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Saccade Preparation Reshapes Sensory Tuning

Highlights

- Target detection improves at the saccade landing position just before saccade onset
- Reverse correlation reveals concurrent changes in feature information processing
- High spatial frequency is enhanced, and orientation tuning is narrowed
- These modulations result in a finer representation of the saccade target

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In Brief

Li et al. show that preparing a saccadic eye movement influences the representation of visual features: just before the eyes move, high spatial frequency information is enhanced, and orientation tuning is narrowed for the saccade target. These findings reveal a finer representation of the saccade target mediated by reshaping feature selectivity.



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Saccade Preparation Reshapes Sensory Tuning

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SUMMARY

Human observers make large rapid eye movementssaccades-to bring behaviorally relevant information into the fovea, where spatial resolution is high. In some visual tasks [1-4], performance at the location of a saccade target improves before the eyes move. Although these findings provide evidence that extraretinal signals evoked by saccades can enhance visual perception, it remains unknown whether and how presaccadic modulations change the processing of feature information and thus modulate visual representations. To answer this question, one must go beyond the use of methods that only probe performance accuracy (d') in different tasks. Here, using a psychophysical reverse correlation approach [5-8], we investigated how saccade preparation influences the processing of orientation and spatial frequencytwo building blocks of early vision. We found that saccade preparation selectively enhanced the gain of high spatial frequency information and narrowed orientation tuning at the upcoming saccade landing position. These modulations were time locked to saccade onset, peaking right before the eyes moved (-50-0 ms). Moreover, merely deploying covert attention within the same temporal interval without preparing a saccade did not alter performance. The observed presaccadic tuning changes may correspond to the presaccadic enhancement [9-11] and receptive field shifts reported in neurophysiological studies [12–14]. Saccade preparation may support transaccadic integration by reshaping the representation of the saccade target to be more fovea-like just before the eyes move. The presaccadic modulations on spatial frequency and orientation processing illustrate a strong perception-action coupling by revealing that the visual system dynamically reshapes feature selectivity contingent upon eye movements.

RESULTS

Humans and primates constantly make large rapid eye movements, saccades, so that behaviorally relevant objects can be positioned at the fovea where acuity is greatest. Reverse correlation enables experimenters to quantify the contribution of different features to performance in perceptual tasks [5-8]. In the present study, we used reverse correlation to assess how saccade preparation affects the way the visual system assigns weights to different spatial frequency (SF) and orientation contents to reach a perceptual judgment (the weights constitute two-dimensional sensitivity kernels). We used a simple detection task of a vertical Gabor target to obtain sensitivity kernels as an approximation to the feature detectors in early stages of visual processing [15]. Observers detected a vertical target embedded in random noise presented at 10° either left or right of fixation (Figures 1A and 1B). To estimate sensitivity kernels, we correlated the behavioral response with the fluctuations of the energy of different SF and orientation components in the random noise. There were two conditions: in the saccade condition, each trial started with a fixation period followed by a saccadic cue presented at fixation. After a short stimulus onset asynchrony (SOA; between cue onset and stimulus onset), the test stimulus was presented at the cued location. Observers were instructed to saccade to the cued location as soon as the cue appeared. In the neutral condition, a neutral cue was presented at fixation informing observers to maintain fixation. The experiment was conducted with the written consent of each observer, and the experimental protocols were approved by the University Committee on Activities involving Human Subjects at New York University.

For the saccade condition, we analyzed observers' performance time locked to saccade onset in each trial. Consistent with previous studies [1–4], we found that observers' performance (*d'*) increased as the test stimuli appeared closer to the saccade onset (Figure 2A), becoming significantly better than the neutral condition within the -50-0 ms period just before saccade onset (t₇ = 4.67, p < 0.05, two-tailed paired t test with Bonferroni correction for the number of time bins; similar results were obtained with a sliding temporal window; Figure S2C).

One might wonder whether such improvement could merely reflect covert endogenous (voluntary) shifts of attention, without the requirement of saccade preparation. Even though it takes \sim 300 ms to deploy endogenous (voluntary) covert attention to a peripheral location ([16] for review see [17])—longer than the longest SOA used here (Figures 1A and 2A)—we ruled out this possibility in a control experiment by measuring performance in a covert attention condition. When the test stimulus location was cued but observers had to maintain fixation, d' did not increase (Figure 2B). A direct comparison between the saccade and the covert attention conditions revealed that the d' presaccadic enhancement (–50 to 0 ms time window)

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Figure 1. Experimental Procedure and Stimulus

(A) Experimental procedure. Each trial started with a 300-ms fixation period followed by the cue presented at the fixation. In the saccade condition, the cue pointed toward the aperture (10° to the left or right of fixation) where the test stimulus would be presented in that trial. In the neutral condition, the cue pointed toward both locations. After a variable delay (SOA uniformly sampled from 12 to 224 ms), the test stimulus (35 ms in duration) was presented at one of the apertures. Observers were instructed to saccade to the cued aperture as fast as possible in the saccade condition and to maintain their fixation at the center throughout each trial in the neutral condition. Observers reported whether the target was present or absent.

(B) Stimulus. In half of the trials, only the noise was presented; in the other half, the target was presented with noise. The test stimulus was the target embedded in random noise. The noise was filtered white noise, and the target was a vertical Gabor with a randomly chosen phase.

observed during saccade preparation significantly differed from covert spatial attention ($t_7 = 3.03$, p < 0.05). In addition, performance in the neutral condition was consistent across the different SOAs used in our study (Figure S2D). Altogether, these results confirmed that saccade preparation is required for performance to improve within such a short time window.

We then extracted the noise image from each trial and filtered each noise image with an array of Gabor filters selective for different SFs and orientations, approximating the feature detectors in early visual cortex [15]. Thus, we transformed the noise from luminance intensity into the energy of different SF and orientation components. The 2D (SF and orientation) sensitivity kernels were obtained by correlating the energy fluctuation of each component and behavioral responses (see Supplemental Experimental Procedures). We computed two sensitivity kernels: the neutral kernel and the presaccadic kernel (Figures 3A and 3B). The presaccadic interval. Each pixel in the kernels represented the sensitivity to a specific SF-orientation component (i.e., how strongly the noise of that component influenced observers' perceptual judgments).

Both the neutral and presaccadic kernels had a peak centered at the target orientation. By subtracting the neutral kernel from the presaccadic kernel, we found that saccade preparation significantly enhanced sensitivity to higher-SF information



(Test stimulus offset minus saccade onset)



Figure 2. Presaccadic Enhancement

(A) Top: observers' performance, indexed by d'. For the saccade condition, the d' was plotted as a function of the time of test stimulus offset relative to saccade onset. The error bars represent ±1 SEM. The neutral baseline was the d' computed from all the trials from the neutral condition, and the blue shading represents ±1 SEM. Bottom: the median of SOA (temporal interval between cue onset and test stimulus onset) distribution of each time bin. The error bars represent ±1 SEM. The dark background represents the trials in which the saccade onset occurred before the offset of the test stimulus.

(B) Covert attention did not improve performance. In the covert attention condition, the 100% valid cue was presented, just like in the saccade condition, but observers had to maintain fixation. Because there was no saccade onset time in this condition, we simulated five time bins corresponding to the five time bins in Figure 2A. We aimed to have the five data points here with the same SOA distribution as the corresponding data points in Figure 2A. We extracted the SOA distribution for each data point in Figure 1A and used the distribution as the constraint to sample the trials from the covert attention condition. For each observer, we computed one d' for each time bin by averaging over 1,000 resampled d'. The error bars denote ± 1 SEM.

See also Figures S1 and S2.



Figure 3. Saccade Preparation Modulates Sensitivity Kernel

(A and B) Group-averaged presaccadic (-50-0 ms from saccade onset) and neutral sensitivity kernels. Each pixel in the kernels is the beta weight estimated from a general linear model, indicating the degree to which the noise at each SF and orientation component correlated with the behavioral judgments. SF is evenly sampled and plotted in log scale.

(C) The difference kernel computed by subtracting the neutral kernel from the presaccadic kernel. The contours in the difference kernel denote the clusters of the components that showed a significant difference between the presaccadic and neutral kernels.

(D) Correlation between the original kernel and reconstructed kernels plotted for each observer. A correlation close to 1 represents high separability between SF and orientation (see Supplemental Experimental Procedures).

around the target orientation (t₇ = 12.88, p < 0.0001, cluster analysis; Figure 3C), increasing the influence of relevant (on-tuned) orientations on behavioral responses. Along with the enhancement of the on-tuned orientation, saccade preparation suppressed the sensitivity of off-tuned orientations (t₇ = -4.88, p < 0.005, cluster analysis), reducing the influence of irrelevant orientations on behavioral responses during saccade preparation. These results revealed that the modulation driven by saccade preparation was not uniform across the feature space. Specifically, the sensitivity change mainly occurred at a higher SF range than the target's SF content, and the orientation sensitivity was either enhanced (vertical) or suppressed (off-vertical), to benefit the detection of the vertical target.

To characterize how these presaccadic changes in visual sensitivity influenced SF and orientation selectivity, we projected the 2D kernels into sensory tuning functions. We first tested whether SF and orientation were two separable dimensions (i.e., whether the shape of orientation tuning was invariant across SF channels and vice versa). By marginal reconstruction [15] (see Supplemental Experimental Procedures and Figure S3), we found a high correlation between the original kernel and the kernel reconstructed by the multiplication of one SF tuning function and one orientation tuning function (Figure 3D), indicating that these two dimensions were separable for each observer. These results, consistent with previous findings in primary visual cortex (V1) [15], justified the extraction of the tuning functions from the 2D kernel. We let each point on the SF tuning function represent the gain of the orientation tuning at each SF and estimated the overall orientation tuning function by averaging the sensitivity of each orientation across SFs (see Supplemental Experimental Procedures and Figure S3). We fit the SF tuning functions using a raised Gaussian and found that saccade preparation shifted the peak sensitivity toward higher SF (Figure 4A), resulting in a finer representation of the signal. This shift was present for each observer and was significant for the individual parameter fits ($t_7 = 5.52$, p < 0.001, two-tailed paired t test; Figure 4B). We investigated the source of the SF tuning shift by testing the gain change on SF channels and confirmed that the shift was due to the gain increment at higher SF ($t_7 = 4.89$, p < 0.005, cluster analysis; shaded area in Figure 4A). This effect also led to a gain increment of the presaccadic orientation tuning functions (t₇ = 2.69, p < 0.05, two-tailed paired t test; Figure 4D). Moreover, orientation tuning width (SD of the best-fit Gaussians) was narrower for presaccadic than neutral trials, resulting in a more selective perceptual representation of the target orientation (Figure 4D). Narrower tuning was present for each (but one) observer and was significant for the individual parameter fits (t₇ = 3.67, p < 0.01, two-tailed paired t test; Figure 4E). This narrowing of tuning width resulted from a combination of both an enhancement of target orientation and a suppression of flanking orientations (clusters outlined in Figure 3C).

To ensure that the observed change of feature selectivity-SF shift and orientation tuning narrowing-was due to saccade preparation, we tested whether these effects were time locked to saccade onset. The number of trials in the presaccadic intervals changed drastically in the early time windows (Figure S1B), so when the trials were divided into equal time bins as in Figure 2A, the number of trials in the earliest time window did not allow for reverse correlation analysis in some observers (e.g., \leq 100 trials [8]). Therefore, for each observer, we sorted all the presaccadic trials into three time bins with equal number of trials and fitted the parameters for each bin. Then, we performed a regression analysis to quantify the temporal trend of the shifts in SF peak and orientation tuning width. The statistical test was based on a null distribution of the slope values, generated by randomly permuting the temporal order of the fitted tuning parameters (see Supplemental Experimental Procedures). We found that the peak SF shifted toward higher values (p < 0.05, permutation test; Figure 4C) and the orientation-tuning width became narrower (p < 0.01, permutation test; Figure 4F) as a function of time relative to saccade onset, providing further evidence that the modulations of sensory tuning were triggered by saccade preparation.

DISCUSSION

Our findings demonstrated a strong coupling between visual representation and motor output: saccade preparation not only

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Figure 4. Saccade Preparation Reshapes Sensory Tuning

(A) Group-averaged SF tuning functions (left panel). The data points are plotted with best-fit raised Gaussians. Error bars denote ±1 SEM. The vertical lines represent the peak frequency (the SF where the fitted function reached its peak). The dashed line represents the target Gabor. The orange shaded area represents the cluster of SF channels that showed a significant difference between the two conditions.

(B) The peak frequency of the presaccadic interval was plotted against the peak frequency of the neutral condition. The dark green data point and error bars represent group mean and ±1 SEM. The light data points represent individual parameter fits.

(C) The peak frequency of spatial frequency tuning of three presaccadic time bins (with equal numbers of trials). The data points are the means of individual parameters, and the error bars denote ±1 SEM. The horizontal position of each data point is determined by the representative time mark of each time bin averaged across observers (see Supplemental Experimental Procedures).

(D) Group-averaged orientation tuning functions (left panel). The data points are plotted with the best-fit Gaussians. Error bars denote ± 1 SEM. The three horizontal bars at the bottom denote the fitted tuning widths (± 1 σ ; the dashed line denotes the width of the target Gabor).

(E) The presaccadic tuning width was plotted against the neutral tuning width. Each data point corresponds to one observer. The dark data point and error bars represent group mean and ±1 SEM. The light data points represent individual parameter fits.

(F) The width of orientation tuning of three presaccadic time bins (with equal numbers of trials). The data points are the means of individual parameters, and the error bars denote ±1 SEM. The horizontal position of each data point is determined by the representative time mark of each time bin averaged across observers (see Supplemental Experimental Procedures).

See also Figures S1 and S3.

enhanced visual sensitivity but reshaped sensory tuning by enhancing the gain of high SF information and narrowing the width of orientation tuning. These modulations are automatic processes driven by extra-retinal preparatory signals related to eye movements and not due to mere covert attention (Figure 2B). Though powerful in its ability to characterize sensory tuning functions, reverse correlation cannot fully pinpoint the specific processing stage(s) for the observed modulations. Modulations in feature selectivity could be due to changes in feature detectors at the encoding stage [7, 8, 18], in the weighting function at the decoding stage, or both [19]. Neurophysiological studies have found that saccade preparation can influence neural responses at multiple stages of processing. For instance, neurons in saccade-related areas such as the superior colliculus and frontal eye fields (FEF) [20, 21] or visual cortical areas V4 [9, 10] and V1 [11] show enhanced responses when a saccade is directed toward the neuron's classical receptive field (cRF; mapped out under steady fixation).

The presaccadic tuning modulations revealed by our study may relate to the shift of receptive fields reported in neurophysiological studies. Two types of presaccadic receptive field shifts have been reported: predictive remapping [12, 14, 22-24] and convergent receptive field shifts [13, 14, 25]. According to both accounts, in our study, the test stimulus in the neutral condition was only processed by the neurons responding to the periphery, but in the presaccadic interval, the test stimulus was processed by a larger group of neurons including those with cRFs selective for more foveal locations. Thus, the contribution of these neurons, sensitive to higher SF, could be responsible for the increased sensitivity to higher SF information observed during saccade preparation. Similarly, these receptive field shifts may support the narrower orientation tuning width we also observed in the saccade condition. Orientation tuning width varies greatly across individual neurons in the visual cortex [26, 27], and the proportion of orientation-tuned neurons is higher in foveal than peripheral regions [28]. The recruitment of a larger neural population with saccade preparation might allow the target to be encoded by a larger population of filters, including those neurons closer to the fovea with a narrower orientation tuning, resulting in a finer representation of the target right before saccade onset.

The visual filters in V1 impose an early constraint on the sensory tuning we measured. Presaccadic receptive field shifts are less pronounced in V1 [24, 29] than in V4 [14, 25], parietal cortex, and FEF [12, 13, 22, 23]. Thus, whether receptive field shifts in V1 could contribute to the presaccadic modulations we observed remains unsettled. Alternatively, the enhanced firing rate at early visual stages [9–11] could already facilitate the encoding or decoding of feature information and result in the tuning modulations we observed. This account does not require a receptive field shift of early visual filters and is consistent with a study showing that the presaccadic enhancement of neural responses in early visual cortex improves discrimination performance of orientation information [30].

Although the presaccadic condition substantially increased the SF tuning peak (by 18%; Figure 4A) and narrowed the orientation tuning width (by 20%; Figure 4D) relative to the neutral condition, these are modest changes when considering the range of SF and orientation content the visual system analyzes. Nevertheless, these tuning modulations were beneficial for the performance as the group-averaged SF and orientation tuning were better aligned with the actual target's SF and orientation width in the presaccadic interval. Given that the gain enhancement we found was consistent (or even more pronounced) at the highest SF tested, we hypothesize that if the target signal contained higher SF, the presaccadic modulation could extend to higher SF. Additionally, we suggest that presaccadic modulations in low-level features revealed in the present and previous studies [1-4] can account for the presaccadic enhancement reported on higher-level object images (e.g., faces [31]).

Presaccadic enhancement has often been considered to be synonymous with a presaccadic attention shift to the saccade target [1, 2]. However, the effects of saccade preparation and covert endogenous spatial attention on performance have been previously dissociated [3, 4], consistent with our study. We found that endogenous attention had no effect within the time window in which significant presaccadic enhancement was observed (Figure 2B), indicating that presaccadic attention can develop more rapidly than endogenous attention [3]. In addition, the tuning modulations we found differ from those observed with endogenous attention. Whereas in the present study we did not characterize the tuning modulation induced by endogenous attention, convergent evidence indicates that it enhances the gain without affecting orientation-tuning or motion-direction-tuning width [7, 18, 32, 33]. Gain enhancement of high SF only emerges when a peripheral, exogenous cue is presented near the target location [34, 35], not when a central, endogenous cue (like ours) is used [36]. These results are consistent with the findings that although the neural correlates of saccade preparation and covert attention share similarities and involve overlapping neural structures, the two phenomena are neurophysiologically distinct [37, 38].

The present study focused on presaccadic modulations at the target location, but saccades influence many other aspects of visual processing (for a review, see [39]). For example, the detection of motion and low SF (<0.5 cpd) information is impaired during saccade execution [40]. The localization of visual objects is compressed toward the saccade target [41], and the spatial precision of stimuli presented distant from the saccade target worsens [42] before saccade onset. Neurophysiological and modeling studies [13, 25] have proposed that the compression of visual space toward the saccade target could be due to the enhanced neural responses at that location. This neural enhancement at the saccade target location seems to lead to many presaccadic perceptual changes, including the ones revealed in the present study.

Saccades induce rapid changes of the retinal images, and how the visual system maintains a stable percept across eye movements has intrigued neuroscientists for decades [43, 44]. Human observers can maintain a stable percept of a saccade target by integrating its presaccadic (in the periphery) and postsaccadic (at the fovea) representations of both SF [45] and orientation [46, 47]. The tuning modulations we found suggest that saccade preparation modifies the representation of the saccade target to be more fovea-like-i.e., higher resolution and finer orientation tuning-just before saccade onset. Perceptual cues are integrated mostly when observers interpret them to arise from the same object [46], and if the presaccadic and postsaccadic images are very different in their SF contents, integration does not occur [48]. Thus, the presaccadic changes of SF and orientation representations reported here may facilitate the integration of the presaccadic and postsaccadic images by reducing the difference between the two (also see discussion in [49]).

To conclude, our results demonstrate that saccade preparation modulates feature representations by selectively enhancing high SF information and sharpening orientation tuning just before we move our eyes. These findings reveal how eye movements reshape feature processing at the site of a saccade target and could represent underlying mechanisms of presaccadic enhancement [1–4] and perceptual stability [43, 45–47] reported in the literature, which illustrate functional benefits of the tight coupling between perception and movements.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and three figures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.04.028.

AUTHOR CONTRIBUTIONS

H.-H.L., A.B., and M.C. conceived and designed the experiments. H.-H.L. performed the experiments and analyzed the data. H.-H.L., A.B., and M.C. wrote the paper.

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Supplemental Information

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Figure S1. Distribution of saccade-related parameters. Related to Figure 2 and Figure 4. (A) Stacked density plots of saccade latency relative to the cue onset for eight

observers. The data points at the top are the means and SDs for individual observers. (B) Density plot of test-stimulus offset time relative to saccade onset. The dashed lines represent the boundaries of 50-ms time bins. The bins from -150 to 100 ms correspond to the time bins in Fig 1. (C) Density plot of saccade landing sites relative to saccade target. The ovals are centered at the averaged saccade landing sites and their radiuses represent ± 1 (inner) and ± 2 (outer) group-averaged standard deviation corresponding to horizontal and vertical axis.



Figure S2. Behavioral performance as a function of time relative to saccade onset. Related to Figure 2. (**A**) Criterion. Positive values represent conservative responses and negative values represent liberal responses. (**B**) Reaction time. The data points are group-averaged median reaction time. Error bars in (**A**) and (**B**) denote ± 1 s.e.m. (**C**) Performance (*d'*) computed for a 30-ms-duration sliding window moving in 5-ms steps. The orange shaded areas denote the time points at which performances significantly differed between saccade and neutral conditions in the cluster analysis. (**D**) Performance (*d'*) as a function of SOA in the neutral condition. Error bars denote ± 1 s.e.m.



Figure S3. Illustration of marginal reconstruction. Related to Figure 4. The orientation tuning function (the bottom curve) was computed by averaging the estimated β values across SF for each orientation channel $o(\theta) = \frac{1}{n_{\omega}} \sum_{\omega} \beta_{\omega,\theta}$. SF tuning (right curve) was computed by averaging the absolute value of β across orientations for each SF channel, $s(\omega) = \frac{1}{n_{\theta}} \sum_{\theta} |\beta_{\omega,\theta}|$.

Supplemental Experimental Procedures

Participants

Eight observers (one of the authors and seven observers naïve to the purpose the experiment; age range: 22-29 years; five females) participated in the experiment. All observers had normal or corrected-to-normal vision. The experiment was conducted with the written consent of each observer and the University Committee on Activities involving Human Subjects at New York University approved the experimental protocols.

Setup

Observers sat in a dimly lit room with the chin rest positioned 57 cm from the monitor. The stimuli were generated by MATLAB (Mathwork) using the Psychophysics Toolbox extensions [S1] and presented on a gamma-correct monitor, with a resolution of 1280X960 pixels and a refresh rate of 85 Hz. An EyeLink 1000 Desktop Mount (SR Research) monitored the gaze position of the right eye.

Procedure

Observers performed a visual detection task in which a test stimulus was presented at one of two positions in each trial, either 10° to the left or to the right of the fixation point. Each of the two positions was marked throughout the entire experiment by placeholders composed of four dots forming a square (3° width) (**Figure 1A**). All the stimuli were presented on a gray background with the luminance set to the middle of the monitor range (14 cd/m²). The target was a Gabor oriented vertically generated by modulating a 1.5 cpd sine wave with a Gaussian envelope (0.8° standard deviation). The phase of the Gabor was randomly determined on each trial. The noise patches

corresponded to white noise randomly generated on each trial and filtered in the SF domain with a band-pass filter (0.75-2.25 cpd). The noise was scaled to have 0.35 root-mean-square contrast. In half of the randomly selected trials, the test stimuli corresponded to the target signal embedded in the noise patch, and in the other half of the trials, only the noise was presented (**Figure 1B**).

Each trial started with a 300 ms fixation period followed by a cue at fixation (Figure 1A). In the saccade condition, the cue was a bar (0.3° in length) pointing to the position (left or right) where the test stimulus was going to be presented (100% valid). Observers were instructed to make a saccade as fast as possible to the center of the cued placeholder. The onset of the cue was followed by the onset of the test stimuli. The SOA (stimulus onset asynchrony) between the cue and the test stimuli was a uniform random distribution ranging from 12 to 224 ms, in discrete steps limited by the refresh rate of the monitor (85 Hz). This temporal interval was chosen based on our previous study [S2] and it had two qualities: 1. The interval allowed presaccadic presentation of the test stimuli in most of the trials. 2. The interval was too short for covert endogenous attention to be deployed at the cued position. In the neutral condition, the cue was composed of two horizontal bars pointing to both placeholders, and observers were required to maintain steady fixation throughout the trial. In each trial, observers reported whether the target was present or absent by pressing one of two buttons at their left (keys A and Z on the keyboard) when the test stimuli were presented at the left location, and one of two other buttons at their right (keys I and < on the keyboard) when the test stimuli were at the right location.

Saccade and neutral conditions were blocked (70 to 80 trials per block) as

intermixing the saccadic and neutral trials could lead to prolonged saccade latency. All other variables (SOA, target positions and presence of the target) were randomized and mixed within each block. Each observer first participated in a training session to be familiarized with the procedure, and a titration procedure was run in this session to measure observers' contrast detection threshold (defined as performance at d'=1 in the neutral condition). The average target contrast across observers was 15% for the first session. We monitored observer's performance for each session, and a titration procedure was performance had improved. This procedure allowed observer's performance to stay constant throughout multiple sessions completed across different days. Observers participated in six more sessions to complete the experiment (\geq 3K trials in total).

To ensure that covert endogenous attention solely did not improve performance under these parameters, all the observers participated in at least four blocks of covert attention condition as a control. The procedure was the same as in the saccade condition, but the cue only served as covert attention cue pointing toward the position of the upcoming target (100% valid). The SOA in the covert attention condition was the same as in the saccade and neutral conditions (ranging from 12 to 224 ms), and thus the temporal uncertainty was the same across conditions. Observers were required to maintain their fixation throughout each trial. The trials in the covert attention condition were used for estimating observers' performance (d') under the presence of the cue without saccade (**Figure 2B**).

We monitored eye position online. Stimulus presentation was contingent upon fixation. If the eye position deviated 1.5° away from the fixation (from the beginning of

the trial to the behavioral response, or to the saccade onset in the saccade condition), that trial was considered as a fixation break. In the saccade condition, if the eye did not land in the target area (2.5° in radius) between 70-400 ms after the saccade cue, that trial was considered as a saccade failure. Trials with fixation break or saccade failure and trials in which the observers used the wrong hand to respond were discarded and repeated at the end of the block.

Data analysis

Eye position. Eye position was analyzed offline. For each time point in a trial, the raw eye position data were first smoothed with a Gaussian and we computed smoothed eye velocity using the eye positions of the five neighboring time points [S3]. Saccades were detected when the eye velocities exceeded the median velocity by 5 SDs for at least 8 ms. Saccade events separated by less than 10 ms were merged as a single event. In the saccade condition, a saccade was considered valid only if the observer's first response saccade left the fixation region and landed within the target region (<2.5° away from the center of the test stimuli) between 70-400 ms after the onset of the saccade cue. Trials that had no valid saccade detected within this temporal range or contained blinks were excluded from analysis. For the neutral condition, trials with saccades detected from the beginning of the trial to 200 ms after the offset of the test stimuli or with blinks were excluded from analysis.

<u>Signal detection analysis.</u> For the saccade condition, we sorted the trials into discrete time bins (50 ms in duration) depending on the interval between target offset and saccade onset (time relative to saccade onset). Observers' performance was evaluated by d' (Z(hit rate)-Z(false alarm rate); **Figure 2A**), criterion (-0.5(Z(hit

rate)+Z(false alarm rate)); **Figure S2A**), and reaction time (**Figure S2B**). The presaccadic d' was also computed at a finer resolution by a 30-ms-duration time window moving in 5-ms steps (**Figure S2C**). For the neutral condition, all the trials were pooled together for analysis.

<u>Covert attention condition</u>. We extracted the SOA distribution for each time bin in saccade condition (**Figure 2A**) and used the distribution as the constraint to resample (with replacement) the trials of the covert attention condition. For each observer, we computed one d' for each time bin by averaging over 1000 resampled d'. Thus, we obtained five d' values of covert attention condition (**Figure 2B**), each with the same SOA distribution matching the corresponding data point in the saccade condition.

Reverse correlation. We used a general linear model (GLM) for reverse correlation analysis [S4]. We first transformed the noise image of each trial from pixel space (luminance intensity of each pixel) to a 2D space defined by the noise energy of components responding to different orientation (varied across all of orientation space, 180°, in steps of 10°) and SF (from 0.75 cpd to 2.25 cpd with 15 points evenly spaced on a log scale). To compute the energy $E_{\omega,\theta}$ of each component, we took the noise image of each trial, and convolved it with two Gabor filters ($g_{\omega,\theta,sin}$ in sine phase and $g_{\omega,\theta,cos}$ in cosine phase) with the corresponding orientation θ and SF ω . The energy was computed as:

$$E_{\omega,\theta} = \sqrt{(S * g_{\omega,\theta,\sin})^2 + (S * g_{\omega,\theta,\cos})^2}$$

in which * represented the cross-correlation operator. We took the energy centered at the test stimuli for analysis.

For each component with preferred orientation θ and preferred SF ω , we estimated the correlation between the energy of that component and behavioral responses using a GLM to predict the binomial dependent variable: $p(yes) = \Psi(\beta_{\omega,\theta}E^*_{\omega,\theta} + b_{\omega,\theta})$

in which p(yes) was the percentage of yes responses in the detection task and Ψ was a cumulative normal distribution. Two free parameters $\beta_{\omega,\theta}$ and $b_{\omega,\theta}$ were fitted. $\beta_{\omega,\theta}$ represented the correlation between the energy and the behavioral report. A zero $\beta_{\alpha\theta}$ indicated that the energy of that component did not influence observers' responses. $b_{\alpha\theta}$ represented a baseline tendency of the observers to respond "present" (i.e. false alarm rate), which was not related to the stimuli. $E^*_{\omega\theta}$ represented the centered-andnormalized energy of each component [S4]. Before applying the GLM, the energy of each component was first sorted into two groups based on whether the target signal was present or absent in each trial, and the mean of the energy was removed for each group. That is, we only used the energy fluctuation induced by the noise and the energy used for analysis was centered at zero for both target-present and target-absent trials. To let the estimated $\beta_{\omega,\theta}$ be comparable across components, we further normalized the energy across all the trials in each component to have a standard deviation of 1. The estimated sensitivity kernel was a 2D matrix *K* in which $K(\omega, \theta) = \beta_{\omega, \theta}$. For each SF, we averaged the components with the same distance (i.e. $+10^{\circ}$ and -10°) from the target orientation (0°) by assuming a symmetric orientation tuning [S5].

Marginal reconstruction and parametric fit of sensory tuning. We evaluated

whether the orientation and SF tuning functions were separable. That is, kernel K can be approximated by multiplication of two vectors, so^{T} , in which s is the SF tuning and o is the orientation tuning function underlying visual detection. Marginal reconstruction was applied [S6]. On the one hand, we observed that beta weights could be negative (with a much weaker amplitude compared to the positive region, see Figure 3A, 3B) for orientations away from the target. On the other hand, the sign of the beta weights was constant across SF. Thus, we consider each point on the SF tuning functions as the gain factor of the orientation tuning function at the corresponding SF channel, and SF tuning was computed by averaging the absolute value of β across orientations for each SF channel, $s(\omega) = \frac{1}{n_{e}} \sum_{\alpha} |\beta_{\omega,\theta}|$. The orientation tuning function was computed by averaging the estimated β values across SF for each orientation channel $o(\theta) = \frac{1}{n} \sum_{\omega, \theta} \beta_{\omega, \theta}$. The orientation-SF separability was then tested by correlating the original kernel K and the reconstructed kernel (so^{T}). We found high correlations between the two kernels (Figure 3D) across observers and experimental conditions, indicating that SF and orientation were separable, and validating the procedure we used for extracting tuning functions.

To fit the orientation tuning width of individual observers (**Figure 4E**), individual orientation tuning functions were scaled between zero and one, and were fit with $G(0,\sigma_{\theta})$, a Gaussian with one free parameter, standard deviation σ_{θ} , representing the orientation tuning width. The gain of the orientation tuning functions was defined as the peak and trough of the functions. Each SF tuning function was fitted by a Gaussian raised to a power: $aG(\mu,\sigma_{\omega})^{p} + b$. μ represented the peak frequency (where the tuning

function reached highest sensitivity; **Figure 4A**). To improve the fit, four free parameters were implemented: σ_{ω} and *p* determined the shape of the SF tuning function while *a* and *b* adjusted the amplitude and baseline of the function. Among all the fitted parameters of SF tuning functions, we only found consistent differences in peak frequency (**Figure 4B**) across conditions. We fit the tuning functions by minimizing the squared error between the fitted tuning function and the data. Note that the statistical tests of all the (SF and orientation) tuning parameters were applied on individual fits; group-aggregated tuning functions (**Figure 4A and 4D**) were fitted and included for presentation purposes only.

Change of tuning parameters as a function of time relative to saccade onset. For each individual observer, we grouped all the presaccadic trials into three bins with equal number of trials (on average, 502 trials per bin per observer), and fitted the peak frequency of SF tuning and orientation tuning width for each time bin. We used the median time (across trials) of each time bin as the representative time mark for each bin (x-axis in **Figure 4C and 4F**). This procedure was applied because there were too few trials in the time window earlier than -100 ms (**Figure S1**), resulting in noisy tuning functions [S4]. We estimated the slopes, representing the temporal trend of the parameters (peak SF frequency and orientation tuning width), by regressing the group-averaged fitted parameters to the group-averaged representative time marks (**Figure 4C and 4F**). We tested whether the slopes deviated from zero by permutation test: We randomly permuted the temporal order of the tuning parameters for each observer and then refitted the slopes. This procedure was repeated 2000 times. We tested whether the original slopes were different from the distributions of the slope from permutation,

which represented the distributions of the slope under the null hypothesis that there is no systematic temporal trend of the tuning parameters.

Cluster analysis. To test the difference between the presaccadic and neutral sensitivity kernels (**Figure 3C**), we first ran a two-tailed paired t-test on each pixel in the kernel independently, and then we grouped the neighboring pixels (distance $\leq \sqrt{2}$ pixel) that showed significant differences (p<0.05 without correction for multiple comparisons) as a cluster and averaged the values of the pixels within each cluster for each observer. A second round of t-tests was applied to each cluster, and Bonferroni correction for multiple comparisons was applied based on the number of clusters tested. In the difference kernel in **Figure 3C**, we plotted the contour of significant clusters by interpolating the p-values (obtained in the first round of t-test) and outlined the boundary of the significant clusters using the criterion of p<0.05. We applied the same cluster analysis procedure to the gain of different SF channels (**Figure 4A**) and the fine-temporal-resolution presaccadic *d'* (**Figure S2C**).

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