Dissociating oculomotor contributions to spatial and feature-based selection

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Submitted 16 April 2013; accepted in final form 1 July 2013

Jonikaitis D, Theeuwes J. Dissociating oculomotor contributions to spatial and feature-based selection. J Neurophysiol 110: 1525–1534, 2013. First published July 3, 2013; doi:10.1152/jn.00275.2013.—Saccades not only deliver the high-resolution retinal image requisite for visual perception, but processing stages associated with saccade target selection affect visual perception even before the eye movement starts. These presaccadic effects are thought to arise from two visual selection mechanisms: spatial selection that enhances processing of the saccade target location and feature-based selection that enhances processing of the saccade target features. By measuring oculomotor performance and perceptual discrimination, we determined which selection mechanisms are associated with saccade preparation. We observed both feature-based and space-based selection during saccade preparation but found that feature-based selection was neither related to saccade initiation nor was it affected by simultaneously observed redistribution of spatial selection. We conclude that oculomotor selection biases visual selection only in a spatial, feature-unspecific manner.

Rapid eye movements, or saccades, direct our gaze to the parts of visual scene we wish to inspect in detail. However, there is more to a saccade than meets the eye, as processes associated with saccade preparation alter visual information processing even before the eye movement starts. In particular, visual selection is biased towards the saccade goal, as perceptual discrimination improves and perceived contrast increases at that location (Hoffman and Subramaniam 1995; Kowler et al. 1995; Deubel and Schneider 1996; Deubel 2008; Jonikaitis and Deubel 2011; Rolfs et al. 2011; Rolfs and Carrasco 2012). These effects are a consequence of saccade preparation, as activity in oculomotor brain structures increases the activity in visual areas representing saccade target location (Moore and Armstrong 2003; Armstrong et al. 2006; Ruff et al. 2006; Armstrong and Moore 2007; Noudoost and Moore 2011), which is accompanied by improved visual selection (Moore and Fallah 2001; Carello and Krauzlis 2004; Moore and Fallah 2004; Ruff et al. 2006). Modulation of visual processing is thought to aid saccade target selection (Moore 1999) by enhancing representations of stimuli to which saccades are planned.

There are two possible explanations of how saccade target selection modulates processing of the visual field. First, saccade target selection could generate feature-unspecific spatial bias (Fig. 1A, top). This hypothesis is based on the idea that signals from feature maps (e.g., luminance, orientation, color, and motion) and top-down signals are combined into a priority map that represents salient and task relevant regions and is used by the saccadic system (Itti and Koch 2000, 2001). Crucially, the priority map represents this information without access to the particular features that made the locations salient or relevant (Fecteau and Munoz 2006). Saccadic target selection relying on a priority map can therefore generate only feature-unspecific spatial biases that lead to spatial attention shifts.

Second, saccade target selection could generate feature-specific bias (Fig. 1A, bottom). This hypothesis is based on observations that the oculomotor system represents feature-matching signals (Bichot and Schall 1999; Egner et al. 2008; Ipata et al. 2009; Greenberg et al. 2010; Liu et al. 2011; Zhou and Desimone 2011) and that feature-based target selection in oculomotor structures precedes selection in earlier visual areas (Zhou and Desimone 2011). Even though these studies suggest such a link, none of them have directly investigated whether this feature-matching signal is related to oculomotor selection. Furthermore, behavioral studies reporting spatial effects of saccade target selection did not measure feature-based selection (Hoffman and Subramaniam 1995; Kowler et al. 1995; Deubel and Schneider 1996; Montagnini and Castet 2007; Deubel 2008; Jonikaitis and Deubel 2011; Rolfs et al. 2011), and the few studies that measured feature-based selection show conflicting results (Born et al. 2012; White et al. 2013).

In the current study, we systematically evaluated the two above alternative explanations. Specifically, two types of selection are expected to modulate perceptual performance in tasks measuring distribution of attentional processing differently. Spatial attention selects a limited number of locations, irrespective of object features (Müller and Rabbitt 1989; Nakayama and Mackeben 1989; Carrasco 2011), and is known to shift to the saccade target even if task requires to attend elsewhere (Kowler et al. 1995; Deubel and Schneider 1996; Deubel 2008). Therefore, one can expect competition between saccade target selection and spatial selection at nonsaccade locations. Feature-based attention (FBA) is assumed to enhance the feature-specific representations throughout the visual field, without an apparent limit on number of locations attended (Martinez-Trujillo and Treue 2004; Melcher et al. 2005; Maunsell and Treue 2006; Wegener et al. 2008; Liu and Mance 2011; White and Carrasco 2011). Therefore, one can measure FBA allocation to nonsaccade locations through the visual field. In two experiments, participants made saccadic eye movements while performing a perceptual discrimination task at different locations across the visual field. We systematically manipulated the role of spatial and feature-based selection. In experiment 1, we measured how space- and feature-guided saccade target selection affected perceptual discrimination at peripheral locations to which saccades were never made. In experiment 2, we quantified the relationship between saccade target selection and perceptual discrimination at the saccade location.
target location by examining differences between spatially and feature-guided saccade target selection.

**METHODS**

**Participants**

In experiment 1, 12 participants completed the Spatial-cue task, 16 completed the Color-cue task, and 9 completed the Combined-cue task. In experiment 2, 10 participants completed the Color-cue task, and 13 completed the Spatial-cue task. Participants' age was between 21 and 30 yr, vision was normal or corrected to normal, and except for the author (D. Jonikaitis) all were naive as to the purpose of the studies. The experiments were all conducted in accordance with the Declaration of Helsinki. Experiments were carried out in Allgemeine und Experimentelle Psychologie, Ludwig-Maximilians Universität München, Munich, Germany. Experiments were designed according to the ethical requirements specified by corresponding institution even though no institutional review board (or corresponding institution) ethics approval was needed for experiments that do not involve invasive methods.

**Setup**

Eye position was recorded with an SR Research EyeLink 1000 tower-mounted eye-tracker (sampling rate of 1,000 Hz), calibrated before each session and whenever necessary. Experiments were controlled by an Apple desktop computer and implemented in Matlab (MathWorks, Natick, MA) using Psychophysics and Eyelink toolboxes (Watson and Pelli 1983; Brainard 1997; Cornelissen et al. 2002). Stimuli were presented at a viewing distance of 70 cm on gamma-linearized 20-in. Sony GDM-F500R screen (1,024 × 768 pixels, vertical refresh rate of 120 Hz).
Procedure

In every task (with exception in the Combined-cue task), participants were asked to make a saccade while we measured perceptual discrimination performance for stimuli presented at different locations in space. We used perceptual discrimination task as a measure of attention allocation to different locations and stimuli (Deubel and Schneider 1996; Rolfs et al. 2011). In experiment 1, we measured attention allocation to peripheral locations while participants made leftward or rightward saccades. The direction of the saccades was cued using a spatial cue, a color cue, or by combining the color and the shape of the cue (see Fig. 1B). In experiment 2, we measured attention allocation to the saccade target while participants made leftward or rightward saccades. The direction of the saccades was cued using a color cue or a spatial cue.

Experiment 1: Spatial-cue task. In this task, we measured whether perceptual discrimination performance at two peripheral locations was affected by whether those locations match or did not match the saccade target color. Figure 1B shows stimulus configuration. Display is composed of a fixation target (black circle: 2.5 cd/m²; diameter: 0.75°) and two potential saccade targets (one green: 29 cd/m²; CIE Xyz 29.0, 0.30, 0.56; one blue circle: 28.5 cd/m²; CIE Xyz 28.4, 0.18, 0.13; presented at 7° to the left or the right of the fixation, diameter 0.75°) and two discrimination-task-related objects (presented 7° above and below the fixation, diameter 2°), all shown on a gray background (73 cd/m², CIE Xyz 75.7, 30.2, 31.8). Discrimination-task-related objects consisted of green and blue square frames containing vertical Gabor patches (frequency: 2.5 cycles-per-degree, 100% contrast, random phase on each presentation, SD of Gaussian window mask covering the Gabor: 0.8°) alternating every 25 ms with noise masks (each pixel gray value from Gaussian distribution with mean of 0.5, where 0 is black and 1 is white).

Each trial started with participants fixating on a fixation target (display duration from Gaussian distribution: 1,000 ms, SD of 300 ms). After the fixation period, a line (length: 0.4°) pointing to the left or to the right indicated the direction of the saccade (display duration: 600 ms, trial repeated at the end of the block if correct saccade was not detected). Between 150 ms before and 450 ms following the saccade-cue onset (time selected randomly), a peripheral probe, a tilted Gabor patch, was presented in the stream. No more vertical Gabor patches were presented after the probe, leaving noise masks alternating with blanks at both locations. At the end of each trial, participants reported the probe orientation (clockwise or counterclockwise from vertical). Participants completed a minimum of three 1-h sessions of the task.

If saccade planning results in an enhancement of processing of features matching saccade target object, we should observe perceptual discrimination improvement at the saccade target color-matching locations. Importantly, we measured FBA at two peripheral locations (upward or downward), to which no saccades had to be directed, in contrast to two studies that measured FBA at locations that were potential saccade targets, thus confounding discrimination benefits arising because of saccade target selection with potential FBA benefits (Gersch et al. 2009; Born et al. 2012).

Experiment 1: Color-cue task. In this task, we measured whether perceptual discrimination performance at two peripheral locations is affected by the locations that match or did not match the saccade target color. Participants made a saccade to a color-matching target (color randomly selected and instructed block-wise, color targets appeared after fixation period). Participants completed a minimum of four 1-h sessions of the task.

Experiment 1: Combined-cue task. In this task, we measured contributions of saccade planning to spatial attention and FBA effects by comparing discrimination performance in saccade and fixation conditions. Saccade target was defined by a combination of color and shape: green or blue, and square or circle (4 possible combinations, target selected randomly and instructed block-wise). Saccades were made if color and shape combination was present (50% of trials, saccade condition), fixation was kept if the combination was absent (50%, fixation condition). Participants completed a minimum of six 1-h sessions of the task.

Experiment 1: threshold procedure. The threshold procedures was completed before each session and task. Stimulus configuration was similar as in above tasks, except for the fixation position (at the center of the display, 7° left or 7° right of the fixation). One-hundred percent valid color cue presented after fixation period (frame around Gabor patch and mask stream changed color) indicated location of the probe (presented 100–200 ms after the cue onset). We used QUEST staircase cases (Watson and Pelli 1983) to adjust the Gabor patch tilt angle needed to reach 82% correct discrimination performance at the cued locations. Two interleaved staircases were run: one for the fixation at the display center (simulating presaccadic display, with probe eccentricity of 7°), and one for the fixation to the left or right of the display center (simulating postsaccadic display, with probe eccentricity of 9.9°). Those threshold values were used during the main task by presenting the appropriate probe tilt depending on whether the eye was at fixation or at the saccade target.

Experiment 2: Spatial-cue task and Color-cue tasks. Discrimination performance was measured at the saccade target location instead of peripheral locations. In both tasks, alternating Gabor patch/mask streams were presented at the saccade target location. Participants completed a minimum of four 1-h sessions of the task.

Experiment 2: threshold procedure. Same as in experiment 1, except that only central fixation was presented (thus stimulating only presaccadic stimulus eccentricity for experiment 2).

Data Analysis

We detected saccades offline using an algorithm based on eye velocity changes (Engbert and Kliegl 2003). Saccades were accepted if end-point and start-point error was <3°, and saccade latency was >100 ms and <500 ms. In experiment 1, we accepted 29,510 trials in the Color-cue task, 13,776 in the Spatial-cue task and 25,165 in the Combined-cue task. In experiment 2 we accepted 19,341 trials in the Color-cue task and 28,748 in the Spatial-cue task.

Probe discrimination performance was calculated for probes shown (using probe offset time) within specified time-bins and is expressed as the percentage of correct orientation discriminations for each time bin (chance level is 50%). Probes presented during the saccade were excluded. Statistical comparisons included repeated-measures ANOVAs and paired t-tests.

RESULTS

Experiment 1

In experiment 1 (Fig. 1B), we investigated whether saccade preparation affected spatial and feature-based selection throughout the visual field. In two versions of the experiment, we measured discrimination performance at two peripheral locations while saccades were directed either to targets selected on the basis of their locations (Spatial-cue task) or of their colors (Color-cue task). Discrimination performance served as a measure of spatial attention allocation at those locations (Müller and Rabbitt 1989; Nakayama and Mackeben 1989; Carrasco 2011). Discrimination performance at the saccade target color-matching location vs. the nonmatching location was used as a measure of feature-based attention (Melcher et al. 2005; Wegener et al. 2008; Liu and Mance 2011; White and Carrasco 2011).

Figure 2A shows temporal dynamics of discrimination performance in the Spatial-cue task. In this task we investigated whether spatially guided saccade preparation coactivates selec-
We observed that feature-guided saccade preparation is associated with an increase in feature-based selection. The FBA effect doubled from 13% after the saccade cue to 3.2% after the saccade cue (150 ms). This paradigm leads to two specific predictions. First, since spatial selection is biased towards saccade target during saccade preparation (Kowler et al. 1995; Deubel and Schneider 1996; Castet et al. 2006; Montagnini and Castet 2007; Deubel 2008), we should observe differences in spatial attention allocation at peripheral locations during saccade condition compared with the fixation condition. Second, if saccade preparation affects feature-specific selection, we should also observe FBA effect size differences during saccade condition compared with fixation condition.

Figure 3A shows the temporal dynamics of discrimination performance in the Combined-cue task. Two findings of note can be seen in this figure. First, discrimination performance at peripheral locations (regardless of target color) increased over time, and differed between fixation and saccade trials. Repeated-measures ANOVA showed that discrimination performance increased by 10.22% on August 27, 2017. http://jn.physiology.org/ Downloaded from

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**Fig. 2. Experiment 1.** A: probe discrimination performance in the Spatial-cue task. Legend depicts color-matching (red) and nonmatching (black) probe locations; saccade is depicted as a large arrow. Error bars represent SE. Lines below the graph represent cumulative saccade onset probability. B: feature-based attention effect (i.e., discrimination performance for the color-matching minus color-nonmatching location) for probes presented [-150 - 0] or [200 - 350] ms in the Spatial-cue task. Statistical comparisons (repeated measures t-test): *significant difference; ns, absence of difference. C and D: Color-cue task, same convention as A and B.
similar magnitude. To further understand the effects of spatial and feature-based selection, we considered them separately for probes presented before saccade cue and after the saccade cue.

Figure 3B shows the spatial attention effects for saccade and fixation conditions. Before the saccade cue appeared (−150–0 ms), discrimination performance at both peripheral locations was comparable for saccade and fixation trials \( t(8) = 0.45, P = 0.65 \). During the saccade target selection interval (200–350 ms, only trials with presaccadic probe presentation) discrimination performance was worse during saccade than fixation trials \( t(8) = 3.64, P < 0.01 \). This analysis shows that saccade preparation redistributed spatial selection through the visual field, as spatial attention was withdrawn from nontarget locations during saccade preparation (Kowler et al. 1995; Deubel and Schneider 1996; Deubel 2008). Figure 3C shows FBA effect for probes presented between −150–0 ms and fixation conditions.

Experiment 2

While experiment 1 found no effects of saccade preparation on FBA throughout the visual field, in experiment 2 we evaluated the relationship between saccade target selection and spatial and feature-based selection at the saccade target location (Fig. 1C). Figure 4 shows probe discrimination performance at saccade target and nontarget locations. Figure 4A shows temporal dynamics of probe discrimination performance in the Spatial-cue task. Discrimination performance increased at both probe locations over time, but much more so at the saccade target location compared with nontarget location. Repeated-measures ANOVA showed main effect of probe presentation time \( F(5,60) = 35.94, P < 0.001 \), main effect of probe location \( F(1,12) = 28.56, P < 0.001 \), and interaction between the two factors \( F(5,60) = 20.43, P < 0.001 \). These
results therefore suggest that saccade target selection resulted in clear spatial attention shift toward that location. Figure 4B shows similar results for the Color-cue task. Repeated-measures ANOVA showed main effect of probe presentation time \( F(5,40) = 23.94, P < 0.001 \), main effect of probe location \( F(1,8) = 103.04, P < 0.001 \), and interaction between the two factors \( F(5,40) = 19.20, P < 0.001 \). These results show that similarly as in the Spatial-cue task attention is shifted toward the saccade target.

To determine the relationship between saccade preparation and spatial and feature-based selection, we evaluated the temporal relationship between saccade initiation and visual selection. We previously reported that spatial selection is coupled to saccade planning: the shorter the saccade latency, the earlier the attention shifts to the saccade goal (Jonikaitis and Deubel 2011). Figure 5A shows discrimination performance at the saccade target location for short and long (below and above median latency for each participant) saccade latencies in the Spatial-cue task. Discrimination performance differed for short latency saccades compared with long latency saccades. Figure 5B shows that discrimination performance for probes presented before the saccade cue \((-150–0 \text{ ms})\) is comparable for trials with short and long latency saccades \( t(12) = 1.01, P = 0.33 \). On the other hand, discrimination performance for probes presented during the saccade preparation \( (50–200 \text{ ms after the cue}) \) was better for short compared with long latency saccade trials \( t(12) = 3.45, P < 0.01 \). Further comparisons of individual participant data (Fig. 5C, circles) suggest that this true for majority of participants, with most of the data points above the unity line when comparing short vs. long saccade latency trial performance for probes presented 50–200 ms after the saccade cue.

Better discrimination performance for probes presented after the saccade cue for short latency saccade trials can be ex-
plained either by an improvement in attentional selection in short saccade latency trials (representing an upward shift in performance function) or by earlier saccade target selection in short saccade latency trials (representing a leftward shift in performance function). We addressed this question by reanalyzing the data with respect to the saccade onset. If our results can be explained by earlier saccade target selection in short latency trials, then locking discrimination performance relative to saccade onset should remove differences between short and long latency trials. Figure 5D shows that discrimination performance for short and long latency saccades does not differ as a function of saccade-cue onset time and only differs as a function of saccade onset time (Fig. 5A). Repeated-measures ANOVA showed main effect of probe presentation time \( [F(3,36) = 54.29, P < 0.001] \), no effect of saccade-cue onset time \( [F(1,12) = 0.002, P = 0.96] \), and no interaction between the two factors \( [F(3,36) = 0.87, P = 0.46] \). In other words, spatial selection varied as a function of the saccade latency, indicating close coupling between saccade initiation and attentional selection.

Temporal coupling between spatial selection and saccade initiation is also supported by reanalysis of previously published data from our lab. Figure 5C, squares and triangles, presents data from three additional experiments utilizing spatial cues (Jonikaitis and Deubel 2011; Rolfs et al. 2011). In all tasks, we observed similar results: spatial attention shifted to the saccade target earlier if saccade latencies were short (all \( P < 0.05 \)) and discrimination performance for short and long latency saccades was comparable before saccade onset (all \( P > 0.05 \)). Combined these results show an association between spatial selection at the saccade target location and saccade latencies.

Notably, we observed different pattern of results in the Color-cue task (Fig. 5, E–H). Figure 5E shows discrimination performance at the saccade target location for short and long saccade latencies in the Color-cue task. Discrimination performance at the saccade target location was comparable for both latency saccades. Figure 5F shows that discrimination performance cannot be distinguished for trials with short and long latency saccades neither for probes presented before the saccade cue \([-150–0 \text{ ms before the cue}, t(9) = 0.89, P = 0.39]\) nor after the saccade cue \([-150–0 \text{ ms before the cue}, t(9) = 0.05, P = 0.95]\). Further comparisons of individual participant data confirm this result (Fig. 5G, circles), as individual participant data are scattered evenly above and below the unity line when comparing short vs. long latency trials performance for probes presented 50–200 ms after the saccade cue. Last, Fig. 5H shows that discrimination performance varied as a function of saccade-cue presentation time and suggests that discrimination performance at the saccade target location did not covary with saccade latencies. This finding further corroborates the independence between saccade target and feature-based selection.

Finally, we reasoned that if the saccades start faster in the color-guided saccade task in experiment 1 (i.e., saccadic latency is short), then FBA might shift earlier to peripheral color-matching locations. However, we neither observed any such effect in the Color-cue task (Fig. 5G, squares) nor in the Combined-cue task (Fig. 5G, triangles). Therefore, saccade target selection was not associated with temporal dynamics of FBA in any of three tasks participants completed.

**DISCUSSION**

In the current study, we evaluated whether saccade target selection biases visual selection in a spatial, feature-unspecific, or a feature-specific manner. We found strong evidence for the first and none for the second alternative. In experiment 1, we observed that spatial (Spatial-cue task) and feature-based attention (Color-cue task) modulated discrimination performance at locations to which saccades were never made. However, when we compared a saccade condition to a fixation condition (Combined-cue task), we observed that saccade preparation affected distribution of spatial processing irrespective of the relevance of the feature. This suggests that saccade target selection biases the perceptual system in a feature-unspecific manner. In experiment 2, we observed that both spatially (Spatial-cue task) and feature (Color-cue task)-guided saccades result in similar discrimination improvement at the saccade target location. However, latencies of the saccades were related to the discrimination performance time course only in the Spatial-cue task (also the case for three other data sets from previously published work; Jonikaitis and Deubel 2011; Rolfs et al. 2011), but not in the Color-cue task (also true for 2 other data sets from experiment 1). This last point indicates separation between saccade target selection and feature-based selection.

We observed feature-based selection in the visual field during feature-guided saccade tasks. Feature-based selection during saccade planning has been observed in a few behavioral studies (Gersch et al. 2009; Born et al. 2012); however, those studies did not measure whether saccade preparation evokes FBA shifts. Further, neurophysiological studies have observed feature-based selection during saccade preparation (Bichot et al. 2005; Zhou and Desimone 2011) and have suggested that it could originate in areas assumed to represent saccade target selection such as the frontal-eye-fields (FEF) or the lateral intraparietal sulcus (Egner et al. 2008; Greenberg et al. 2010; Liu et al. 2011; Zhou and Desimone 2011). Our findings clarify those results, in showing that even though feature-based selectivity is apparent during saccade planning, saccade planning is unlikely to directly affect feature-specific selectivity.

We based this conclusion on the following observations. First, in the Spatial-cue task of experiment 1, saccade target selection did not lead to concomitant feature-specific activation, ruling out automatic coupling between these two processes. Second, in the Combined-cue task of experiment 1, saccade target selection biased spatial selection irrespective of object features, thus showing different effects of saccade planning on spatial and feature-based selection. Third, in the Color-cue tasks of both experiments 1 and 2, shorter saccade latencies were not associated with earlier selectivity at the feature-matching locations, thereby ruling out the possibility that saccade target selection could directly bias feature-specific activation. Combined these findings suggest that even though feature-specific selection is clearly observed during saccade preparation, saccade target selection alters spatial, but not feature-specific, processing.

Our results are consistent with the notion that there are two selection mechanisms: a spatial one that is closely related to saccade target selection and a feature-based one that is not driven by the oculomotor selection. Spatial selection mechanism could be described as a priority map, which represents top-down attentional selection and bottom-up salience at each location in space (Itti and Koch 2000; Thompson and Bichot 2005; Fecteau and Munoz 2006; Bisley and Goldberg 2010),
calculated as a summed spatial signal across all feature space, without feedback to feature-specific signals. In this view, saccade target selection can bias only spatial selection, irrespective of feature specific values. Such priority maps have been demonstrated in psychophysical studies (Donk and van Zoest 2008; Zehetleitner et al. 2011), have been formalized in computational models (Iitti and Koch 2000), and have been suggested to be located in saccade planning areas such as FEF, lateral intraparietal sulcus, or superior colliculus (SC) (Thompson and Bichot 2005; Fecteau and Munoz 2006; Bisley and Goldberg 2010). In parallel to spatial selection, feature-based selection could assign higher weights to task-relevant features, resulting in enhanced representations at all feature-matching locations. This selection mechanism could still be used to guide saccades in a spatial manner, as only feature-matching locations would provide higher weighted signal and nonmatching locations would be tagged with lower weights. If this interpretation is correct, then the origin of the feature-based visual biases remain unknown, even though few studies have observed independent spatial and feature-based attentional modulations using behavioral and neurophysiological paradigms (Treue and Martinez-Trujillo 1999; Hayden and Gallant 2005, 2009; Cohen and Maunsell 2011).

Neurophysiological findings are inconclusive concerning the contributions of oculomotor structures to feature-based selection. Those studies that suggest such a contribution have not demonstrated direct causality, as has been demonstrated for spatial attention using transcranial magnetic stimulation, inactivation, or microstimulation (Moore and Fallah 2001; Ruff et al. 2006; van Ettinger-Veenstra et al. 2009; Lovejoy and Krauzlis 2010; Zenon and Krauzlis 2012). In addition, the relationship between feature-based selection and saccade target selection within FEF, intraparietal sulcus, or SC remains unclear, as few studies distinguish visual feature selection from saccade target selection (Gottlieb et al. 1998; Sato et al. 2001; Shadlen and Newsome 2001; Sato and Schall 2003; Juan et al. 2004). Indeed, it has been shown that even in experimental situations when object features/identity are task relevant, FEF neurons seem to robustly represent spatial selection signals (Monosov et al. 2010, 2011; Clark et al. 2012).

However, even though oculomotor structures have been demonstrated to modulate spatial selection, the relationship between spatial selection and saccade preparation is less direct than suggested by models proposing direct equivalence between two (Rizzolatti et al. 1987; Sheliga et al. 1997). Separate neural populations within FEF mediate visual target selection and saccade preparation (Sato and Schall 2003; Thompson et al. 2005; Schafer and Moore 2011; Gregoriou et al. 2012), effectively dissociating spatial attention and saccade preparation. Further, as distinct neural populations within FEF are interconnected with visual cortex and with the SC, areas that are considered to be recipients of visual selection and saccade preparation signals, respectively (Pouget et al. 2009; Gregoriou et al. 2012), it is visual selection cells that likely mediate spatial selection via connections to visual processing areas (Gregoriou et al. 2012). However, as there is a close behavioral association between spatial selection and saccade preparation (Kowler et al. 1995; Deubel and Schneider 1996; Baldauf et al. 2006; Jonikaitis and Deubel 2011), oculomotor structures might be best regarded as a functional network underlying spatial selection and saccade preparation (Awh et al. 2006), even though dissociable visual and saccade preparation signals can be observed within that network. How feature-based selection interacts with this network underlying spatial selection and saccade preparation still remains to be defined, even though our findings suggest stronger dissociation between feature-based selection and saccade preparation than between spatial selection and saccade preparation.

Dissociating two separate mechanisms for spatial saccade target selection and feature-specific biases might offer behavioral advantages. In foraging situations, which require the selection of as many task-relevant objects as possible, information about task-relevant features with every intervening eye movement could simply be lost due to spatial bias induced by the saccade planning. This is especially evident in situations where perceptual discrimination performance at nonsaccade locations decreases during saccade preparation and is associated with impoverished moving stimulus tracking (Jonikaitis et al. 2009) or memory (Bays and Husain 2008) at attended locations after the saccade. Limited interactions between saccade target selection and feature-based selection, on the other hand, could leave unimpaired selectivity for task relevant features, even in the case of intervening eye movements. In this view, dissociation between saccade planning and feature-based selection offers an adaptive advantage and supports the ability to react to constantly changing visual world despite intervening eye movements.

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