p^2 = .033, BF₁₀ = .191, did not reach significance. Importantly, however, there was a significant two-way interaction between cue type and cue validity, F(1, 21) = 30.619, p = .00002, $\eta_p^2 =$.593, $BF_{inclusion} = 772.99$. In line with previous work on featurebased cueing effects (e.g., Folk & Remington, 1999; Folk et al., 1992; Folk et al., 1994; Gibson & Amelio, 2000; Gibson & Kelsey, 1998; Yantis & Egeth, 1999), there was a samelocation benefit for target-colored cues, such that RTs were faster when target-colored cues were presented in the same location as targets (M = 737 ms, SD = 70 ms) than when they were presented in a different location (M = 776 ms, SD = 77 ms), t(21) = -3.671, $p = .001, d = -.783, BF_{10} = 24.779$. Results also revealed a samelocation cost for distractor-colored cues. RTs were slower when cues were presented in the same location as the target (M = 783ms, SD = 83 ms) than when they were presented in a different location (M = 755 ms, SD = 75 ms), t(21) = 3.933, p = .0008, d = .0008.839, BF₁₀ = 43.694.



	Experiment 1		Experiment 2		Experiment 3	
	Cue absent	Cue present	Cue absent	Cue present	Cue absent	Cue present
0	69%	49%	83%	41%	67%	44%
Unaware	69%	49%	83%	41%	67%	44%
1	14%	13%	9%	13%	15%	15%
2	9%	14%	4%	11%	6%	8%
3	9%	25%	5%	34%	13%	33%
Aware	32%	52%	18%	58%	33%	56%

Table 1 Awareness ratings for cue-absent and cue-present trials in Experiments 1–3

The other two-way interactions did not reach significance, awareness and cue validity, F(1, 21) = 1.251, p = .276, $\eta_p^2 = .056$, BF_{inclusion} = .498; awareness and cue type, F(1, 21) = .169, p = .685, $\eta_p^2 = .008$, BF_{inclusion} = .756. Finally, the three-way interaction between awareness, cue type, and cue validity did not reach significance, F(1, 21) = .171, p = .683, $\eta_p^2 = .008$, BF_{inclusion} = .244, suggesting that the same-location benefit for target-colored cues and the same-location cost for distractor-colored cues were not differentially affected by awareness.

An analogous ANOVA on error rates (see Table 2) revealed a significant main effect of awareness, F(1, 21) =5.758, p = .026, $\eta_p^2 = .215$, $BF_{10} = 2,441.679$. Mean error rates were higher when participants were aware of the cue (M = 16.31%, SD = 16.72) than when they were unaware of the cue (M = 10.21%, SD = 9.57). None of the other main effects or interactions reached significance, suggesting there was no speed-accuracy trade-off. Main effect of cue type, F(1, 21) = .905, p = .352, $\eta_p^2 = .041$, BF₁₀ = .213; main effect of cue validity, F(1, 21) = 2.879, p =.105, η_p^2 = .121, BF₁₀ = .231; Awareness × Cue Type, F(1, 21) = .208, p = .653, η_p^2 = .010, BF_{inclusion} = .103; Awareness × Cue Validity, F(1, 21) = .558, p = .463, $\eta_p^2 = .463$.026, BF_{inclusion} = .108; Cue Type × Cue Validity, F(1, 21)= 2.228, p = .150, $\eta_p^2 = .096$, BF_{inclusion} = .032; Awareness × Cue Type × Cue Validity, F(1, 21) = .031, p = .862, $\eta_p^2 = .862$ $.001, BF_{inclusion} = .004.$

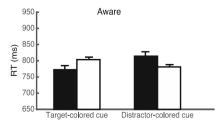
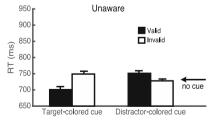


Fig. 2 Mean correct RTs to targets in Experiment 1, shown as a function of cue color, cue condition, and cue awareness. Cue color either matched the target color (target-colored cue) or was a distractor color (distractor-colored cue). Cue location either matched the target location (valid) or was different from the target location (invalid). The aware condition included trials in which participants reported having some awareness of the

Discussion

The results from Experiment 1 demonstrate that attention can be oriented to task-relevant cues even when those cues are not consciously perceived, and that the magnitude of this orienting effect is largely independent of cue awareness. Task-irrelevant cues caused a same-location cost. Interestingly, the magnitude of the cost was also independent of cue awareness, a finding that is not consistent with Lamy et al. (2015), who found a same-location cost for aware cues, but not for unaware cues (see, however, Schoeberl et al., 2018). Given that we used the same methodological design as Lamy et al., this finding is surprising. Having said this, the same location cost for unaware cues is a small effect. Thus, as we used a larger sample and had observers perform more trials than did Lamy et al., our results likely reflect that we simply had more statistical power to uncover this small effect.

In Experiment 1, feature-based cueing effects were operationalized in terms of RT differences between valid and invalid cues. Response times, however, represent the final outcome of several information-processing stages, from initial encoding and selection of sensory inputs to response execution (Schmidt, 1988). It is possible that some of these processes are modulated by cue awareness, while others remain largely independent of it. We investigated this possibility in Experiment 2 by comparing neural activity associated with consciously perceived versus unperceived cues.



cue (i.e., awareness ratings of 1, 2, or 3). The unaware condition included only those trials in which participants indicated they were not aware of the cue (i.e., an awareness rating of 0). The small arrow on the right indicates the mean reaction time for the no-cue condition. Error bars represent within-subjects standard errors of the mean



Table 2 Mean reaction times and error rates for the different cue color and awareness conditions of Experiment 1

Cue validity	Target-colored cue				Distractor-colored cue			
	Unaware		Aware		Unaware		Aware	
	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)
Valid Invalid	701 (16) 749 (17)	9.0 (2.6) 9.8 (2.1)	772 (19) 804 (18)	16.4 (4.0) 15.7 (3.6)	751 (15) 728 (15)	12.0 (2.6) 10.1 (2.5)	814 (24) 781 (19)	18.0 (4.2) 15.2 (3.5)

Note. Standard errors are given in parentheses

Experiment 2

In Experiment 2, we employed EEG to examine the timing and magnitude of cue-related evoked responses in an analogous feature-based cueing paradigm to that employed in Experiment 1. We focused our analyses on the N2pc component, consistent with previous investigations of spatial orienting (Eimer, 1996; Kiss et al., 2008; Luck & Hillyard, 1994; Woodman & Luck, 1999, 2003b).

Method

Participants

Twenty new individuals participated in Experiment 2 (17 females, mean age = 21.00 years, SD = 1.00).

Apparatus, stimuli, and procedure

The stimuli and procedure were similar to those of Experiment 1, except for the following changes. Our aim in Experiment 2 was to measure an N2pc to the cue displays. Thus, to accommodate the measurement of N2pc responses, all cue and target stimuli $(.05^{\circ} \times .05^{\circ})$ were lateralized so that they appeared at the top left, bottom left, top right, and bottom right corners (2.5° distant from fixation; see Fig. 3) of the display. Cuepresent trials consisted of a target-colored cue, a distractorcolored cue, and two neutral cues. As in Experiment 1, target and distractor colors were consistent throughout the experiment. For observers searching for red or green targets, cues were red or green. For observers searching for blue or yellow targets, cues were blue or yellow. To ensure that any cuerelated N2pc response was driven by top-down attentional biasing and not by stimulus differences, target-colored cues and distractor-colored cues were always presented in opposite hemifields (left/right). Target displays consisted of one targetcolored T, one distractor-colored T, and two white Ts. As with the cue display, each hemifield contained one colored T shape (target or distractor). The CFS mask was presented at 20 or 22 Hz (10 participants each). Participants completed 12 blocks of 64 trials (for a total of 768 experimental trials; 368 more than in Lamy et al., 2015).

For observers searching for red or green targets, one cue was red and one cue was green (640 trials; 83%), or no cue was presented (128 trials; 17%). For observers searching for blue or yellow targets, one cue was blue and one cue was yellow (640 trials; 83%), or no cue was presented (128 trials; 17%). During the target display, two T shapes changed color. For participants searching for red or green, one T shape was red (CIE: 607, .365, 43 cd/m²) and one was green (CIE: .294,

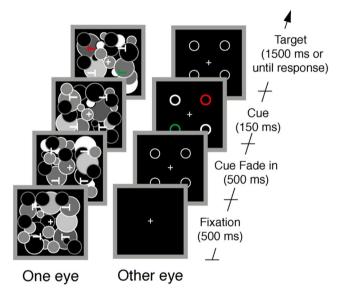


Fig. 3 Schematic of individual trial events in Experiment 2. Participants' task was to report the orientation of the target T shape and to indicate whether they were aware of a colored cue. A flickering mask display (20 or 22 Hz) and four white T shapes (two rotated 90° clockwise and two rotated 90° counterclockwise) were presented to one eye throughout the experiment. Each trial began with a 500-ms fixation cross, followed by a 500-ms period in which the cue placeholders faded in to the suppressed eye. Colored cues were then presented to the suppressed eye for 150 ms. All placeholders thickened, and on cue-present trials, two of the four placeholders changed color so that one matched the target color (targetcolored cue) and another matched the distractor color (distractor-colored cue). Neutral cues remained white. These colored circles were always presented in different hemifields. In the immediately following target display, two of the four T shapes changed color such that one matched the target color (target) and another was the distractor target (distractor). The target display was presented for 1,500 ms or until response. Participants first indicated the orientation of the target T shape as quickly and as accurately as possible, and then reported, without time pressure, their perception of the cue on a scale from 0 (not aware of the cue) to 3 (clearly aware of the cue). (Color figure online)



.651,158 cd/m²). For participants searching for blue or yellow, one T shape was blue (CIE: .144, .083, 17 cd/m²) and one was yellow (CIE: .396, .561,198 cd/m²). The other two T shapes remained white.

Electroencephalography EEG data were recorded continuously from 64 active Ag/AgCl scalp electrodes. The electrodes were arranged according to the international standard 10–10 system for electrode placement (Oostenveld & Praamstra, 2001) using a nylon cap. Eye movements were monitored using bipolar horizontal and vertical electrooculography (EOG). EEG and EOG signals were amplified by Biosemi Active Two amplifiers and sampled at 1024 Hz with 24-bit A/D conversion. Standard reference and ground electrodes were used during recording.

Off-line preprocessing of the EEG data was performed using Brain Electrical Source Acquisition (BESA 5.3; MEGIS Software GmbH, Gräfelfing, Germany). Noisy channels were identified via visual inspection and replaced by interpolation of the voltages recorded at all other scalp electrodes. A maximum of four electrodes were interpolated for each participant. Data were then subjected to a 0.1 Hz highpass filter and a 100 Hz low-pass filter. The data were rereferenced to the average of all 64 scalp electrodes and segmented into 1-s epochs spanning 200 ms before cue onset to 800 ms after cue onset. The average voltage in the 200-ms precue interval was used as a baseline for each epoch. Epochs with excessive noise from eye blinks or other muscle activity were identified by visual inspection and rejected from further analysis. An average of 18% of epochs were rejected using this criterion, with no more than 25% rejected for any individual participant. Incorrect trials were also excluded from the analysis. The remaining epochs were averaged for each participant separately for each condition.

The N2pc response to the cue was quantified within the time period of 200–300 ms after cue onset. This time window was chosen to match that of Lien, Ruthruff, Goodin, and Remington (2008), who conducted a similar experiment (but without the awareness manipulation), and is also consistent with those adopted in previous research on the N2pc (e.g., Eimer, 1996; Hopf et al., 2006b; Luck & Hillyard, 1994; Wascher & Wauschkuhn, 1996; Wauschkuhn et al., 1998). The N2pc was calculated as the mean amplitude from electrodes contralateral to the target-colored cue minus the mean amplitude for the homologous electrodes ipsilateral to the target-colored cue. To determine electrode sites for analysis, we calculated the average response for each electrode site during the cue-related time window, separately for trials in which the target-colored cue was presented in the right visual hemifield and trials in which the target-colored cue was presented in the left visual hemifield. We then collapsed across hemispheres such that responses contralateral to the targetcolored cue were represented in the right hemisphere and responses ipsilateral to the target-colored cue were represented in the left. We chose the three electrode sites with the highest responses in the right hemisphere (P8, P10, and PO8) and the homologous electrode sites in the left hemisphere (P7, P9, PO7) for analysis.

Results

Behavioral analysis

The behavioral results from Experiment 2 replicated those of Experiment 1. Awareness ratings can be seen in Table 1. We found faster RTs to targets that were validly cued by target-colored cues than by neural cues. This pattern of results was found for both aware and unaware target-colored cues. We also found slower RTs to targets that were validly cued by distractor-colored cues than by neutral cues. This pattern of results was found for both aware and unaware distractor-colored cues. Again, we grouped cue-present trials rated 1, 2, and 3 to form the aware trials, and those rated 0 as the unaware trials.

Figure 4 shows mean correct RTs as a function of awareness (aware or unaware) and cue condition (target-colored cue in target location, distractor-colored cue in target location, or neutral cue in target location). To analyze these patterns statistically, we conducted a 2 (awareness) \times 3 (cue condition) repeated-measures ANOVA on mean correct RTs (see Table 2). Results revealed a significant main effect of awareness, F(1, 19) = 26.444, p = .00006, $\eta_p^2 = .582$, $BF_{10} = 9.274e+6$. Mean correct RTs were faster for unaware trials

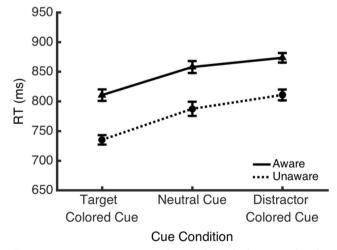


Fig. 4 Mean correct RTs to targets in Experiment 2, shown as a function of cue condition and cue awareness. Target location either matched the target-colored-cue location (target-colored cue), the distractor-colored-cue location (distractor-colored cue), or a neutral cue location (neutral cue). The aware condition included trials in which participants reported having some awareness of the cue. By contrast, the unaware condition included only those trials in which participants indicated they were not aware of the cue. Error bars represent within-subjects standard errors of the means



(M = 778 ms. SD = 115) than for aware trials (M = 847 ms. SD)= 111). There was also a significant main effect of cue condition, F(2, 38) = 27.429, p = .00000004, $\eta_p^2 = .591$, BF₁₀ = 4,419.50. Follow-up tests using Bonferroni correction revealed that RTs were faster when targets were presented in the same location as the target-colored cue (M = 773 ms, SD= 104) than when they were presented in a neutral cue location (M = 823 ms, SD = 118), t(19) = -4.743, p = .0001, d =-1.060, BF₁₀ = 204.13). Furthermore, RTs were slower when distractor-colored cues were presented in the same location as the target (M = 842 ms, SD = 122) than when they were presented in the location of a neutral-colored cue, t(19) =3.811, p = .001, d = .852, BF₁₀ = 31.69. The interaction between awareness and cue condition was not significant, F(2,38) = .496, p = .530 (Greenhouse–Geisser corrected), η_p^2 = .025, $BF_{inclusion} = .615$, suggesting that the effect of cue condition did not depend on awareness. Thus, top-down attentional settings were involved in feature-based cueing even when cues were not consciously perceived.

A further ANOVA on error rates (see Table 3) revealed no significant main effect of awareness, F(1, 19) = .182, p = .675, $\eta_p^2 = .009$, BF₁₀ = .270, but a significant main effect of cue condition, F(2, 38) = 5.823, p = .006, $\eta_p^2 = .235$, $BF_{10} = .670$. Follow-up tests using Bonferroni correction revealed that the main effect of cue condition was driven by a significantly higher mean error rate for trials in which the target was located in the distractor-colored-cue location (M = 9.40%, SD = 6.21) than for trials in which the target was located in the targetcolored-cue location (M = 7.21%, SD = 6.38), t(19) = -3.462, p = .003, d = -.774, BF₁₀ = 15.948. The interaction between awareness and cue condition was also significant, F(2, 38) =5.328, p = .009, $\eta_p^2 = .219$, BF_{inclusion} = .180. This significant interaction was followed up by evaluating the simple main effects of cue condition separately for aware and unaware trials. Mean error rates did not differ between cue conditions for aware trials, $F(2, 38) = 1.172, p = .321, \eta_p^2 = .058$, but they did differ significantly between cue condition for unaware trials, F(2, 38) = 11.71, p = .0001, $\eta_p^2 = .381$. We performed follow-up t tests with Bonferroni correction, to assess these differences. For unaware cues, error rates were significantly lower when targets were located in the same location as targetcolored cues (M = 5.85%, SD = 4.39) than when targets were located in the same location as distractor-colored cues (M = 9.52%, SD = 5.36), t(19) = -4.144, p = .0006, d = .927, BF₁₀ = 61.551, or when targets were located in the same location as neutral cues (M = 8.55%, SD = 5.47), t(19) = -3.203, p = .005, d = -.716, BF₁₀ = .9.694. Thus, the interaction between awareness and cue condition appears to be driven by fewer errors in the unaware target-colored-cue condition. Overall these results suggest there was no speed–accuracy trade-off in Experiment 2.

ERP analysis

As we were interested in the effect of awareness on the neural signatures of attentional orienting, we focused our ERP analyses on cue-related responses. The ERP data were analyzed as a function of cue awareness (aware or unaware) and electrode laterality (contralateral or ipsilateral to the target-colored cue location). An N2pc component was evident for both aware and unaware trials, but with a slightly larger negative amplitude for the aware trials (see Fig. 5). ERP data for the cuerelated response were submitted to a 2 (awareness) × 2 (electrode laterality) repeated-measures ANOVA on the mean response during the cue-related N2pc time window.

There was a significant main effect of awareness on cueevoked ERP magnitude, F(1, 19) = 10.14, p = .005, $\eta_p^2 = .005$.348, BF₁₀ = 11.330. Responses were more negative for aware trials (M = -.968, SD = 1.109) than for unaware trials (M =-.520, SD = 1.384). There was also a significant main effect of electrode laterality, F(1, 19) = 20.65, p = .0002, $\eta_p^2 = .521$, $BF_{10} = 1,293.948$. Responses at electrode sites contralateral to the target-colored cue (ipsilateral to distractor-colored cue) were more negative (M = -1.062, SD = 1.325) than responses at electrode sites ipsilateral to the target-colored cue (contralateral to distractor-colored cue; M = -.426, SD = 1.178), indicating a significant N2pc response. Critically, there was also a significant interaction between awareness and electrode laterality, F(1, 19) = 13.66, p = .002, $\eta_p^2 = .418$, BF_{inclusion} = 3.310. To investigate whether there was an N2pc to both aware and unaware trials, we followed up this interaction with pairwise t tests. When participants were aware of the cue, mean ERPs were significantly more negative at electrode sites contralateral to the target-colored-cue location (M = -1.384,

Table 3 Mean reaction times and error rates for the different cue and awareness conditions of Experiment 2

Cue condition	Unaware		Aware		
	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)	
Target-colored cue	735 (24)	5.8 (1.0)	810 (24)	8.6 (2.2)	
Distractor-colored cue	811 (30)	9.5 (1.2)	874 (28)	9.3 (1.9)	
Neutral	787 (27)	8.5 (1.2)	858 (27)	7.9 (1.6)	

Note. Standard errors are given in parentheses



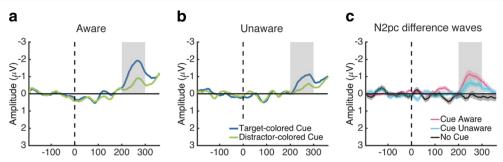


Fig. 5 Grand average event-related potentials (ERPs) for target-colored cues, averaged across posterior electrode sites (P7/P8, P9/P10, PO7/PO8) contralateral to the target-colored cue location (blue) and distractor colored cue location (green), as a function of awareness (aware vs. unaware).

a Average ERPs when participants were aware of the cue. b Average ERPs when participants were unaware of the cue. c Difference waves calculated by subtracting ipsilateral from contralateral ERPs for the aware (magenta), unaware (cyan), and no-cue trials (black), showing the cue-induced N2pc. Cue onset is at time zero. Shaded areas represent analyzed

time window for the cue-related response (200–300 ms after cue onset). Data have been smoothed using a sliding boxcar for display only. All analyses were performed on the unsmoothed data. Note that here the label *Target-colored cue* represents responses that were contralateral to the target-colored cue, but also ipsilateral to the distractor-colored cue; likewise, the label *distractor-colored cue* represents responses that were contralateral to the distractor-colored cue, but also ipsilateral to the target-colored cue. (Color figure online)

SD=1.204) than at electrode sites ipsilateral to the target-colored-cue location (M=-.553, SD=1.181), t(19)=-5.206, p=.00005, d=-1.164, BF₁₀ = 514.330. Critically, this pattern was also found for unaware trials. When participants were unaware of the cue, mean ERPs were significantly more negative at electrode sites contralateral to the target-colored-cue location (M=-.740, SD=1.580) than responses at electrode sites ipsilateral to the target-colored-cue location (M=-.300, SD=1.315), t(19)=-3.172, p=.005, d=-.709, BF₁₀ = 9.136. Thus, there was a significant N2pc to target-colored cues both when participants were aware of the cue and also when the cue was not consciously perceived; however, the magnitude of the N2pc was greater for aware cues (mean difference = -.805, SD=.598) than for unaware cues (mean difference = -.428, SD=.514; see Fig. 5c).

The difference in N2pc magnitude between aware and unaware cues was driven by a larger negative response at electrode sites contralateral to aware target-colored cues than those contralateral to unaware target-colored cues, t(19) = -4.082, p = .0006, d = -.913, BF₁₀ = 514.330. Responses at electrode sites contralateral to the distractor-colored cue (ipsilateral to the target colored cue) did not differ between aware and unaware conditions, t(19) = -1.771, p = .093, d = -.396, BF₁₀ = 9.136. Thus, the difference in N2pc magnitude between aware and unaware cues was likely driven by differences between processing aware and unaware target-colored cues, but not between aware and unaware distractor-colored cues.

Discussion

In Experiment 2 we recorded EEG while participants performed a behavioral task with stimuli and design similar to that used in Experiment 1. We found an RT benefit for valid versus invalid target-colored cues, with no difference in the magnitude of this feature-based cueing effect for cue-aware and cue-unaware trials. These findings are consistent with our Experiment 1 findings and those of Lamy et al. (2015). We also found an RT cost for valid versus invalid distractor-colored cues. We found no difference in the magnitude of this same location cost for cue-aware and cue-unaware trials. Our finding that the same location cost does not depend on awareness aligns with recent research by Schoeberl et al. (2018), in which the authors found that valid cues that mismatched the observers' goals produced a same location cost for unaware cues.

The ERP data revealed an N2pc response to both aware and unaware cues. The N2pc is thought to reflect target enhancement (Eimer, 1996; Shedden & Nordgaard, 2001). Thus, the results from Experiment 2 suggest that attention was allocated to the location of items that share features with observers' task goals even in the absence of awareness. 1 Interestingly, the magnitude of the N2pc response in Experiment 2 was larger for cue-aware trials than for cue-unaware trials. This magnitude difference was driven by a larger negative response at electrode sites contralateral to aware target-colored cues than those contralateral to unaware target-colored cues. Responses at electrode sites contralateral to the distractor-colored cue did not differ between aware and unaware cues. Thus, our findings suggest that neural measures of target processing are modulated by awareness, but those associated with distractor suppression are not—a finding that is reversed in relation to the behavioral results reported in Lamy et al. (2015).



¹ There was no N2pc in no-cue trials (p > .05). Thus, there was a neural difference between unaware cue-present trials and unaware no-cue trials. It might be argued that participants' actual level of awareness, as indexed by subjective ratings, differed between unaware cue-present and unaware cue-absent trials. In interpreting the awareness ratings, however, we followed the reasoning of Lamy et al. (2015) and took the participants' subjective awareness ratings in the cue-present trials at face value—that is, when participants gave a zero rating, we defined their experience as *unaware of the cue*.

In Experiment 2, each trial involved the presentation of a target-colored cue in one hemifield and a distractor-colored cue in the opposite hemifield. We reasoned that by using these balanced displays, any lateralized effects would be attributable to influences from participants' current task set as opposed to stimulus-driven effects. There was, however, a downside to using such a balanced-display design. As the N2pc is by definition a difference between contralateral and ipsilateral responses, the balanced displays used in Experiment 2 may have yielded N2pc waveforms that reflected a combination of responses elicited by the target-colored cue and the simultaneously presented distractor-colored cue. Consistent with this, Hickey, Di Lollo, and McDonald (2009) have suggested that the N2pc is a combination of two ERP components: the N_T , a negative ERP component associated with target enhancement, and the P_D, a positive ERP component associated with distractor suppression (e.g., Cosman, Lowe, Woodman, & Schall, 2018; Gaspelin & Luck, 2018b). Although in Experiment 2 we were able to measure neural responses separately for contralateral and ipsilateral electrode sites, we were not able to determine whether these responses reflected processing of the target-colored cue, the distractor-colored cue, or a combination of both. We sought to address this issue in Experiment 3.

Experiment 3

While much of the literature on feature-based cueing has focused on attentional allocation in terms of the selective enhancement of task-relevant information (e.g., Wolfe, 1994), suppression of task-irrelevant information is also a key component of selective processes (Braithwaite & Humphreys, 2003; Lleras, Kawahara, Wan, & Ariga, 2008). Indeed, a large volume of research supports the idea that selective attention both modulates activity in sensory processing areas by enhancing relevant features (Bisley & Goldberg, 2010; Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990; Corbetta & Shulman, 2002; Desimone & Duncan, 1995; Fries, Reynolds, Rorie, & Desimone, 2001; Gruber, Muller, Keil, & Elbert, 1999; Hillyard & Anllovento, 1998; Kastner, Deweerd, Desimone, & Ungerleider, 1998; Kastner & Ungerleider, 2000; Luck, Woodman, & Vogel, 2000; Raz & Buhle, 2006; Reynolds & Chelazzi, 2004; Siegel, Donner, Oostenveld, Fries, & Engel, 2008; Tallon-Baudry, Bertrand, Henaff, Isnard, & Fischer, 2005; Treue, 2003) and suppressing irrelevant features (Andersen & Muller, 2010; Chelazzi, Miller, Duncan, & Desimone, 1993; Hopf et al., 2006a; Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985; Reynolds, Chelazzi, & Desimone, 1999; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Vanduffel, Tootell, & Orban, 2000; Worden, Foxe, Wang, & Simpson, 2000). This idea that selection involves both enhancement and suppression is central to prominent theories of attention, such as the biased competition model (Desimone & Duncan, 1995) and the notion of priority maps (Itti & Koch, 2001).

In Experiment 3, we tested whether the N2pc response reported in Experiment 2 is the result of an N_T to the targetcolored cue, a PD to the distractor-colored cue, or a combination of both components. The design was similar to that employed in Experiment 2, except that only one cue was presented on each cue-present trial (either a target-colored or a distractor-colored cue). This design allowed us to investigate lateralized neural responses separately for target-colored and distractor-colored cues under aware and unaware conditions. In line with our findings from Experiments 1 and 2, we expected to observe an RT benefit for valid target-colored cues and an RT cost for valid distractor-colored cues, for both aware and unaware trials. For the ERPs, we expected to observe an N_T to target-colored cues, which would be larger in magnitude for aware trials than for unaware trials. We also predicted a P_D in response to distractor-colored cues, but not target-colored cues.

Method

Participants

Twenty-four new individuals participated in Experiment 3 (12 males, mean age = 21.37 years, SD = 1.53).

Apparatus, stimuli, and procedure

The stimuli and procedure were the same as those of Experiment 2, with the following exceptions. To accommodate the measurement of the N_T and P_D components, cuepresent trials consisted of a single target-colored cue in one of the four locations, with three neutral cues in the remaining locations (320 trials; 41.67%), or a single distractor-colored cue in one location with three neutral cues (320 trials; 41.67%). In an additional 128 trials (16.67%), no cue was presented. The CFS mask was presented at 20 Hz for each participant.

Electroencephalography

Off-line preprocessing of the EEG data was performed using EEGLAB (Delorme & Makeig, 2004). Muscle, eye movement, and blink artifacts were identified and removed using independent component analysis. Incorrect trials were also excluded from the analysis. An average of 18% of epochs were rejected using this criterion, with no more than 25% rejected for any individual participant. The remaining epochs were averaged for each participant separately for each condition.



The N_T responses to the target-colored cue and the P_D responses to the distractor colored cue were quantified within the time period of 200–300 ms after cue onset. The N_T was calculated as the mean amplitude from electrodes contralateral to the target-colored cue minus the mean amplitude for the homologous three electrodes ipsilateral to the target-colored cue. The P_D was calculated as the mean amplitude from electrodes contralateral to the distractor-colored cue minus the mean amplitude for the homologous three electrodes ipsilateral to the distractor-colored cue. To determine electrode sites for analysis, we calculated the average response for each electrode site during the cue-related time window, separately for trials in which the cue was presented in the right visual hemifield and trials in which the cue was presented in the left visual hemifield. We then collapsed across hemispheres such that responses contralateral to the cue were represented in the right hemisphere and responses ipsilateral to the cue were represented in the left. We chose the three electrode sites with the highest responses in the right hemisphere (P8, P10, and PO8) and the homologous electrode sites in the left hemisphere (P7, P9, PO7) for analysis.

Results

Data from five participants were excluded from the analysis because these individuals reported being aware of the cue on more than 50% of no-cue trials. Data from the remaining 19 participants were included in the following analyses.

Behavioral analysis

Awareness ratings are presented in Table 1. As in Experiments 1 and 2, we grouped cue-present trials rated 1, 2, and 3 together to form the aware trials, and those rated 0 as the unaware trials.

Figure 6 shows mean correct RTs as a function of awareness (aware or unaware), cue type (target-colored cue or distractor-colored cue), and cue validity (valid or invalid). We conducted a 2 (awareness) × 2 (cue type) × 2 (cue validity) ANOVA on mean correct RTs (see Table 4). There was a

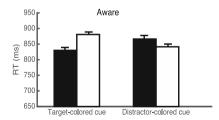


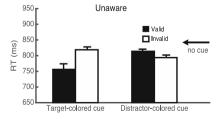
Fig. 6 Mean correct RTs to targets in Experiment 3, shown as a function of cue color, cue condition, and cue awareness. Cue color either matched the target color (target-colored cue) or was a distractor color (distractor-colored cue). Cue location either matched the target location (valid) or was different to the target location (invalid). The aware condition

significant main effect of awareness, F(1, 18) = 28.473, $p = .000045 \, \eta_p^2 = .613$, BF₁₀ = 2.464e+7), with mean correct RTs faster when participants were unaware of the cue ($M = 796 \, \text{ms}$, $SD = 117 \, \text{ms}$) than when they were aware of the cue ($M = 855 \, \text{ms}$, $SD = 109 \, \text{ms}$).

The main effects of cue type, F(1, 18) = .569, p = .460, η_p^2 = .031, BF₁₀ = .221, and cue validity, F(1, 18) = 4.113, p =.058, $\eta_{\rm p}^2 = .186$, BF₁₀ = .660, did not reach significance. Again, however, there was a significant two-way interaction between cue type and cue validity, F(1, 18) = 26.414, p =.000069, $\eta_p^2 = .595$, BF_{inclusion} = 3048.43. Specifically, there was a same-location benefit for target-colored cues, such that RTs were faster when target-colored cues were presented in the same location as targets (M = 793 ms, SD = 126 ms) compared with when they were presented in a different location (M = 850 ms, SD = 124 ms), t(18) = -4.192, p = .000548,d = -.962, BF₁₀ = 62.505. Results also revealed a samelocation cost for distractor-colored cues. RTs were slower when cues were presented in the same location as the target (M = 840 ms, SD = 107 ms) than when they were presented in a different location (M = 818 ms, SD = 117 ms), t(18) = 2.518, $p = .021, d = .578, BF_{10} = 2.775.$

The other two-way interactions did not reach significance, awareness and cue type, F(1, 18) = 3.591, p = .074, $\eta_p^2 = .166$, BF_{inclusion} = .600; awareness and cue validity, F(1, 18) = .412, p = .529, $\eta_p^2 = .022$, BF_{inclusion} = .974. Finally, the three-way interaction between awareness, cue type, and cue validity did not reach significance, F(1, 18) = .127, p = .726, $\eta_p^2 = .007$, BF_{inclusion} = .334, suggesting that the same-location benefit for target-colored cues and the same-location cost for distractor-colored cues were not differentially affected by awareness. Thus, as in the previous two experiments, we found behavioral evidence for feature-based cueing effects and distractor costs even when the evoking events were not consciously perceived.

We ran an analogous ANOVA on error rates (see Table 4). There were no significant main effects of awareness, F(1, 18) = .134, p = .719, $\eta_p^2 = .007$, BF₁₀ = .194; cue type, F(1, 18) = 1.426, p = .248, $\eta_p^2 = .073$, BF₁₀ = .321; or cue validity, F(1, 18) = .279, p = .604, $\eta_p^2 = .015$, BF₁₀ = .209. There was,



included trials in which participants reported having some awareness of the cue. By contrast, the unaware condition included only those trials in which participants indicated they were not aware of the cue. The small arrow on the right indicates the mean reaction time for the no-cue condition. Error bars represent within-subjects standard errors of the means



Table 4 Mean reaction times and error rates for the different cue color and awareness conditions of Experiment 3

Cue validity	Target-colored cue				Distractor-colored cue			
	Unaware		Aware		Unaware		Aware	
	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)	RT (ms)	Error rate (%)
Valid Invalid	756 (34) 819 (29)	7.3 (7) 10.8 (11.5)	830 (26) 881 (29)	9.4 (8.2) 9.9 (8.5)	814 (26) 794 (28)	9.2 (6.7) 7.8 (6.2)	867 (25) 841 (27)	8.9 (9.1) 8.2 (8.3)

Note. Standard errors are given in parentheses

however, a significant interaction between cue type and cue validity, F(1, 18) = 8.042, p = .011, $\eta_p^2 = .309$, BF_{inclusion} = .300. Follow-up pairwise t tests revealed that this two-way interaction was because there were more errors when invalid cues were target colored (M = .104, SD = .099) than when they were distractor colored (M = .080, SD = .070), but this difference did not survive Bonferroni correction with an alpha level of .0125, t(18) = -2.322, p = .032, d = -.533, BF₁₀ = 2.006. None of the other interactions were significant (Awareness × Cue Type, F(1, 18) = .148, p = .705, $\eta_p^2 = .008$, BF_{inclusion} = .028; Awareness × Cue Validity, F(1, 18) = .912, p = .352, $\eta_p^2 = .048$, BF_{inclusion} = .026; Awareness × Cue Type × Cue Validity, F(1, 18) = 2.229, p = .153, $\eta_p^2 = .110$, BF_{inclusion} = .008.

ERP analysis

The ERP data were analyzed as a function of cue awareness (aware or unaware), electrode laterality (contralateral or ipsilateral to the cue location), and cue condition (target-colored cue or distractor-colored cue). As seen in Fig. 7, starting approximately 200 ms after cue onset, a negative component (N_T) was evident for all conditions, but with a slightly larger negative amplitude for the target-colored cue trials than the distractor-colored cue trials. Interestingly, starting approximately 350 ms after cue onset, a positive component (P_D) was also evident for distractor-colored cue trials, but not for target-colored cue trials. To capture the sequence of these laterality effects, we analyzed mean ERP amplitudes during two time windows: An earlier time window focused on the N_T component (200 to 300 ms after cue onset, to match the cuerelated time window analyzed in Experiment 2), and a later time window focused on the P_D component (350 to 500 ms after cue onset). Past research has shown that the PD component can vary over a broad time range that depends on the evoking stimulus and experimental task (e.g., Burra & Kerzel, 2014; Cosman et al., 2018; Gaspar & McDonald, 2014; Gaspelin & Luck, 2018a; Hickey et al., 2009; Hilimire et al., 2011; Sawaki, Geng, & Luck, 2012; Sawaki & Luck, 2010). To be sure any P_D effect was not cancelled out by the opposite polarity of the N_T component, we chose a time window that was outside the N_T time window. Note also that the cue-related ERP responses were always collapsed across valid and invalid trials (with respect to subsequent target location), so any evoked activity arising from the subsequent onset of target events was effectively cancelled out.

ERP data for the N_T and P_D responses were submitted to separate 2 (awareness) \times 2 (electrode laterality) \times 2 (cue condition) repeated-measures ANOVAs on the mean amplitude for each participant during each time window.

N_T component There was no significant main effect of awareness on cue-evoked ERPs during the earlier time window, F(1,18) = .011, p = .918, η_p^2 = .001, BF₁₀ = .175. Responses did not differ between aware trials (M = -.090, SD = .931) and unaware trials (M = -.104, SD = .664). There was a significant main effect of electrode laterality, F(1, 18) = 18.402, p = .000441, $\eta_p^2 = .506$, $BF_{10} = 1.254e + 6$. Responses at electrode sites contralateral to the cue were more negative (M = -.439, SD = .942) than responses at electrode sites ipsilateral to the cue (M = .246, SD = .703). There was also a significant effect of cue condition, F(1, 18) = 5.096, p= .037, η_p^2 = .221, BF₁₀ = 1.762. Overall responses for targetcolored cue trials were more negative (M = -.236, SD = .854) than those for distractor colored-cue trials (M = .043, SD = .745). There was no significant interaction between cue condition and electrode laterality, F(1, 18) = 2.739, p = .115, $\eta_p^2 = .132$, $BF_{inclusion} = .861$, between cue condition and awareness, $F(1, \frac{1}{2})$ 18) = 1.247, p = .279, $\eta_p^2 = .065$, BF_{inclusion} = .112, or between awareness and cue laterality, F(1, 18) = 1.420, p = .249, η_p^2 =.073, $BF_{inclusion}$ = .146. There was, however, a significant three-way interaction between cue condition, awareness, and electrode laterality, F(1, 18) = 9.639, p = .006, $\eta_p^2 = .349$, BF_{inclusion} =.050. To investigate this three-way interaction, we analyzed the interaction between cue condition and cue laterality at each awareness level.

For aware trials, there was no significant effect of cue condition, F(1, 18) = 1.854, p = .190, $\eta_p^2 = .093$, $BF_{10} = .359$. There was, however, a significant effect of cue laterality, F(1, 18) = 13.943, p = .002, $\eta_p^2 = .436$, $BF_{10} = 2,443.150$, as well as a significant interaction between cue condition and cue laterality, F(1, 18) = 9.643, p = .006, $\eta_p^2 = .349$, $BF_{inclusion} = 1.231$. To investigate whether there was an N_T to both target-colored and distractor-colored cues for aware trials, we followed up this interaction with pairwise t tests. On target-



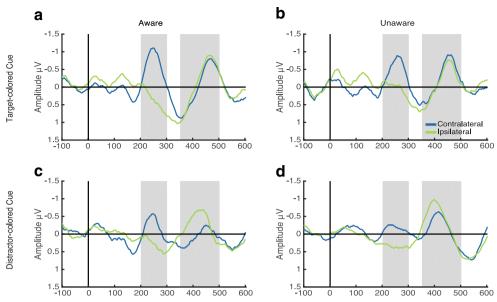


Fig. 7 Grand average event-related potentials (ERPs) in response to cue events, averaged across posterior electrode sites (P7/P8, P9/P10, PO7/P08) contralateral to the cue location (blue) and ipsilateral to the cue location (green). The ERPs are shown as a function of awareness (aware vs. unaware) and cue condition (target-colored cue vs. distractor-colored cue). a Average ERPs when a target-colored cue was presented and participants were aware of the cue. b Average ERPs when a target-colored cue was presented and participants were unaware of the cue. c Average

ERPs when a distractor-colored cue was presented and participants were aware of the cue. **d** Average ERPs when a distractor-colored cue was presented and participants were unaware of the cue. Cue onset is at time zero. Shaded areas represent analyzed time windows for the cue-related response (200–300 ms after cue onset and 350–500 ms). Data have been smoothed using a sliding boxcar for display only. All analyses were performed on the unsmoothed data. (Color figure online)

colored cue trials, mean ERPs were significantly more negative at electrode sites contralateral to the cue location (M = -.720, SD = 1.445) than at electrode sites ipsilateral to the cue location (M = .349, SD = .962), t(18) = -3.950, p = .000939, d = -.906, BF₁₀ = 39.032. This pattern was also found for distractor-colored cue trials, such that ERPs were significantly more negative at electrode sites contralateral to the cue location (M = -.255, SD = 1.054) than at electrode sites ipsilateral to the cue location (M = .267, SD = .850), t(18) = -2.872, p = .010, d = -.659, BF₁₀ = 5.145. We performed permutation tests, which verified these results (see the Supplemental Material).

To determine whether the magnitude of the N_T response differed between target-colored and distractor-colored cues for aware trials, we computed a difference score by subtracting responses at ipsilateral electrode sites from responses at contralateral sites, separately for target-colored and distractor-colored cue trials. The magnitude of this difference (i.e., the size of the N_T) was greater for target-colored cues (mean difference = -1.069, SD = 1.180) than for distractor-colored cues (mean difference = -.522, SD = .792), t(19) = -3.105, p = .006, d = -.712, BF₁₀ = 7.859. Thus, there was a significant N_T to both target-colored and distractor-colored cues in aware trials, but the magnitude of the response was larger for target-colored cues. There was no evidence of a P_D component during this earlier time window.

For the unaware trials, there was a significant effect of cue condition, F(1, 18) = 5.775, p = .027, $\eta_p^2 = .243$, BF₁₀ = 2.386. There was also a significant effect of cue laterality, $F(1, 18) = 14.493, p = .001, \eta_p^2 = .446, BF_{10} = 118.123, but$ there was no significant interaction between cue condition and cue laterality, $F(1, 18) = .062, p = .807, \eta_p^2 = .003, BF_{inclusion}$ = 1.030. Pairwise t tests showed that on target-colored cue trials, mean ERPs were significantly more negative at electrode sites contralateral to the cue location (M = -.588, SD =1.086) than at electrodes insilateral to the cue location (M =.014, SD = .712), t(18) = -2.597, p = .018, d = -.596, BF₁₀ = 3.171. This pattern was also found for distractor-colored cues in unaware trials, such that mean ERPs were significantly more negative at electrode sites contralateral to the cue location (M = -.194, SD = .709) than at electrodes ipsilateral to the cue location (M = .354, SD = .822), t(18) = -4.379, p = .822.000362, d = -1.005, BF₁₀ = 89.846. Thus, there was a significant N_T to both target-colored and distractor-colored cues, but this did not differ between the two cue conditions. Once again there was no evidence of a P_{D} component during this earlier time window.

P_D **component** There was no significant effect of awareness on cue-evoked ERPs during the later time window (350 to 500 ms after cue onset), F(1, 18) = .763, p = .394, $\eta_p^2 = .041$, BF₁₀ = .298. Responses did not differ between aware trials (M = -.114, SD = .821) and unaware trials (M = -.232,



SD = .902). In addition, there was no significant main effect of electrode laterality, F(1, 18) = 3.653, p = .072, $\eta_p^2 = .169$, $BF_{10} = .396$. Responses did not differ between electrode sites contralateral to the cue (M = -.099, SD = .817) and those at electrodes ipsilateral to the cue (M = .246, SD = .838). Finally, there was no significant effect of cue condition, F(1, 18) =.057, p = .815, $\eta_p^2 = .003$, BF₁₀ = .186. Overall responses for target-colored-cue trials (M = -.150, SD = -.682) did not differ from those for distractor-colored-cue trials (M =-.196, SD = 1.091). There was, however, a significant interaction between cue condition and electrode laterality, F(1, 18)= 6.002, p = .025, $\eta_p^2 = .250$, BF_{inclusion} = .562. To investigate whether there was a PD to both target-colored and distractorcolored cues, we followed up this interaction with pairwise t tests (collapsed across the awareness condition). In targetcolored-cue trials, mean ERPs did not differ between electrode sites contralateral to the cue location (M = -.151, SD = .720) and electrode sites insilateral to the cue location (M = -.150, SD = .730), t(19) = -.013, p = .990, d = -.003, $BF_{10} = .238$. In contrast, in distracter-colored-cue trials, ERPs were significantly more positive at electrode sites contralateral to the cue location (M = -.048, SD = 1.133) than at electrode sites ipsilateral to the cue location (M = -.343, SD = 1.077), t(19) =3.693, p = .002, d = .847, BF₁₀ = 23.795. Thus, there was a significant PD for distractor-colored cues, but not for targetcolored cues. None of the other interaction terms approached significance (Cue Condition \times Awareness), F(1, 18) = .288, p= .598, η_p^2 = .016, BF_{inclusion} = .026; Awareness × Electrode Laterality, F(1, 18) = 2.204, p = .155, $\eta_p^2 = .109$, BF_{inclusion} = .049; Cue Condition \times Awareness \times Electrode Laterality, F(1,18) = .149, p = .704, $\eta_p^2 = .008$, BF_{inclusion} = .003. We performed permutation tests, which verified these results (see the Supplemental Material).

Discussion

In line with the findings of Experiments 1 and 2, we found an RT benefit for valid versus invalid target-colored cues, with no difference in magnitude between cue-aware and cue-unaware trials. Target-colored cues and distractor-colored cues elicited an N_T response for both cue-aware and cue-unaware trials. In line with our findings from Experiment 2, the magnitude of the N_T response to target-colored cues was reliably larger for cue-aware trials than for cue-unaware trials. We also found that distractor-colored cues elicited an equivalent P_D response for both cue-aware and cue-unaware trials, whereas targetcolored cues did not elicit a reliable P_D. Thus, at the neural level, target processing is modulated by awareness, but distractor processing is not. Taken together, the results of Experiment 3 suggest that top-down task goals can elicit selective enhancement of task-relevant features (as measured by the N_T) and active suppression of task-irrelevant features (as measured by the P_D), even in the absence of cue awareness.

Interestingly, enhancement occurred earlier (200–300 ms after cue onset) than suppression of task-relevant features (350–500 ms after cue onset), suggesting that the N2pc results reported in Experiment 2 are not likely to reflect a combined $N_{\rm T}$ and $P_{\rm D}$ response.

General discussion

A key debate in the visual attention literature concerns how attention and perceptual awareness are related. Some researchers propose that attention and consciousness are intimately linked (Chun & Wolfe, 2000; Cohen et al., 2012; De Brigard, & Prinz, 2010; Mack & Rock, 1998; Merikle & Joordens, 1997; Mole, 2008; O'Regan & Noe, 2001; Posner, 1994; Prinz, 2011; Velmans, 1996), whereas others suggest that the two processes can act independently (Baars, 1997, 2005; Bachmann, 2006; Block, 2005; Dehaene et al., 2006; Iwasaki, 1993; Kentridge, Heywood, & Weiskrantz, 1999b; Kentridge et al., 2004; Koch, 2004; Koch & Tsuchiya, 2007; Lamme, 2003; Maier et al., 2008; Naccache et al., 2002; van Boxtel et al., 2010; Watanabe et al., 2011; Woodman & Luck, 2003). Here, we investigated the independent effects of spatial attention and perceptual awareness on feature-based cueing effects. Specifically, we were interested in whether the relationship between attention and perceptual awareness was consistent across behavioral and neural signatures of feature-based cueing effects. Previous research has shown that behavioral measures of feature-based cueing effects are independent of perceptual awareness (e.g., Ansorge & Neumann, 2005; Hsieh et al., 2011; Ivanoff & Klein, 2003; Lamy et al., 2015), but there has been little work on the effects of attention and perceptual awareness on neural measures of feature-based cueing effects.

In Experiment 1, we ran a direct replication of Lamy et al. (2015, Experiment 1), in which participants searched for a color-defined target that was preceded by a cue that was masked via CFS. Like Lamy et al. (2015), we found an RT benefit for valid target-colored cues, the magnitude of which did not differ between aware and unaware cues. We also found an RT cost for distractor-colored cues, which did not differ with cue awareness. This latter finding is in contrast to that of Lamy et al. (2015), who found an RT cost for distractor-colored cues on aware trials but not on unaware trials. Our findings suggest that when measured behaviorally, attentional mechanisms of selective enhancement and active suppression appear to act independently from perceptual awareness. Importantly, we replicated these behavioral results across all three experiments.

In Experiment 2, we presented a pair of colored cues, one in each visual hemifield, and found that target-colored cues evoked an N2pc response for both consciously perceived and unperceived cues. The magnitude of this N2pc response was larger for aware cues than for unaware ones. The N2pc is widely assumed to index attentional orienting to a specific location in



space (Heinze et al., 1990; Luck, 2005; Luck & Hillyard, 1994; but other processes have also been implicated; see Naughtin, Mattingley, & Dux, 2016). Since both aware and unaware cues in our study produced a significant N2pc response, it seems reasonable to conclude that selective attention is required to resolve competition between goal-relevant and distractor stimuli even when those stimuli are not consciously perceived.

In Experiment 3, we presented just one cue (either target colored or distractor colored) within each cue display, and measured N_T and P_D responses to the cue stimuli. We found an N_T to target-colored and distractor-colored cues when observers were both aware and unaware of those cues. In line with predictions, the magnitude of the N_T response was larger for aware target-colored cues than for unaware target-colored cues. Interestingly, we also found an N_T to distractor-colored cues, the magnitude of which did not differ between aware and unaware trials. Previous research has found that the N2pc/N_T response is evoked when stimuli are goal relevant, but not when stimuli are task irrelevant (Eimer & Kiss, 2008; Eimer et al., 2009; Kiss et al., 2008; Lien et al., 2008). Thus, our finding of an N_T response to distractor-colored cues might seem unexpected. However, one important component of our design is that we asked participants to report their awareness of the cue on every trial. Thus, all cues, both target colored and distractor colored, were relevant to the awareness task in our experiments. Previous research has shown that cues that have some taskrelevant features produce an N2pc response, even when those cues do not share all task-relevant features (Kiss, Grubert, & Eimer, 2013). Given that an N_T is typically not found for distractor-colored cues in feature-based cueing studies, our finding of an N_T response to distractor-colored cues highlights how different this version of the paradigm is from the original paradigm introduced by Folk et al. (1992). The presence of the N_T response to distractor-colored cues suggests that attention was directed to the location of the distractor-colored cue. This finding might seem contradictory to our observation of a samelocation RT cost for distractor-colored cues. We suspect that the N_T response reflects an early stage of processing, whereas the RT measure captures a later stage in the stimulus-response chain (as we discuss in detail below).

In Experiment 3, we also observed a P_D response to distractor-colored cues that occurred later in time than the N_T response. The magnitude of the P_D response did not differ between aware and unaware cues. Importantly, we found no evidence of a P_D response to target-colored cues. The timing of the P_D in our study was somewhat later than has been observed previously (Burra & Kerzel, 2014; Gaspar & McDonald, 2014; Gaspelin & Luck, 2018a; Hickey et al., 2009; Hilimire et al., 2011; Sawaki et al., 2012; Sawaki & Luck, 2010). According to the signal suppression hypothesis (Sawaki & Luck, 2010), top-down suppression is typically initiated even before a stimulus is presented. Thus, once participants are informed of their task goal (e.g., "Find the red T

shape and ignore the green T shape"), top-down signals act to enhance firing rates of neurons involved in processing goal-relevant features (e.g., red), and to attenuate the firing of neurons involved in processing goal-irrelevant features (e.g., green; e.g., Maunsell & Cook, 2002). When a target-colored cue is then presented, neurons involved in processing critical stimulus features are more likely to fire and neurons involved in processing goal-irrelevant stimuli are less likely to fire (Hamker, 2005; Treue & Martínez-Trujillo, 1999). As all cues were relevant to the awareness task in our experiments, however, active suppression was not required until after cue onset. Thus, it is possible that cues were initially enhanced in order to perform the cue awareness task, but then were quickly suppressed for target processing and rapid response.

Relationship between attention and perceptual awareness

Lamy et al. (2015) found an RT benefit for target-colored cues that was independent of perceptual awareness, and an RT cost for distractor-colored cues that depended on perceptual awareness. Across the three experiments presented here, we failed to replicate the independent effects of perceptual awareness on RT costs. Given that we used the same methodological design as Lamy et al., this finding is surprising. We note that the RT cost for unaware cues is quite small in numerical terms (mean cost of 23 ms across the three experiments). As we used a larger sample and had observers perform more trials than did Lamy et al. (2015), we may have simply had more statistical power to find this small effect. Interestingly, a recent paper by Schoeberl et al. (2018) also found that the same location cost was independent of cue awareness. Thus, converging evidence suggests that, when measured behaviorally, the attentional mechanisms of selective enhancement and active suppression both appear to be independent of awareness.

Interestingly, our neural data provide a different story as to the relationship between attention and perceptual awareness. We found that the neural responses associated with enhancement (the N2pc/N $_{\rm T}$; Hickey et al., 2009) were dependent on awareness, whereas the neural response associated with suppression (the P $_{\rm D}$; Hickey et al., 2009) was independent of awareness. Thus, our findings suggest that while the neural signatures of top-down enhancement of sensory processes are modulated by awareness, the neural signatures of top-down suppression are not.

Overall our findings have two important implications for understanding the relationship between attention and perceptual awareness. The first is that conclusions about the manner in which attention and awareness relate are likely contingent on how any effects on behavior and brain activity are measured. The variance in neural responses and the variance in RT measures might be assumed to arise from a common source. Thus, it might be expected that the pattern of ERP responses would



match those of the behavioral responses (i.e., RTs). The N2pc/N $_{\rm T}$ component, however, represents an early stage in the stimulus–response chain, whereas RTs represent the final outcome of that chain (or conceivably one of many consequences of stimulus processing). It is possible, therefore, that N2pc/N $_{\rm T}$ amplitude is determined by one stage of processing, whereas the RT effect is determined by later processing stages involved in decision-making, response selection, and/or execution. Our findings suggest that these later stimulus-processing stages are largely independent of the magnitude of responses during the early processing of visual features.

The second implication of our work is that the mechanisms of selective attention are likely the combination of (at least) two processes—selective enhancement and active suppression—and these processes seem to relate in different ways to perceptual awareness. While the neural measures of selective enhancement appear to depend on awareness, the neural measures of active suppression do not.

To claim that perceptual awareness is entirely independent of attention, it must be shown that all forms of attentional bias involved in all stages of processing are independent of whether a stimulus will be consciously perceived. Our findings suggest that the relationship between attention and perceptual awareness is a complex one that depends on the type of processing involved in any given task. Future research on the relationship between attention and perceptual awareness should focus on how these different mechanisms interact at different stages of the information processing hierarchy.

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