

# Saccadic eye movements do not disrupt the deployment of feature-based attention

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**The tight link of saccades to covert spatial attention has been firmly established, yet their relation to other forms of visual selection remains poorly understood. Here we studied the temporal dynamics of feature-based attention (FBA) during fixation and across saccades. Participants reported the orientation (on a continuous scale) of one of two sets of spatially interspersed Gabors (black or white). We tested performance at different intervals between the onset of a colored cue (black or white, indicating which stimulus was the most probable target; red: neutral condition) and the stimulus. FBA built up after cue onset: Benefits (errors for valid vs. neutral cues), costs (invalid vs. neutral), and the overall cueing effect (valid vs. invalid) increased with the cue–stimulus interval. Critically, we also tested visual performance at different intervals after a saccade, when FBA had been fully deployed before saccade initiation. Cueing effects were evident immediately after the saccade and were predicted most accurately and most precisely by fully deployed FBA, indicating that FBA was continuous throughout saccades. Finally, a decomposition of orientation reports into target reports and random guesses confirmed continuity of report precision and guess rates across the saccade. We discuss the role of FBA in perceptual continuity across saccades.**

## Introduction

According to the Greek myth, Orpheus was allowed to release his dead wife Eurydice from the underworld on one condition—not to look at her before they reached the world of the living. But Orpheus set his gaze on her and Eurydice vanished instantly. The myth suggests that as soon as the eyes land on a new

position, attention is deployed. But does this hold for all flavors of attention?

Saccadic eye movements are a characteristic feature of human vision. Occurring several times per second, they play a vital role in the deployment of resources in visual information processing. First and foremost, saccades select objects of interest for high-acuity vision in the fovea—the most densely sampled part of the retina, which is highly overrepresented in cortical visual processing. In addition, saccades are tightly coupled to covert spatial attention. It is widely accepted that when a stimulus is presented before the onset of a saccadic eye movement, participants are better at identifying it when its location coincides with the target of the saccade compared to other locations (Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). Indeed, this presaccadic shift of attention even biases visual short-term memory performance, selectively retaining visual features seen at locations that become the targets of saccades (Ohl & Rolfs, 2017).

Despite the significant bias that saccade preparation imposes on covert spatial selection, some attention can be deployed to locations other than the movement target without a decrement in saccadic latency or accuracy (Kowler et al., 1995). For the voluntary deployment of attention, however, this flexibility strongly declines before saccade initiation, when attention is captured at the saccade target (Montagnini & Castet, 2007). Indeed, just before saccadic eye movements, spatial attention can be split among more than one spatial location, but only provided that these locations are themselves potential movement goals (Baldauf & Deubel, 2008; Gersch, Kowler, & Doshier, 2004; Godijn & Theeuwes, 2003; Rolfs et al., 2011).

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Evidence has accumulated that the allocation of spatial attention before saccades plays a key role in perceptual continuity across saccades—that is, the visual system’s ability to deal with the massive displacement of objects on the retina that saccades unavoidably entail (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Rolfs, 2015). An instant before the execution of a saccade, attention shifts towards the future retinal locations of currently attended objects (Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013; Puntiroli, Kerzel, & Born, 2015; Rolfs et al., 2011; Szinte, Carrasco, Cavanagh, & Rolfs, 2015; Szinte, Jonikaitis, Rolfs, Cavanagh, & Deubel, 2016). This remapping of attention has been associated with benefits in visual processing at these locations after saccade landing (Jonikaitis et al., 2013) and the facilitation of secondary saccades toward them (Puntiroli et al., 2015; Rolfs et al., 2011). Indeed, recent evidence suggests that attention is available at relevant locations within no more than 30 ms after saccade landing (Yao, Ketkar, Treue, & Krishna, 2016), although a direct link to remapping of attention has yet to be established (visual sensitivity was not probed at the remapped location of the attended target). Together, these results suggest that timely updating of attention across saccades tracks relevant locations in a scene, ensuring continuity of perception and movement planning.

But do saccades influence spatial selection only? And is covert spatial selection the only attentional mechanism supporting trans-saccadic vision? Another flavor of visual selection is feature-based attention (FBA)—the enhancement of processing of a specific feature (e.g., looking for the flying, shiny hair of President Trump in a football field full of his supporters). FBA does not exert its effect on a specific location, but ubiquitously boosts a specific feature across the entire visual field (Bichot, Cave, & Pashler, 1999; White & Carrasco, 2011) and across the visual cortex (Saenz, Buracas, & Boynton, 2002; Treue & Martínez Trujillo, 1999). Indeed, this spatial invariance of FBA appears to make it an ideal attentional mechanism to avoid the costs of retinal shifts of relevant objects when the eyes move.

Few studies thus far have tried to investigate the interplay between saccades and FBA. In most of these studies, experimenters used a visual discrimination task to probe performance at a number of locations on a screen while participants prepared a saccade to one of these locations. Critically, each of these locations carried a particular but irrelevant feature (e.g., they were colored or had a particular motion direction), such that the probed location could be either congruent or incongruent with the saccade target (probing spatial attention) and its feature could either coincide or not coincide with the feature at the saccade target (probing FBA). In these tasks, saccades clearly biased spatial

attention but had little effect on FBA (Born, Ansorge, & Kerzel, 2012; Jonikaitis & Theeuwes, 2013; White, Rolfs, & Carrasco, 2013). That is, visual performance was higher at the saccade target location than at any other location, but there was little or no increase in sensitivity for other locations that incidentally carried the same feature as the target. Similarly, postsaccadic visual search for a colored target does not benefit from making the saccade to a target of the same color (Eymond, Cavanagh, & Collins, 2016). In contrast, robust global selection of the feature at the saccade target was observed in these paradigms if the color of the saccade target was relevant for the task (i.e., when it defined the saccade target; Born et al., 2012; Jonikaitis & Theeuwes, 2013). Moreover, this effect was slightly larger and more reliable when the feature remained constant across trials (Born et al., 2012) and when the features at the probe and target locations had coincided on a previous trial (White et al., 2013).

Together, these studies suggest a dissociation of FBA from spatial selection before saccades. However, it remains unclear whether and how FBA contributes to transsaccadic vision: Not a single published study thus far (that we are aware of) has investigated the continuity of FBA across saccades. It is interesting to note that, in the absence of saccades, it takes 300–500 ms for FBA to exert its effect on performance in a visual detection task (detection of a speed increment in one of four moving-dot patterns; Liu, Stevens, & Carrasco, 2007). If FBA were not continuous across saccades, therefore, vision would benefit from it mainly toward the end of each 300-ms fixation. In contrast, previous studies of presaccadic spatial selection have shown rapid attention shifts within 60 ms (Rolfs & Carrasco, 2012) to 150 ms (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006). Moreover, all previous studies of FBA in relation to saccades have involved clear spatial components: Features (e.g., color or motion direction) were linked to particular objects and locations in space. Under these circumstances, spatial updating of attention (as already discussed) could aid transsaccadic visual processing, alleviating the need to maintain a focus of FBA across an eye movement. In the current study, therefore, we explicitly isolated FBA from spatial components (cf. Kalogeropoulou, Jagadeesh, Ohl, & Rolfs, 2016) to assess its dynamics during fixation and its continuity across saccadic eye movements.

We asked participants to report the exact orientation of one of two sets of Gabors (black or white, and spatially interspersed) on a continuous scale. We cued FBA with a color cue indicating which of the two sets of gratings was the most probable one to be probed for report. Cues colored black and white were valid 75% of the time and invalid (drawing attention to the nontarget orientation) otherwise. To test for benefits

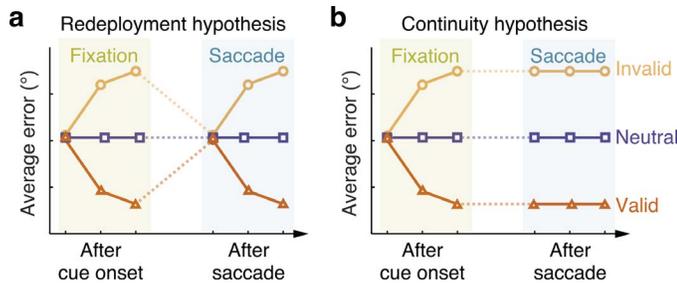


Figure 1. Scenarios of how saccades may affect the deployment of feature-based attention. (a) According to the redeployment hypothesis, cueing effects will revert to their initial state upon saccade execution. (b) According to the continuity hypothesis, feature-based attention will be readily deployed upon saccade landing (i.e., the cueing effects will be preserved after saccade execution).

and costs of the attentional deployment, we also included neutral cues (colored red), not providing information about the color of the target stimulus. To establish the time course of FBA, we tested performance at different intervals between the onset of the cue and the stimulus (cue–stimulus interval [CSI]). Critically, we also tested (on other trials) performance for stimuli presented at different intervals after a saccade (saccade–stimulus interval [SSI]) when FBA had been fully established before saccade initiation (by presenting the saccade target after the longest CSI). This protocol allowed us to investigate the continuity of FBA across saccadic eye movements. That is, if the saccade interrupts the deployment of FBA, attentional cueing effects would need to build up again at the beginning of the new fixation (redeployment hypothesis; Figure 1a). In contrast, if FBA is continuous across the saccade (continuity hypothesis; Figure 1b), this would provide support for its potential role in trans-saccadic processing. Across a number of performance variables, partly derived from mixture modeling of the data, we find clear evidence for the continuity hypothesis.

## Methods

### Participants

We recruited 12 participants (ages 20–36 years; 10 women, two men; three left-eye dominant, nine right-eye dominant; one left-handed, 11 right-handed) for participation in the experiment. We decided upon this number based on the sample size in previous studies on FBA (Herrmann, Heeger, & Carrasco, 2012; Kalogeropoulou et al., 2016). All participants were unaware of the purpose of the study and participated in exchange

for a fixed monetary payment of 7 euros per session (1 hr each), and a bonus of 21 euros after completion of all 10 sessions. The Ethics Committee of the German Society for Psychology approved the study, and participants provided written consent before participation. The study was conducted in accordance with the Declaration of Helsinki (2008).

### Experimental setup

Participants sat in a dimly lit room with their head positioned on a chin rest, at a distance of 57 cm from a VIEWPixx/3D monitor (1920 × 1080 pixels, 120-Hz vertical refresh rate). An EyeLink 1000 Desktop Mount (SR Research, Ottawa, Ontario, Canada) recorded the position of the dominant eye at 1000 Hz. The eye tracker was calibrated before each session (standard 9-point grid covering a square region enveloping the full extent of all stimulus locations) and whenever necessary. For stimulus presentation, online gaze control, and response collection, we used MATLAB (MathWorks, Natick, MA), including the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and the EyeLink Toolbox (Cornelissen, Peters, & Palmer, 2002) running on a Linux machine. Manual reports were collected using a PowerMate USB (Griffin Technology, Nashville, TN).

### Stimuli and procedure

During fixation trials (Figure 2a, left), participants had to maintain fixation at a centrally presented filled red circle (diameter = 0.2° visual angle [dva]). After 300 ms of fixation, a precue appeared for 100 ms (a ring with a diameter of 1.0 dva, width of 0.12 dva, and color defined by experimental condition), either informing participants about the color of the stimulus that would most likely have to be reported (black or white; 75% validity) or not providing any advance information (red; neutral cue). After a CSI of 0, 150, or 350 ms, the memory array—consisting of two sets of differently colored and oriented gratings (one black, one white; gratings of the same color all shared the same orientation)—was briefly flashed for 150 ms. At 500 ms after stimulus offset, one set of gratings (the positions of the gratings did not coincide with the positions occupied in the stimulus array; see below) colored black or white was presented and participants were asked to rotate (using a volume knob) their orientation (initial orientation drawn from a uniform distribution ranging from 0° to 180°; all individual gratings had the same orientation) until they matched the orientation of the corresponding stimulus the participants had just seen. Finally, when the participants pressed the knob, the

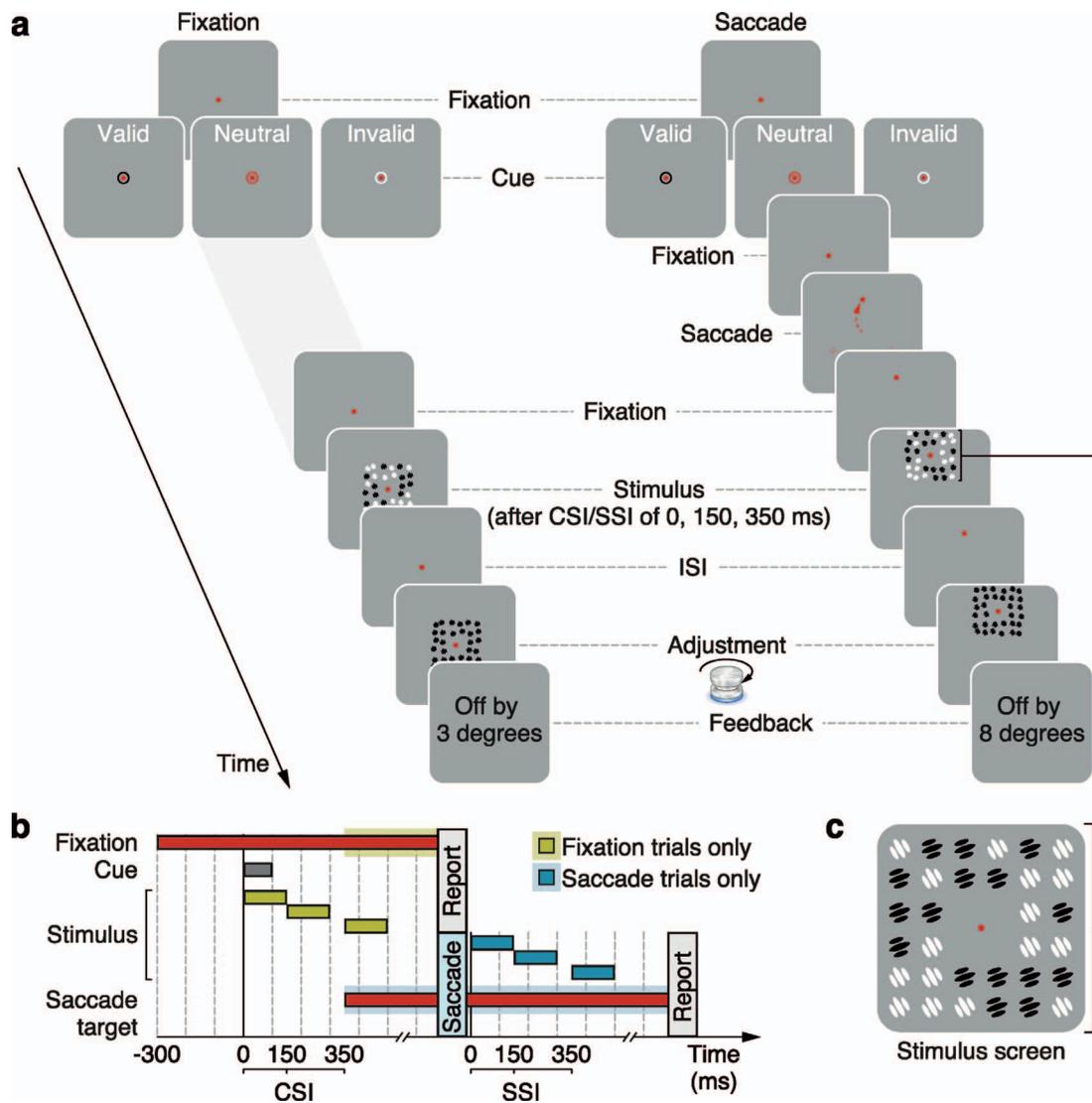


Figure 2. Experimental protocol. (a) Trial procedure for the fixation and saccade conditions. Each trial began with a fixation point (red dot, 300 ms) followed by a brief cue (ring around the fixation point, 100 ms) that was either informative (black or white; 75% validity) or neutral (red) as to the color of the target stimulus. In fixation trials, the stimulus screen (150 ms) appeared after a cue–stimulus interval (CSI) of 0, 150, or 350 ms. In saccade trials, 350 ms after cue onset the fixation point jumped randomly to one vertex of an imaginary equilateral triangle ( $0^\circ$ ,  $-120^\circ$ ,  $120^\circ$  relative to vertical) within a circle (radius of  $4^\circ$  of visual angle) centered at the screen's center and observers executed a saccade within 300 ms. Upon saccade landing (i.e., as soon as the eyes landed inside a circular area of radius  $2^\circ$  of visual angle centered on the target), and after a saccade–stimulus interval (SSI) of 0, 150, or 350 ms, the stimulus screen appeared (150 ms). At 500 ms after the stimulus screen went off (ISI), the response screen appeared, consisting of all 32 gratings with the same orientation and color (defining the target color) but not at the same position (see Stimuli and procedure). By rotating a knob, participants had to indicate the orientation the target had on the stimulus screen. Pressing the knob saved their report, and they received written feedback on the screen of how many degrees their report was off. (b) Timeline of stimulus events. (c) Schematic of the stimulus screen, which consisted of 32 gratings, colored half black and half white (randomly assigned). Gratings of the same color also shared the same orientation. The orientations were randomly drawn from a uniform distribution with a difference between the orientations of the two sets of  $60^\circ$  to  $120^\circ$ .

response was saved and participants received visual feedback regarding their exact error (in the range of  $0^\circ$  to  $90^\circ$ ).

Apart from blocks of fixation trials, observers also completed blocks with saccades executed between the cue and the stimulus (Figure 2a, right). Saccade trials

were identical to fixation trials up to the disappearance of the precue. Three-hundred and fifty ms after the onset of the precue (the longest CSI), the fixation spot was displaced to one of three saccade target locations. These saccade target locations formed an imaginary equilateral triangle around the initial fixation location,

placed on an imaginary circle at an eccentricity of 4 dva (radius) from the center of the screen, at  $0^\circ$ ,  $-120^\circ$ , and  $120^\circ$  relative to vertical. Upon saccade landing (detected online), the stimulus (identical to that used in fixation trials) was shown after one of three SSIs corresponding in duration to the three CSIs (0, 150, and 350 ms).

In both fixation and saccade trials, we controlled fixation behavior using an online eye-tracking routine. Trials were aborted automatically when eye position left the fixation region (2-dva radius) during periods of instructed fixation. In saccade trials, after saccade target onset, the target-directed saccade was identified online as the first saccade that left the fixation region within 300 ms and landed in the new, circular fixation area (2-dva radius around the saccade target) within 300 ms of saccade initiation. When no saccade was detected, the trial was aborted. Participants repeated aborted trials at the end of a block.

The stimulus (Figure 2c) consisted of 32 (16 black and 16 white) gratings (spatial frequency = 3.8 c/dva) arranged on a  $9 \times 9$  dva<sup>2</sup> regular grid centered at fixation. Each grating was either the positive (white) or the negative (black) lobe of a sine-wave grating, fading out in a Gaussian window ( $SD = 0.16^\circ$ ). The minimum distance between the center of the screen and the center of its closest neighboring grating was 2.7 dva. We randomly jittered (uniform distributions, ranging from 0 to 0.5 dva) the horizontal and vertical position of each grating in each interval and trial. The spatial uncertainty associated with the locations of individual Gabors, their eccentricity, small size, and high spatial frequency required observers to allocate attention globally over the whole visual display, to encode the orientation of the full set of gratings rather than the orientation of a single one (Herrmann et al., 2012; Kalogeropoulou et al., 2017). The orientations of the target and nontarget sets of gratings varied independently with a distance in the range from  $60^\circ$  to  $120^\circ$ , drawn from a uniform distribution.

Each observer was tested in 10 experimental sessions (each session consisting of 24 blocks, with 20 trials per block), contributing a total of 4,800 trials to the data set, such that the least frequent condition (invalid or neutral precue) had a minimum of 160 reports.

## Statistics

To assess the impact of cueing condition (valid vs. neutral vs. invalid), time interval (0 vs. 150 vs. 350 ms CSI or SSI), and eye-movement condition (fixation vs. saccade) on performance, we conducted three-way repeated-measures analyses of variance (rmANOVA) on each dependent variable. For guess rates, we used arcsine-transformed data in all rmANOVAs, as pro-

portions could not be assumed to be normally distributed.

We calculated 95% confidence intervals (CIs) using a bootstrap technique (Efron & Tibshirani, 1993). To generate each of the 10,000 bootstrap data sets, we first resampled the number of reports  $N$  that each participant provided in a given condition exactly  $N$  times (with replacement), fitted the model, and obtained the parameters of the best fit (for the angular error, we simply computed the average error for the resampled trials). Then we averaged these bootstrapped parameters across the 12 participants, resulting in one bootstrap data set. We repeated this procedure 10,000 times and obtained 2.5 and 97.5 percentiles of a given dependent variable across the 10,000 bootstrap data sets. These 10,000 bootstrap data sets were also used to compute the 95% CIs of differences between two conditions by simply subtracting the parameter values of the first condition's 10,000 bootstrap data sets from those of the second condition and determining the 2.5 and 97.5 percentiles of the resulting distribution of differences.

## Eye-movement analysis

Eye position was recorded from the onset of the fixation point until the presentation of the feedback screen. We confirmed the response saccades off-line by transforming recorded eye positions into 2-D velocity space. Successive eye positions were classified as saccades if they exceeded the median velocity by five standard deviations for at least 8 ms (Engbert & Mergenthaler, 2006). Moreover, saccadic events that were separated by less than 10 ms were merged into a single saccade.

We included all saccade trials that fulfilled the following criteria: (a) The landing position of the saccade was no more than 2 dva away from the center of the saccade target; (b) there were no secondary saccades ( $>1$  dva) after landing at the target; (c) there were no missing recordings of the eye tracker before a saccade; and (d) there were no missing recordings after a saccade. For fixation trials, we applied the following inclusion criteria: (a) Gaze remained inside a circular area of 2 dva from the fixation dot; (b) no saccades larger than 2 dva occurred during fixation; and (c) no eye-position data were lost during stimulus presentation. Applying these criteria, we discarded 6.6% of the valid trials, 5.7% of the neutral trials, and 6.2% of the invalid trials.

The online saccade detection (see earlier) was used to trigger the display of the stimulus contingent on saccade landing (see earlier). To determine any discrepancies between the intended, nominal SSI (as implemented online) and the true SSI, we also

performed an off-line analysis of saccade landing times, which we defined as the time of the first eye-position sample after the response saccade. Indeed, saccade landing as detected online preceded saccade landing as detected off-line by 18 ms on average, resulting in a stimulus onset that preceded the nominal SSI by 19 ms on average. This discrepancy was negative (i.e., on average, stimuli were present right upon saccade landing) and an order of magnitude smaller than the duration of the stimulus itself (150 ms), and overall performance in each cueing condition did not vary significantly as a function of the true SSI. We therefore report all data as a function of the nominal SSI.

## Results

### Saccade parameters

In a first step, we analyzed basic parameters of the eye movement in the saccade task. The mean saccade amplitude across conditions and subjects was 3.9 dva (95% CI [3.8, 4.0]), and remained within the small range of 3.7–4.3 dva for all nine combinations of the three time intervals (0, 150, 350 ms) and the three conditions (valid, invalid, neutral). A two-way ANOVA on time interval (SSI) and cueing condition showed no main effects ( $F_s > 1.57$ ,  $p_s > 0.092$ ) and no interaction between time interval and cueing condition,  $F(4, 44) = 2.40$ ,  $p = 0.064$ .

Similarly, saccade latencies were highly consistent across conditions, ranging between 156 and 160 ms for all nine combinations of the three SSIs and the three cueing conditions, and averaging to 159 ms overall (95% CI [152, 167]). A two-way ANOVA showed a main effect of condition,  $F(2, 22) = 4.91$ ,  $p = 0.017$ , reflected in slightly faster saccade latencies in the neutral condition (157 ms; 95% CI [151, 164]) as compared to the valid (160 ms; 95% CI [152, 168]) and invalid (160 ms; 95% CI [153, 168]) conditions. There was no main effect of time interval (SSI),  $F(2, 22) = 1.25$ ,  $p = 0.307$ , and no interaction between time interval (SSI) and cueing condition,  $F(4, 44) = 0.94$ ,  $p = 0.452$ .

Finally, as the time of saccade landing was critical to the control of stimulus timing in the saccade condition, we also assessed saccade durations as a function of cueing condition and SSI. The average saccade duration ranged between 70 and 72 ms across all nine combinations of the three SSIs and the three cueing conditions, and averaged to 71 ms overall (95% CI [66, 76]). A two-way ANOVA showed no significant main effects—cueing condition:  $F(2, 22) = 1.11$ ,  $p = 0.346$ ; time interval:  $F(2, 22) = 3.34$ ,  $p = 0.054$ . Whereas the interaction was statistically significant,  $F(4, 44) = 3.66$ ,

$p = 0.011$ , this effect was of little practical importance, as the means across conditions differed by no more than 2 ms.

The high consistency of these saccade parameters alleviates potential concerns about comparability of visual performance across experimental conditions in our task.

### Performance in the orientation-adjustment task

In our feature-cueing paradigm, a precue oriented observers' attention either correctly to a target orientation (valid precue), incorrectly to the distractor orientation (invalid precue), or to both orientations (neutral precue). If observers were able to deploy FBA, we would observe a benefit in performance for the valid condition compared to the neutral condition. Similarly, the successful deployment of FBA might entail a cost in performance for the invalid compared to the neutral condition. We hypothesized that benefits and costs of the deployment of FBA take time to build up (see also Liu et al., 2007). An eye movement, planned and executed after the successful deployment of FBA, may or may not interrupt this process and thus necessitate (or not) a redeployment of FBA upon saccade completion (see Figure 1). We assessed these predictions by (a) analyzing the time course of accuracy in the orientation-adjustment task, (b) decomposing participants' orientation reports into different sources of errors (report precision and the rate of guesses), and (c) assessing the continuity of FBA cueing effects across saccades for each of these variables.

### Time course of accuracy

We calculated the mean angular error of the observers' orientation reports for each condition and each interval (Figure 3a, left panel; individual data shown in right panel). The results of a  $3 \times 3 \times 2$  rmANOVA are summarized in Table 1 (Angular error); we found main effects of all three factors: cueing condition, time interval, and eye-movement condition. Moreover, there were interactions between time interval and cueing condition and between time interval and eye-movement condition, but no interaction between cueing and eye-movement condition. Critically, there was a significant three-way interaction among all three factors, indicating a difference in the time course of the cueing effects between the fixation and the saccade trials. Indeed, separate two-way rmANOVAs for the two eye-movement conditions (Table 1) revealed a significant interaction between cueing condition and time interval in the fixation condition but not the saccade condition. That is, whereas the cueing effect increased with the CSI during fixation, this deployment

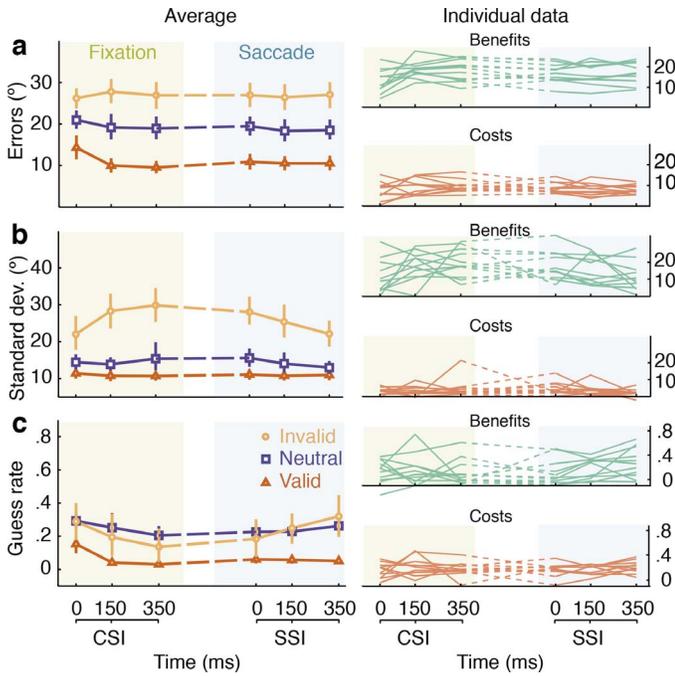


Figure 3. Average performance (left column) as a function of cueing condition, time interval, and eye-movement condition, and individual cueing effects (right column) as a function of time interval and eye-movement condition. Benefits are the difference between the neutral and valid conditions; costs are the difference between the invalid and neutral conditions. Rows show (a) overall accuracy, as well as the model-based decomposition of responses into (b) standard deviation, the inverse of precision, and (c) guess rate. The error bars are bootstrapped 95% confidence intervals.

of FBA remained stable across all SSIs after the saccade (Figure 3a).

**Decomposition of orientation reports into different sources of errors**

Next, we investigated the source of changes in accuracy, using a number of models (increasing in complexity) to decompose orientation reports into target reports (with variable precision), random guesses, and a potential contribution of nontarget reports (see Figure 4). For each participant and each of the 18 combinations of cueing condition, time interval, and eye-movement condition, we fitted the distribution of responses (i.e., the difference between the orientation report and the actual target orientation) with five different probabilistic mixture models to find the model that best describes their performance (Table 2).

*Model I Target reports only:* Here we assumed that participants report targets only (i.e., they never guess), such that the distribution of reports  $p(\theta)$  can be described by

$$p(\theta) = \Phi_{\mu, \kappa},$$

where  $\theta$  is the difference between the reported value and the target value,  $\Phi$  is a von Mises probability density function (i.e., a circular Gaussian) with mean  $\mu$  (target orientation) and spread parameter  $\kappa$  (which relates to the standard deviation  $\sigma = \sqrt{1/\kappa}$ ).

*Model II Target reports and random guesses:*

$$p(\theta) = (1 - \gamma) \Phi_{\mu, \kappa} + \gamma \frac{1}{2\pi},$$

in addition to target reports, features a uniform distribution of random guesses that make up the proportion  $\gamma$  of all reports.

*Model III Target reports, random guesses, and nontarget reports:*

$$p(\theta) = (1 - \gamma - \beta) \Phi_{\mu, \kappa} + \beta \Phi_{\delta, \kappa} + \gamma \frac{1}{2\pi},$$

adds another von Mises distribution, centered at the distractor orientation  $\delta$ , that has the same spread  $\kappa$  as the target distribution, making up the proportion  $\beta$  of all reports. This model is equivalent to the one proposed for visual short-term memory performance by Bays, Catalao, and Husain (2009). It has also been most successful in our previous study on the impact of FBA in visual short-term memory (Kalogeropoulou et al., 2016).

*Model IV Target reports, random guesses, and nontarget reports with different spread:*

$$p(\theta) = (1 - \gamma - \beta) \Phi_{\mu, \kappa_T} + \beta \Phi_{\delta, \kappa_N} + \gamma \frac{1}{2\pi},$$

is identical to Model III except that the distribution of nontarget reports was allowed to have a different spread ( $\kappa_N$ ) from that of the target distribution ( $\kappa_T$ ).

*Model V Target reports, random guesses, and orthogonal nontarget reports:* Finally, Model V is identical to Model III except that we assume that participants strategically reported nontargets as 90° off from the target orientation:

$$p(\theta) = (1 - \gamma - \beta) \Phi_{\mu, \kappa} + \beta \Phi_{\mu+90^\circ, \kappa} + \gamma \frac{1}{2\pi}.$$

The von Mises distribution centered 90° off the target orientation ( $\mu + 90^\circ$ ) had the same spread  $\kappa$  as the target distribution, making up the proportion  $\beta$  of all reports.

A formal model comparison using the Akaike information criterion (Akaike, 1974) revealed largely equivalent model fits for Models II through V, with a slight advantage for Model II (see Akaike information criteria reported in Table 2). For the sake of simplicity, therefore, we modeled response distributions as a composition of target reports and random guesses. As a consequence, we obtained two additional dependent

Source	$df_H$	$df_E$	Angular error			Standard deviation			Guess rate		
			MS	$F$	$p$	MS	$F$	$p$	MS	$F$	$p$
Three-way rmANOVA											
Participants	11		245.48			154.97			0.109		
Cueing condition	2	22	4,537.6	145	<0.001	4,449	78.75	<0.001	0.758	17.13	<0.001
Time interval	2	22	31.97	8.37	0.002	0.64	0.04	0.962	0.024	2.26	0.127
Eye-movement condition	1	11	15.66	5.37	0.040	22.04	0.992	0.341	0.001	0.06	0.809
Cueing condition × Time interval	4	44	16.91	4.37	0.004	14.2	0.92	0.459	0.006	0.55	0.700
Cueing condition × Eye-movement condition	2	22	2.27	1.18	0.324	11.5	0.670	0.520	0.022	1.75	0.197
Time interval × Eye-movement condition	2	22	12.62	6.33	0.006	140.65	5.17	0.014	0.150	8.13	0.002
Cueing condition × Time interval × Eye-movement condition	4	44	16.73	5.29	0.001	87.07	4.15	0.006	0.019	1.30	0.285
Error	44		3.17			20.97			0.015		
Post hoc two-way rmANOVA (reported if three-way interaction was significant)											
Fixation											
Participants	11		126.14			104.09					
Cueing condition	2		2,214.2	148.27	<0.001	2,456.4	78.9	<0.001			
Time interval	2		40.69	13.5	<0.001	66.15	2.42	0.112			
Cueing condition × Time interval	4	44	32.67	6.01	<0.001	75.03	3.06	0.026			
Error	44		5.44			24.5					
Saccade											
Subjects	11		122.25			73.12					
Cueing condition	2	22	2,327.7	127.17	<0.001	2,004.0	47.22	<0.001			
Time interval	2	22	3.9	1.39	0.269	75.14	4.55	0.022			
Cueing condition × Time interval	4	44	0.97	0.61	0.659	26.24	2.21	0.083			
Error	44		1.6			11.86					

Table 1. Repeated-measures analyses of variance (rmANOVAs) for three dependent variables of performance: angular error, standard deviation, and guess rate. *Notes:* Bold  $p$  values indicate significant effects (i.e.,  $p < 0.05$ ). MS, mean sum of squares.

variables—standard deviation (i.e., the inverse of precision) and guess rate—that we examined as a function of our experimental conditions.

First, we computed  $3 \times 3 \times 2$  rmANOVAs with the factors of cueing condition, time interval, and eye-movement condition for the parameter of standard deviation (Table 1); we found a main effect of cueing condition and no main effect of time interval or eye-movement condition. For the standard deviation, there was a significant interaction between time interval and eye-movement condition, but not between time interval and cueing condition or between cueing condition and eye-movement condition. Most importantly, there was a significant three-way interaction, suggesting that the time course of cueing effects differed between the two eye-movement conditions. Indeed, separate post hoc two-way rmANOVAs (Table 1) showed significant two-way interactions between cueing condition and time interval for fixation but not saccade trials. Figure 3b suggests the origin of this difference: During fixation, the standard deviation of reports rapidly increased with increasing CSI for the unattended gratings (invalid condition) with respect to the neutral

condition, whereas it decreased slightly for the attended one (valid condition). These benefits and costs remained largely constant across saccades, suggesting that the deployment of FBA was not interrupted by the eye movement (see also the next subsection).

For the parameter of guess rate (Table 1), we observed a main effect of cueing condition and no main effect of time interval or eye-movement condition. There was an interaction between time interval and eye-movement condition, but we found no interaction between time interval and cueing condition nor between cueing and eye-movement condition. Finally, there was no three-way interaction. Figure 3c shows that guess rates were comparable between the neutral and invalid cueing conditions and considerably lower for the valid condition. Moreover, guess rates decreased across time during fixation, whereas they remained largely constant across saccades.

Together these results suggest that cueing of FBA had effects on both the number of random guesses and the precision of target orientation reports. Benefits for the attended orientation included a reduced guess rate and increased precision relative to a neutral cue. Costs

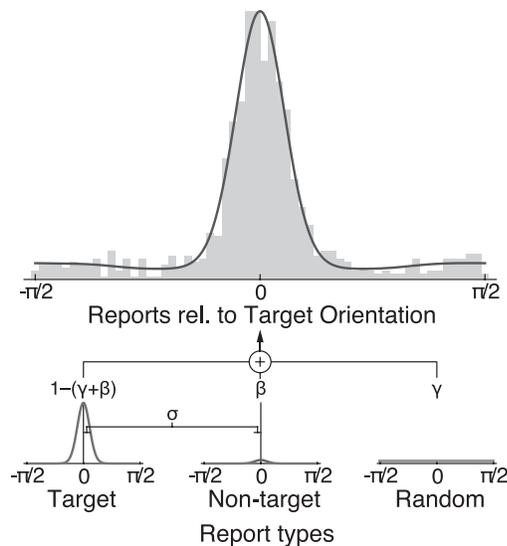


Figure 4. Example distribution of orientation reports, including the fit of a mixture model. The model comprised nontarget reports and random guesses in addition to target reports, each associated with a certain probability ( $\gamma$ ,  $\beta$ , and  $1 - [\gamma + \beta]$ , respectively). Here, target and nontarget reports were assumed to have the same precision, captured by its inverse, the standard deviation  $\sigma$ . Note that in the overall fit (top panel), the nontarget reports are distributed across a range of angles, due to the variable relation between target and nontarget orientations.

of unattended orientations were largely due to a decrease in precision.

### Continuity of FBA cueing effects across saccades

Here we turn toward one of the main questions of this study and assess the continuity of FBA across a saccade in a quantitative fashion. For each of the dependent variables of performance—absolute angular error, standard deviation, and guess rate—we computed the impact of cueing on performance by taking differences for each pair of cueing conditions for each time interval and each participant. These pairs of conditions capture three cueing effects: the benefit of cueing the target grating (Neutral – Valid), the cost of cueing the nontarget grating (Invalid – Neutral), and the overall effect of FBA (Invalid – Valid). If attention were continuous across the saccade (Figure 1b), then the cueing effects right after the saccade (0-ms SSI) should correspond closely to those for the longest CSI (350 ms) during fixation, because FBA had time to build up in the fixation leading up to the saccade. In that scenario, the cueing effects right after the saccade (0-ms SSI) should be predicted best by the cueing effects observed when FBA was fully deployed (350-ms CSI in the fixation condition). If, however, the saccade interrupted the deployment of FBA, cueing effects

Rank	Model number	Number of parameters	Average AIC
1	II	2	484.8
2	V	5	486.2
3	III	3	486.3
4	IV	4	487.9
5	I	1	514.2

Table 2. Rank order of models fit to individual data, listed with number of parameters and average Akaike information criteria (AIC).

would have to build up once more (Figure 1a). In that scenario, the cueing effects right after the saccade (0-ms SSI) should be predicted best by the cueing effects right after cue onset (0-ms CSI in the fixation condition). We examined these scenarios for each dependent variable using two types of analyses. First, we correlated postsaccadic cueing effects with those observed at different CSIs during fixation (Figure 5, scatter plots). Second, we assessed the similarity of cueing effects in different time windows as deviations from the unity line (Figure 5, corner-density plots and confidence intervals therein).

For absolute angular error (Figure 5a through c), cueing effects right after the saccade (0-ms SSI) were more strongly correlated to those in the 350-ms CSI ( $R^2 = .72$ ,  $p < 0.001$ ) than to those in the 0-ms CSI ( $R^2 = .48$ ,  $p < 0.001$ ). Indeed, the correlation between the 0-ms intervals in fixation and saccade trials (CSI and SSI, respectively) was very similar to the correlation between the 0-ms and 350-ms CSIs ( $R^2 = .31$ ,  $p < 0.001$ ), thus reflecting primarily between-subjects variance in the size of cueing effects.

Indeed, as shown in Table 3, the cueing effects (i.e., benefits, costs, and overall effects) observed upon saccade landing (0-ms SSI) could not be distinguished from those 350 ms after cue onset (350-ms CSI), but were consistently larger than those at 0 ms after cue onset (0-ms CSI). To quantify the similarity between cueing effects during fixation and across saccades, we assessed deviations of the correlation from the unity line. The more similar cueing effects are in two time intervals, the closer the data points should be to the unity line. The deviations were around zero for the combination 350-ms CSI and 0-ms SSI (all 95% CIs above corner densities in Figure 5a include zero), indicating a strong continuity of FBA across the saccade. In contrast, for the combination of 0-ms CSI and 0-ms SSI (Figure 5b), most data points fell above the unity line, indicating that cueing effects were larger upon saccade landing than right after cue onset. These differences were significant (i.e., the 95% CI did not overlap with 0) for costs and for the overall cueing effect. The deviation was not significant for benefits, which was due to the fact that benefits did not increase significantly from the 0-ms to the 350-ms CSI. Indeed,

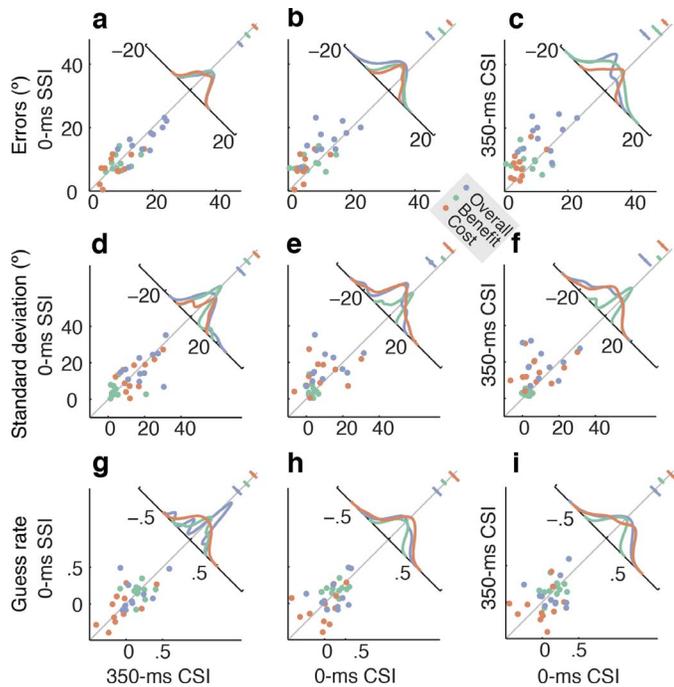


Figure 5. Predicting cueing benefits (green), costs (red), and overall effects (blue) for three performance variables: absolute angular error (a–c), standard deviation (d–f), and guess rate (g–i). The left column (a, d, g) shows predictions of cueing effects immediately after the saccade (0-ms saccade–stimulus interval) based on those observed when feature-based attention was fully established (350-ms cue–stimulus interval [CSI]). The middle column (b, e, h) shows predictions of cueing effects immediately after the saccade (0-ms saccade–stimulus interval) based on those observed immediately after cue onset (0-ms CSI). For comparison, the right column (c, f, i) shows predictions of cueing effects long after cue onset (350-ms CSI) based on those observed immediately after cue onset (0-ms CSI). This latter comparison is a quantification of how strongly cueing effects developed after cue onset; if they did not change in magnitude, deviations from the unity line are insignificant. Each dot in the scatter plot represents one participant; the corner-density functions show the distribution relative to unity (dashed line). Error bars above the density functions show 95% confidence intervals for the deviation from the unity line.

deviations between 0-ms CSI and 0-ms SSI can only be expected if the combination of 0-ms and 350-ms CSI also yields a significant deviation. This comparison (Figure 5c) yielded significant deviations from the unity line for costs but not for benefits.

Similarly, for standard deviation (Figure 5d through f), cueing effects right after the saccade (0-ms SSI) were more strongly correlated to the 350-ms CSI ( $R^2 = .47$ ,  $p < 0.001$ ) than those in the 0-ms CSI ( $R^2 = .21$ ,  $p = 0.005$ ). Again, the correlation between the 0-ms CSI and the 0-ms SSI was very similar to the correlation between the 0-ms and 350-ms CSI during fixation ( $R^2 =$

.15,  $p = 0.02$ ), thus reflecting primarily between-subjects variance in the size of cueing effects.

Table 3 shows that, as was the case for angular error, the cueing effects for standard deviation observed upon saccade landing (0-ms SSI) were very similar to those long after cue onset (350-ms CSI), but were consistently larger than those at 0 ms after cue onset (0-ms CSI). Deviations from the unity line were indistinguishable from zero for the comparison between the 350-ms CSI and 0-ms SSI (Figure 5d) for benefits, costs, and the overall cueing effect. In contrast, the comparison of the 0-ms CSI and the 0-ms SSI (Figure 5e) yielded consistently larger differences, suggesting that the 350-ms CSI predicted the 0-ms SSI more accurately than the 0-ms CSI. The difference was significant for the overall effect only (i.e., the 95% CI did not overlap with 0), as was expected based on the evolution of the cueing effects during fixation. That is, for the combination of 0-ms and 350-ms CSI (Figure 5f), we found the same pattern of deviations, supporting the hypothesis that FBA needs time to build up and then remains at that level throughout a saccade.

Finally, for guess rates (Figure 5g through i), cueing effects right after the saccade (0-ms SSI) were again more highly correlated to those at the 350-ms CSI ( $R^2 = .34$ ,  $p < 0.001$ ) than those at the 0-ms CSI ( $R^2 = .21$ ,  $p = 0.005$ ). However, in some cases participants differed wildly in their guess rates for different intervals, reducing the magnitude of the correlation between the respective cueing effects. The correlation between the 0-ms and 350-ms CSI during fixation was indeed very low ( $R^2 = 0.09$ ) and insignificant ( $p = 0.068$ ).

Moreover, as we already reported, the average cueing effects on guess rate remained largely constant across time (see previous section), such that differences from the unity line were not expected. Indeed, Table 3 shows that the cueing effects observed upon saccade landing (0-ms SSI) could not be distinguished from those at 350 ms after cue onset (350-ms CSI), nor from those right after cue onset (0-ms CSI). In none of the comparisons did cueing effects differ significantly from the unity line (all 95% CIs in Figures 5g through i overlap with 0). The guess rate, therefore, could not be used to assess evidence for or against the continuity of FBA across a saccade, as any such assessment relies on the change of the magnitude in cueing effects after cue onset (i.e., from 0-ms to 350-ms CSI).

Overall, we saw a very clear pattern of results: Cueing effects immediately after the saccade did not resemble those right after cue onset. Instead, post-saccadic performance reflected the full-fledged cueing effects that were established half a second after the onset of a cue during fixation (i.e., 350-ms CSI + 150-ms stimulus duration). These results suggest that saccades did not interfere with the deployment of FBA.

Dependent variable	Cueing effect	0-ms CSI		350-ms CSI		0-ms SSI	
		Mean	95% CI	Mean	95% CI	Mean	95% CI
Angular error (°)	Benefit	6.66	[4.25, 9.11]	9.39	[7.93, 11.09]	8.59	[7.36, 10.02]
	Cost	5.23	[3.79, 7.09]	7.94	[5.81, 10.43]	7.47	[5.38, 9.46]
	Overall	11.88	[8.89, 14.98]	17.33	[14.57, 19.99]	16.07	[13.66, 18.42]
Standard deviation (°)	Benefit	3.01	[2.00, 4.05]	4.71	[2.61, 7.99]	4.52	[2.83, 6.63]
	Cost	7.57	[2.24, 13.63]	14.46	[10.60, 18.78]	12.45	[8.18, 16.94]
	Overall	10.58	[5.78, 16.09]	19.17	[14.90, 23.61]	16.97	[12.70, 21.75]
Guess rate	Benefit	0.14	[0.07, 0.21]	0.17	[0.11, 0.23]	0.16	[0.11, 0.22]
	Cost	0.00	[−0.13, 0.11]	−0.07	[−0.18, 0.05]	−0.04	[−0.16, 0.07]
	Overall	0.14	[0.03, 0.023]	0.11	[0.01, 0.22]	0.12	[0.02, 0.24]

Table 3. Cueing effects for angular error, standard deviation, and guess rate for three time windows: 0-ms cue–stimulus interval (CSI), 350-ms CSI, and 0-ms saccade–stimulus interval (SSI).

### On the origin of early cueing effects

A surprising aspect of our data was the finding that the deployment of attention occurred very early after cue onset (see Figure 3, 0-ms CSI). At first glance, this may appear inconsistent with previous findings suggesting that FBA takes at least 300 ms to exert its effects on visual sensitivity (Liu et al., 2007). A closer inspection of the individual data suggests that the time course of cueing effects for each participant followed one of two patterns—showing either an early cueing effect (at 0-ms CSI) or a relatively late onset (at 150-ms CSI). These two patterns of results were each observed in about half the participants in our study, and we thus decided to subdivide our sample into early- and late-onset groups, based on a median split of the overall effect at 0-ms CSI.

The late-onset group built up attention slowly (Figure 6a), as would be expected based on previous work on FBA in motion perception (Liu et al., 2007). A  $3 \times 3 \times 2$  rmANOVA with factors of cueing condition, time interval, and eye-movement condition showed a main effect of precueing,  $F(2, 10) = 56.76, p < 0.001$ , and no main effects of time interval,  $F(2, 10) = 2.43, p = 0.138$ , or eye-movement condition,  $F(1, 5) = 0.73, p = 0.431$ , for average angular error. There was an interaction between cueing condition and time interval,  $F(4, 20) = 8.89, p < 0.001$ , but no other two-way interaction ( $F_s < 1.85, p_s > 0.20$ ). Importantly, this group showed the three-way interaction among all three factors,  $F(4, 20) = 12.43, p < 0.001$ , indicating a difference in the time course of the cueing effects between the fixation and saccade trials. Equivalent analyses for standard deviation—three-way interaction:  $F(4, 20) = 3.33, p = 0.030$ —were consistent with this interpretation. Guess rate showed no main effects ( $F_s < 3.53, p_s > 0.069$ ) and no three-way interaction,  $F(4, 20) = 1.14, p < 0.367$ , but a two-way interaction between time interval and eye-movement condition,  $F(4, 20) = 5.51, p < 0.024$ .

In contrast, for the early-onset group (Figure 6b) the effect of the cue was fully developed right after cue onset (0-ms CSI). We observed a main effect of cueing condition,  $F(2, 10) = 83.55, p < 0.001$ , and a main effect of time interval,  $F(2, 10) = 5.86, p = 0.021$ , but no main effect of eye-movement condition,  $F(1, 2) = 1.23, p = 0.318$ . There was an interaction between time interval and eye-movement condition,  $F(2, 10) = 6.88, p = 0.013$ , but no other two-way interaction ( $F_s < 1.69, p_s >$

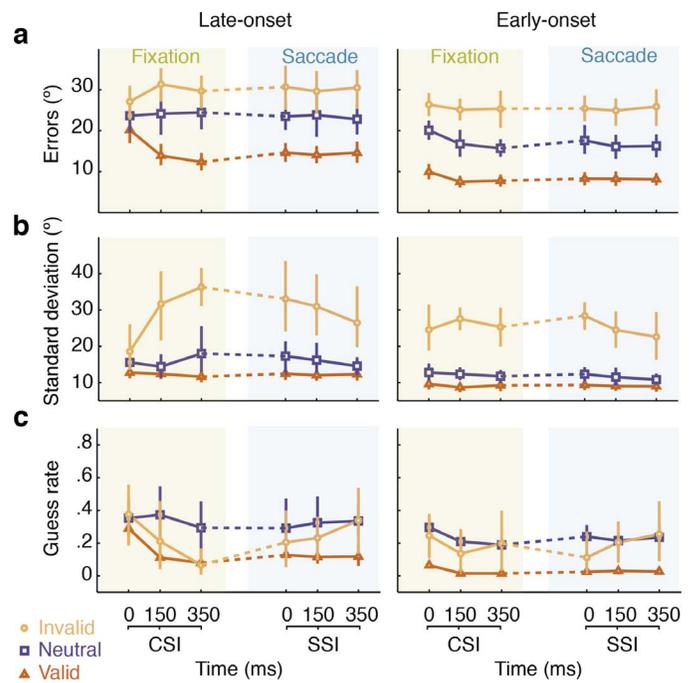


Figure 6. Performance of the late-onset group (left column) and the early-onset group (right column) captured by absolute angular error (a), standard deviation (b), and guess rate (c) as a function of cueing condition, time interval, and eye-movement condition. The data have been split into two groups using a median split of the overall cueing effect on angular error in the 0-ms cue–stimulus interval condition. Error bars are bootstrapped 95% confidence intervals.

0.19). Importantly, there was no three-way interaction,  $F(4, 20) = 0.51$ ,  $p = 0.732$ . The absence of any interaction between cueing condition and either time interval or eye-movement condition shows that, for this group, cueing effects remained constant across time during fixation and across the eye movement. Again, equivalent analyses for the standard deviation—three-way interaction:  $F(4, 20) = 1.84$ ,  $p = 0.161$ —were consistent with this interpretation. This group showed a main effect of cueing condition on guess rate,  $F(2, 10) = 5.78$ ,  $p < 0.021$ , as well as a two-way interaction of time interval and eye-movement condition,  $F(2, 10) = 4.58$ ,  $p = 0.038$ , but no three-way interaction,  $F(4, 20) = 0.98$ ,  $p = 0.440$ .

These results suggest that participants in the early-onset group used a slightly different strategy to solve the task than participants in the late-onset group. We speculate that these observers used the precue in hindsight (i.e., similar to a retrocue) to deploy attention to the internal representation of the stimuli in visual short-term memory (Kalogeropoulou et al., 2017; see Discussion) rather than as a precue to increase sensitivity during stimulus encoding. Importantly, both groups show a clear continuity of FBA effects across a saccadic eye movement.

## Discussion

Feature-based attention is a cardinal selection mechanism of the visual system. However, very few studies have explored this mechanism in active vision—when eye movements frequently interrupt the visual-processing stream. To fully understand the architecture of attentional processes, therefore, we need to study FBA in the presence of eye movements. Here we assessed the deployment of FBA during fixation and across saccades. We devised a dual task, combining a simple color-cueing task—in which participants had to pay attention to and report the orientation of one of two sets of colored gratings with a rotating knob (continuous report task)—with the instruction to make an eye movement. FBA is known to develop over tenths of a second after the onset of a cue (Liu et al., 2007). Through varying the interval between the cue and the stimulus, therefore, this paradigm allowed us to distinguish between two possible scenarios of how saccades may affect the deployment of FBA: (a) Attentional cueing effects return to their initial levels such that a redeployment of FBA is necessary after a saccade (redeployment hypothesis; Figure 1a) and (b) FBA is continuous across the saccade, such that attentional cueing effects remain fully developed after saccade landing (continuity hypothesis; Figure 1b). Our

data show clear evidence for the second hypothesis: FBA was deployed continuously across saccades.

To arrive at this conclusion, we first assessed the effects of cueing on participants' performance for three different time intervals after cue onset during fixation (CSI = 0, 150, and 350 ms). We found that cueing effects increased across time and involved both benefits from validly cueing the target stimulus and costs from invalidly cueing the nontarget stimulus. Attention was thus drawn toward the cued orientation relative to the neutral condition (in which no stimulus was cued) and away from the uncued orientation. We then compared this time course of FBA during fixation to that following a saccade (SSI = 0, 150, and 350 ms). Importantly, the eye movement was initiated once FBA was fully deployed (CSI > 350 ms). In the saccade trials, we did not find any evidence for an interaction between time interval and cueing condition: Cueing effects on the mean angular error remained at the same level across time.

The nature of the continuous reports collected from observers enabled us to use mixture modeling to further decompose errors into two components: standard deviation (which translates to precision, its inverse) and guess rate (Figure 3). Both variables corroborated the results obtained from the average error. Cueing effects on precision changed across time for the fixation trials (increasing with CSI) but not the saccade trials (constant across SSI). The guess rate did not show an interaction in either eye-movement condition.

An unexpected aspect of our findings is that FBA cueing effects developed rapidly and were noticeable even when the stimulus appeared simultaneously with the cue (0-ms CSI). At first sight, this result appears inconsistent with previous work (Liu et al., 2007) showing that FBA takes 300 ms to exert its effect on visual performance. It appears likely that the early cueing effects observed here resulted from two differences between our study and that by Liu et al. First, we used a colored cue to draw attention to the orientation of the gratings of that color. In contrast, Liu et al. used a symbolic arrow cue to signal the location or direction of motion of a potential target stimulus. We speculate that the direct (bottom-up) correspondence between the cue and the stimulus feature in our study was processed faster than the symbolic (top-down) information provided in the other study. Second, Liu et al. used a simple detection task, in which observers had to report the presence or absence of a speed change in a motion stimulus. In our study, by contrast, observers had to report the exact orientation of a stimulus they had just seen. The necessity of providing a continuous report may have caused observers to rely more strongly on an iconic or visual short-term memory of the stimulus. Consistent with this idea, we have previously shown that feature cues can be used retrospectively and induce

cueing effects even when the cue lags the stimulus by a second (Kalogeropoulou et al., 2017). Indeed, a closer look at the individual data (Figure 3a, right column) suggests that some participants appeared to exhibit this early onset of FBA, whereas others did not.

To better understand this result, we split our sample of participants into two groups according to their overall cueing effect at 0-ms CSI (i.e., the difference in the average error between invalid and valid trials). Indeed, half of our participants showed an early onset of the cueing effects (FBA was already deployed at 0-ms CSI; Figure 6, right column) and half showed a late onset (FBA deployed at 150-ms CSI; Figure 6, left column). We speculate that early-onset participants might have used the precue in hindsight—after the stimulus (and the cue) had disappeared. Using this introspective retrocue may have helped retrieve the stimulus orientation from visual short-term memory, resulting in an advantage for the attended over the unattended stimulus. Using a similar paradigm in a previous study (Kalogeropoulou et al., 2017), we showed that retrocueing of FBA lowers the guess rate but does not increase the precision of orientation reports from visual short-term memory. Our data here are consistent with this finding: The effect of cueing on precision was more pronounced in the late-onset group than the early-onset group (Figure 6b), and only the early-onset group exhibited a significant effect of cueing on the guess rate (Figure 6c).

The significant differences in performance in fixation and saccade trials shed more light on the role of FBA in transsaccadic vision. Our data show a continuity of performance across saccades (Figure 3), regardless of the group (late- or early-onset; see Figure 6). Indeed, fully established cueing effects, observed long after cue onset (350-ms CSI), predict the postsaccadic effects (0-ms SSI) more precisely and more accurately than the early cueing effects (0-ms CSI) do (Figure 5). With their marked time course of FBA, the late-onset group allowed for the most rigorous test of the alternative hypotheses (Figure 1) and supported continuity in the deployment of FBA rather than redeployment of FBA after the saccade. These results are consistent with those of a recent study in the realm of spatial attention (Yao et al., 2016; see also Rolfs & Szinte, 2016) that used very brief stimuli to show attentional effects as early as 30 ms after saccade landing. The stimuli in our study had a longer presentation duration (150 ms). It could be argued that this duration might have been long enough to redeploy FBA while the stimulus was on the screen. We do not think this was the case, however, as stimulus durations were the same during fixation and after the saccade, yet performance right after the saccade differed systematically from performance right after cue onset. More specifically, the presence of a time course of FBA during fixation—that

was not observed following a saccade—allows us to reject the redeployment hypothesis in favor of transsaccadic continuity.

Our results speak to an intriguing question in active vision: Why is perception continuous (and visually guided action unimpaired) despite the large disruptions and displacements that saccades cause in the visual input? Previous studies have shown that spatial attention rapidly selects saccade targets before the onset of the movement (Castet et al., 2006; Deubel, 2008; Rolfs & Carrasco, 2012) and that feature information such as motion survives the saccade (Fallah & Reynolds, 2012). Due to the retinotopic organization of the visual-processing machinery, spatial attention requires an updating process that remaps the attentional landscape each time we execute a saccade (Cavanagh et al., 2010; Rolfs & Szinte, 2016), and this remapping of attention has received considerable empirical support (Jonikaitis et al., 2013; Puntiroli et al., 2015; Rolfs et al., 2011; Szinte et al., 2015). In contrast to that, FBA is independent of space, and exerts its effects broadly across the visual field (White & Carrasco, 2011). Its global nature and our finding that saccades do not disrupt its deployment make FBA an ideal candidate to sustain perceptual continuity across eye movements.

## Conclusion

FBA needs time to fully develop its effect on visual performance. For it to be a useful mechanism in active observers, therefore, its continuity across frequent eye movements appears critical. Indeed, we found that once FBA is deployed, saccades do not cause interference with this deployment and attention need not be redeployed upon saccade landing. This finding sheds more light on a nonspatial aspect of attentional selection that could act as a key player in transsaccadic perception.

*Keywords:* visual attention, feature-based attention, eye movements, visual short-term memory

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ZK and MR developed the study concept and the study design. ZK performed data collection, and performed data analysis and interpretation under the supervision of MR. ZK drafted the manuscript, and MR provided critical revisions. Both authors approved the final version of the manuscript for submission.

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## References

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*(6), 716–723.
- Baldauf, D., & Deubel, H. (2008). Properties of attentional selection during the preparation of sequential saccades. *Experimental Brain Research*, *184*(3), 411–425.
- Bays, P. M., Catalao, R. F. G., & Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of Vision*, *9*(10):7, 1–11, doi:10.1167/9.10.7. [PubMed] [Article]
- Bichot, N. P., Cave, K. R., & Pashler, H. (1999). Visual selection mediated by location: Feature-based selection of noncontiguous locations. *Perception & Psychophysics*, *61*(3), 403–423.
- Born, S., Ansorge, U., & Kerzel, D. (2012). Feature-based effects in the coupling between attention and saccades. *Journal of Vision*, *12*(11):27, 1–17, doi:10.1167/12.11.27. [PubMed] [Article]
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- Castet, E., Jeanjean, S., Montagnini, A., Laugier, D., & Masson, G. S. (2006). Dynamics of attentional deployment during saccadic programming. *Journal of Vision*, *6*(3):2, 196–212, doi:10.1167/6.3.2. [PubMed] [Article]
- Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, *14*(4), 147–153.
- Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers*, *34*(4), 613–617.
- Deubel, H. (2008). The time course of presaccadic attention shifts. *Psychological Research*, *72*(6), 630–640.
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837.
- Efron, B., & Tibshirani, R. J. (1993). *An Introduction to the bootstrap*. New York: Chapman and Hall/CRC.
- Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(18), 7192–7197.
- Eymond, C., Cavanagh, P., & Collins, T. (2016). Feature-based attention across saccades and immediate postsaccadic selection. *Attention, Perception, & Psychophysics*, *78*(5), 1293–1301.
- Fallah, M., & Reynolds, J. H. (2012). Contrast dependence of smooth pursuit eye movements following a saccade to superimposed targets. *PLoS ONE*, *7*(5), 1–9.
- Gersch, T. M., Kowler, E., & Doshier, B. (2004). Dynamic allocation of visual attention during the execution of sequences of saccades. *Vision Research*, *44*(12), 1469–1483.
- Godijn, R., & Theeuwes, J. (2003). Parallel allocation of attention prior to the execution of saccade sequences. *Journal of Experimental Psychology: Human Perception and Performance*, *29*(5), 882–896.
- Herrmann, K., Heeger, D. J., & Carrasco, M. (2012). Feature-based attention enhances performance by increasing response gain. *Vision Research*, *74*, 10–20.
- Jonikaitis, D., Szinte, M., Rolfs, M., & Cavanagh, P. (2013). Allocation of attention across saccades. *Journal of Neurophysiology*, *109*, 1425–1434.
- Jonikaitis, D., & Theeuwes, J. (2013). Dissociating oculomotor contributions to spatial and feature-based selection. *Journal of Neurophysiology*, *110*(7), 1525–1534.
- Kalogeropoulou, Z., Jagadeesh, A. V., Ohl, S., & Rolfs, M. (2017). Setting and changing feature priorities in Visual Short-Term Memory. *Psychonomic Bulletin & Review*, *24*, 453–458.
- Kowler, E., Anderson, E., Doshier, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*(13), 1897–1916.

- Liu, T., Stevens, S. T., & Carrasco, M. (2007). Comparing the time course and efficacy of spatial and feature-based attention. *Vision Research*, *47*(1), 108–113.
- Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision*, *7*(14):8, 1–16, doi:10.1167/7.14.8. [PubMed] [Article]
- Ohl, S., & Rolfs, M. (2017). Saccadic eye movements impose a natural bottleneck on visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *43*, 736–748.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442.
- Puntiroli, M., Kerzel, D., & Born, S. (2015). Perceptual enhancement prior to intended and involuntary saccades. *Journal of Vision*, *15*(4):2, 1–20, doi:10.1167/15.4.2. [PubMed] [Article]
- Rolfs, M. (2015). Attention in active vision: A perspective on perceptual continuity across saccades. *Perception*, *44*(8–9), 900–919.
- Rolfs, M., & Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. *The Journal of Neuroscience*, *32*(40), 13744–13752.
- Rolfs, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. *Nature Neuroscience*, *14*(2), 252–256.
- Rolfs, M., & Szinte, M. (2016). Remapping attention pointers: Linking physiology and behavior. *Trends in Cognitive Sciences*, *20*(6), 399–401.
- Saenz, M., Buracas, G. T., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience*, *5*(7), 631–632.
- Szinte, M., Carrasco, M., Cavanagh, P., & Rolfs, M. (2015). Attentional tradeoffs maintain the tracking of moving objects across saccades. *Journal of Neurophysiology*, *113*, 2220–2231.
- Szinte, M., Jonikaitis, D., Rolfs, M., Cavanagh, P., & Deubel, H. (2016). Pre-saccadic motion integration between current and future retinotopic locations of attended objects. *Journal of Neurophysiology*, *116*, 1592–1602.
- Treue, S., & Martínez Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, *399*(6736), 575–579.
- White, A. L., & Carrasco, M. (2011). Feature-based attention involuntarily and simultaneously improves visual performance across locations. *Journal of Vision*, *11*(6):15, 1–10, doi:10.1167/11.6.15. [PubMed] [Article]
- White, A. L., Rolfs, M., & Carrasco, M. (2013). Adaptive deployment of spatial and feature-based attention before saccades. *Vision Research*, *85*, 26–35.
- Yao, T., Ketkar, M., Treue, S., & Krishna, B. S. (2016). Visual attention is available at a task-relevant location rapidly after a saccade. *eLife*, *5*(e18009), 1–12.