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# Ultra-fine resolution of pre-saccadic attention in the fovea

## Highlights

- Pre-microsaccadic attention effects are highly localized at the microsaccade goal
- Pre-microsaccadic enhancements are reduced when microsaccades are less accurate
- Before microsaccade onset, sensitivity decreases at the preferred locus of fixation

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## In brief

Guzhang et al. examine the resolution of pre-saccadic attention at the foveal scale, and they show that fine visual discrimination enhancements associated with pre-microsaccadic attention are highly localized around a 0.17°-region centered on the saccade goal. This enhancement is accompanied by a drop in acuity at the preferred locus of fixation.

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# Ultra-fine resolution of pre-saccadic attention in the fovea

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## SUMMARY

Microsaccades, the tiny gaze relocations that occurr during fixation, have been linked to covert attention deployed degrees away from the center of gaze. However, the link between attention and microsaccades is deeper in that it also unfolds at the foveal scale. Here, we have examined the spatial grain of pre-microsaccadic attention across the 1° foveola. Through the use of high-precision eye-tracking and gaze-contingent display system that achieves arcminute precision in gaze localization, we have shown that the spotlight of attention at this scale can reach a strikingly high resolution, in the order of 0.17°. Further, when a microsaccade occurs, vision is modulated in a peculiar way across the foveola; whereas fine spatial vision is enhanced at the microsaccade goal location, it drops at the very center of gaze, where acuity is normally highest. These results reveal the finesse of the visuomotor system and of the interplay between eye movements and attention.

## INTRODUCTION

Humans use large saccades to shift their gaze and sample the visual scene with the foveola, the tiny 1° region of the retina capable of achieving high spatial resolution. Contrary to the classical textbook view, positing that at each fixation the visual system simply acquires a high-resolution snapshot of the visual input at the center of gaze, foveal vision is an active process.[1–9] During fixation, the eyes are never stationary. Besides ocular drift, tiny saccades less than half a degree in size, known as microsaccades, continually occur. Humans perform microsaccades in a variety of everyday tasks, ranging from reading[10–12] to exploring fine details,[3,4,13,14] at rates varying from 0.5 to 2 microsaccades per second.[10,13,15,16] Given their pervasiveness, understanding the effects that these small eye movements have on fine spatial vision at the center of gaze is crucial.

Although these eye movements were previously thought to be useless for the visual system[17] or a simple refreshing mechanism to prevent visual fading,[18,19] it has been shown that microsaccades can be voluntarily generated, that their precision and accuracy is comparable to that of saccades,[20–23] and that they are controlled by the same neural structures driving larger saccades.[24,25] Moreover, in natural viewing conditions when our fovea is exposed to a rich visual input, the visuomotor system actively uses microsaccades to explore complex foveal stimuli.[3,4,13,14] Further, by shifting the preferred locus of fixation (PLF) on the detail of interest, microsaccades effectively counteract non-uniform vision across the foveola.[3,4] Notably, the benefits of microsaccades do not only stem from precise relocation of the PLF but are also exerted before the onset of the eye movement; microsaccade preparation leads to a perceptual enhancement at the microsaccade target location within the foveola.[26]

The presence of a deeper link between microsaccades and attention, which goes beyond the reported effects of microsaccades in the visual periphery[15,27–37] and extends them to the central foveal region, raises new questions critical to the understanding not only of foveal vision but also of the mechanisms underlying attention at this scale. One longstanding question regards the degree to which the attentional spotlight can be narrowed down. In the case of pre-saccadic attention, how narrowly tuned can its effects be around the saccade goal? Mirosaccades are aimed at targets already in the foveola, where visual resolution is highest and is ideal to address this question. Further, because the PLF is just arcminutes away from a microsaccade goal, it is important to understand whether and how visual perception is altered at this location before the microsaccade onset.

Addressing these questions is technically challenging, primarily because microsaccadic shifts can be as small as a quarter of a degree.[20,38–41] Hence, probing fine discrimination around the microsaccade target location requires not only precise eye-tracking but also accurate gaze localization, something that is beyond the capability of commercial video-based eye-trackers. To circumvent these problems, here we used a high-precision eye-tracker,[42–44] coupled with a system for gaze-contingent display control capable of localizing the line of sight with arcminute precision.[3,45] Our findings reveal the spatial resolution of overt attention and the complex nature of foveal vision, which


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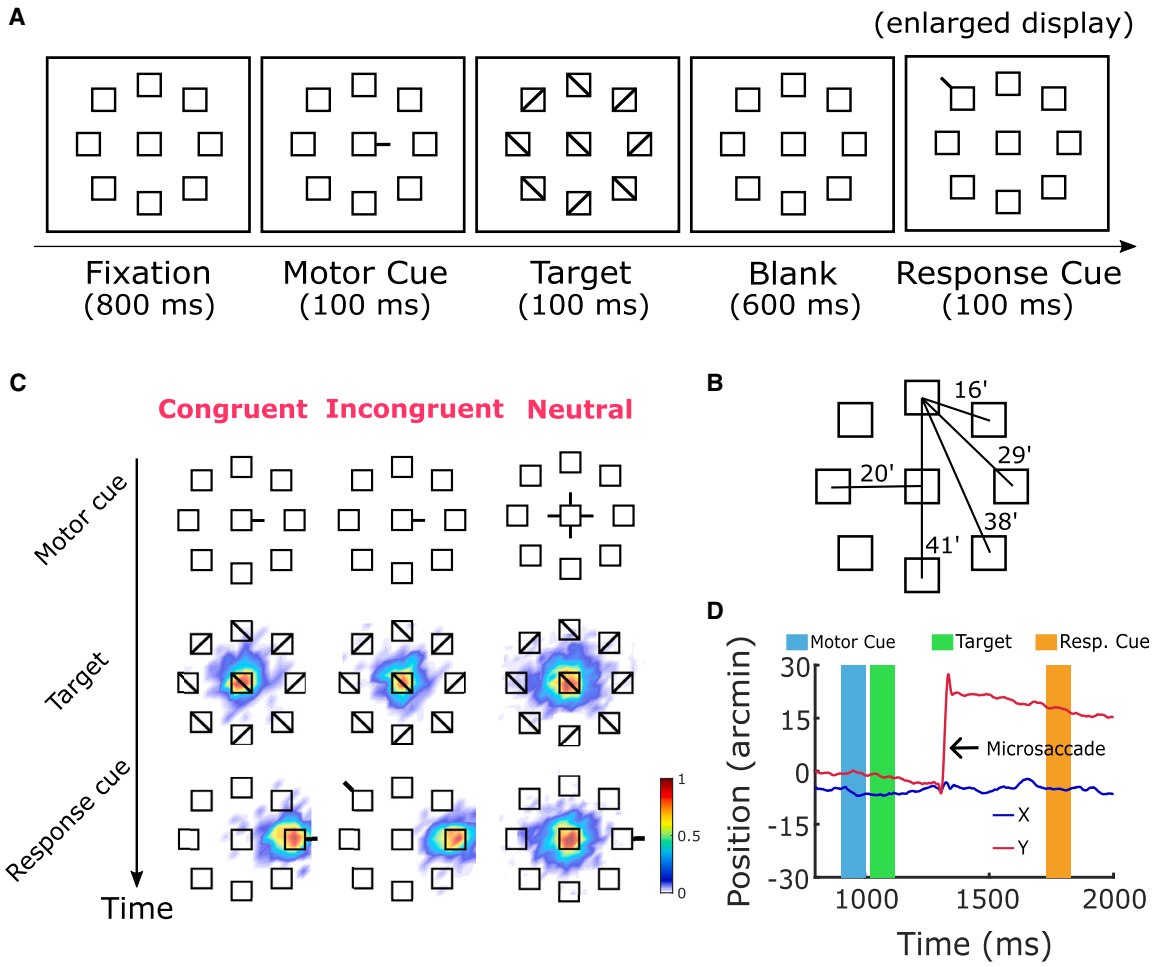


**Figure 1. Experimental protocol**

(A) Trials started with eight location placeholders displayed foveally on the monitor and arranged in a circle, with an additional one at the center of the array. Observers were instructed to maintain fixation at the center and then shift their gaze, via a microsaccade, toward the location indicated by a motor cue as soon as possible. Immediately following the motor cue and before the microsaccade onset, nine fine spatial stimuli tilted (±45°) were briefly displayed, one at each location. At the end of the trial, a response cue appeared, and observers were instructed to report the orientation of the stimulus that was previously presented at the location indicated by this cue.

(B) Spatial arrangement of stimuli.

(C) In congruent/incongruent trials, the response cue pointed to the same/different location as the motor cue. In neutral trials, a non-directional cue instructed observers to maintain their gaze at the center of the stimulus array. Heatmaps represent two-dimensional (2D) average distributions of gaze position during the course of the trial.

(D) An example of eye movements during the course of a typical trial.

See also Figures S1 and S2.

is continuously reshaped by the interplay of microsaccades and fine spatial attention.

## RESULTS

To examine the degree by which the effects of pre-microsaccadic attention extend around the saccade goal, we used a 2AFC fine visual discrimination task in which observers were asked to discriminate the orientation of a small target (7.5′ × 1.4′, tilted ±45°) presented a few hundred milliseconds before the onset of a visually guided microsaccade. Stimuli, including the target, were presented foveally and arranged in a circular pattern with a radius of 20′ around the central fixated location. Upon microsaccade landing, a response cue appeared and observers reported the orientation of the stimulus previously presented at the location indicated by this cue (Figures 1A and 1B). Eye movements were monitored at high resolution, using either an analog or a digital Dual Purkinje Image eye-tracker,[42–44] to ensure that observers maintained the gaze within a 10″10′ window around the fixation point when stimuli were presented and that microsaccades were promptly performed after the presentation of the motor cue.

Microsaccades were prompted by a motor cue, pointing to one of four equally probable cardinal directions. The motor cue and response cue could either indicate the same location (congruent condition) or different locations (incongruent

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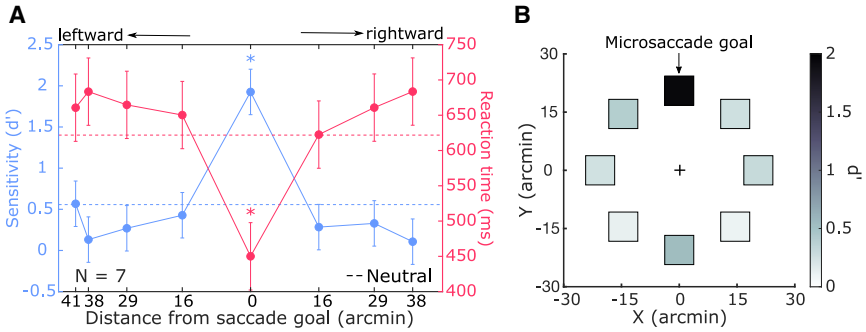


**Figure 2. Perceptual enhancement resulting from pre-microsaccadic attention**

(A) Average performance (blue) and manual reaction times after the presentation of the response cue (red) across all observers at various distances from the saccade goal location. Dashed lines represent performance in neutral condition. Error bars represent group means and within-subject 95% confidence intervals[46] (n = 7).

(B) Same results shown in (A), displayed in a 2D spatial layout with respect to the saccade goal location.

See also Figure S3.

condition). Approximately 10%–20% of the time that a motor cue was presented, the trial was congruent. As a result, there was little incentive for the observers to systematically prioritize the saccade goal over other locations; the probability of being tested at the saccade goal location was only slightly higher than the probability of being tested at another location (≈10%–11%). In a control condition (neutral condition), observers were instructed to maintain their gaze at the center of the array throughout the duration of the trial (Figure 1C). The directional cue condition (incongruent and congruent trials) and the neutral condition had the same probability of occurrence in the task. Importantly, in all conditions, stimuli appeared foveally approximately at the same distance (20′) from the center of gaze. Hence, conditions differed only in the motor behavior after the target presentation and in the microsaccade landing position with respect to the response cue location (Figures 1D and S1). In congruent and incongruent trials, observers were capable of shifting their gaze precisely to nearby stimuli based on the motor cue, with an average landing error of 5.46′ ± 1.52′. The average latency of microsaccades was 396 ± 48 ms, which is in line with what has been reported in previous work[26] (Figure S2).

## The spatial grain of pre-microsaccadic perceptual enhancements

To understand how fine spatial vision changes across the foveola immediately before a microsaccade, we examined visual discrimination as a function of the distance between the microsaccade goal and the target, i.e., the stimulus presented at the location indicated by the response cue (Figures 1A and 1B). Our findings show that the perceptual enhancement associated with microsaccade preparation was highly localized; performance at the microsaccade goal location, measured as $d'$, was higher compared with all other locations, including those only 16′ (center-to-center distance) away from the microsaccade goal (Figures 2A and 2B, 1.93 ± 0.61 at the saccade target, 0.43 ± 0.35 and 0.28 ± 0.28 for the locations surrounding the saccade target; Tukey's HSD post hoc tests, saccade goal vs. all other locations, $p < 0.0001$). When compared with the neutral condition in which observers maintained fixation, performance at the microsaccade goal location increased by approximately 1.37 units of $d'$ (Figures 2A and 2B; 1.93 ± 0.61, 0.29 ± 0.23, and 0.56 ± 0.27 for congruent, incongruent, and neutral conditions respectively; $F(2, 12) = 57.09$, $p < 0.0001$; congruent vs. incongruent and neutral, $p < 0.0001$, incongruent vs. neutral condition, $p = 0.2714$). Not only was fine spatial vision enhanced at the microsaccade target location, but observers were also faster at discriminating stimuli presented at this location. Hence, the increase in sensitivity at the saccade goal was not the result of a speed-accuracy trade-off (Figure 2A; manual reaction times; 450 ± 142, 650 ± 221, and 623 ± 189 ms for a distance of 16′ leftward and rightward respectively; Tukey's HSD post hoc tests, congruent vs. all other locations, $p < 0.0001$).

Note that performance at the microsaccade goal location for horizontal and vertical microsaccades was comparable; pre-microsaccadic attention significantly improved performance along both meridians (Figure S3; 2.07 ± 0.52 vs. 1.10 ± 0.64 for pre-microsaccadic vs. neutral along the horizontal meridian and 1.85 ± 0.91 vs. 0.33 ± 0.35 for pre-microsaccadic vs. neutral along the vertical meridian; multiple t test with Holm-Bonferroni correction: $p = 0.0041$ and $p = 0.0041$ for pre-microsaccadic vs. neutral at horizontal and vertical meridians respectively). Interestingly, similar to the asymmetry in performance reported in the visual periphery, where visual sensitivity is higher along horizontal than vertical meridian,[47,48] observers' ability to discriminate fine spatial details was better at locations along the horizontal than the vertical meridian in the neutral condition, when observers were simply fixating (1.10 ± 0.64 vs. 0.33 ± 0.35 for horizontal vs. vertical meridian in neutral condition; multiple t tests with Holm-Bonferroni correction: $p = 0.0502$). However, differently from what reported for pre-saccadic attention,[47,48] this asymmetry was reduced when stimuli were presented before microsaccade onset (2.07 ± 0.52 vs. 1.85 ± 0.91 for horizontal vs. vertical meridian in pre-microsaccadic condition; multiple t test with Holm-Bonferroni correction: $p = 0.5021$).

Experiment 1 poses a high memory load on subjects, all stimuli appear at the same time and are gone by the time the response cue is presented. Therefore, memory selection may have contributed to the enhancement reported here.[49–52] To ease the memory burden, subjects may have chosen to prioritize the saccade goal location. This strategy would not improve the overall performance in the task, but it may be more efficient given that this prioritization may benefit saccade accuracy. If observers opted to prioritize processing at the saccade goal in experiment 1, we would anticipate similar performance at the initially cued location in all the congruent trials. As illustrated in Figure 4A (see also Figure S5), when observers did not perform a microsaccade in congruent trials, performance was lower compared with when they executed microsaccades (1.65 ± 0.49 vs. 0.97 ± 0.41 for ms. vs. no ms., respectively; $F(2, 8) = 25.65$, $p = 0.0003$; Tukey's HSD post hoc test, ms. vs. no ms., $p = 0.0092$).

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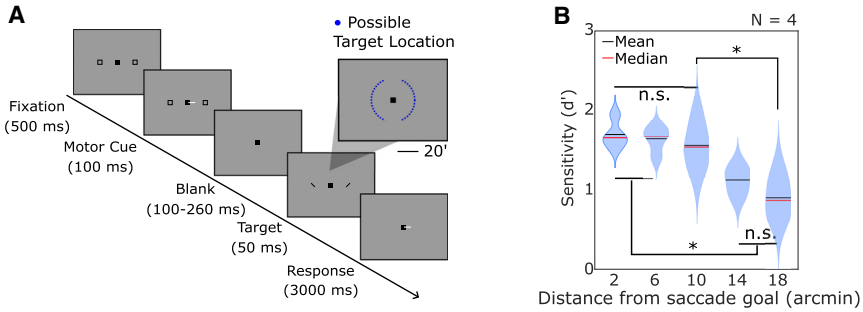


**Figure 3. Resolution of pre-microsaccadic attention at a finer grain**

(A) Experimental protocol for experiment 2. Trials started with two location placeholders displayed foveally ±20′ from the central fixation marker. Observers were instructed to maintain fixation at the center and then shift their gaze, via a microsaccade, toward the location indicated by a motor cue as soon as it appeared. After a variable delay before the onset of the microsaccade, two fine spatial stimuli tilted ±45° were briefly displayed. Stimuli could appear at any location along an arch centered on the microsaccade goal and subtending a radius of 20′. Observers were instructed to report the orientation of the stimulus that was previously presented in the same hemifield, indicated by the initial motor cue.

(B) Average performance for targets presented 0′–20′ away from the saccade goal. Performance is calculated within individual observers using a non-overlapping binning window of 4′ from 0′to 20′. The shaded regions represent the kernel density estimation showing the distribution shape of the data.

See also Figure S4.

Interestingly, performance in the absence of microsaccades was higher compared with the neutral trials in which a non-directional cue was presented and subjects maintained fixation (1.65 ± 0.49, 0.97 ± 0.41, 0.44 ± 0.22 for microsaccade, no microsaccade, and neutral conditions respectively; $F(2, 8) = 25.65$, $p = 0.0003$; no microsaccade vs. neutral, $p = 0.0354$). These results suggest that, although pre-microsaccadic attention is the main contributor to the effect reported in experiment 1, it is likely that a small part of this effect is the consequence of subjects prioritizing the saccade goal to ease the memory burden—a strategy that could be used whenever a directional cue is presented. As a result, when a microsaccade is performed, the perceptual enhancement is sizably larger than when a microsaccade is not executed.

The results shown in Figures 2A and 2B indicate that the focus of pre-microsaccadic attention may have a radius smaller than 16′, which inevitably raises the question of whether attention is uniform within this 16′ window or whether the resolution of attention is even finer. To address this question, we probed attention at a finer grain in experiment 2. In addition, to reduce the memory burden, in this experiment we displayed only two stimuli at a time. The two stimuli were presented at the same eccentricity to the left and to the right with respect to the fixation marker but at random locations within ± 20′ from the microsaccade goal (Figure 3A). To minimize uncertainty and the memory load further, we informed observers that the test target always appeared in the initially cued hemifield. The optimal strategy in this task would be to prioritize whatever stimulus appears on the cued hemifield; i.e., performance should be equally high at all possible locations tested in that hemifield, no matter how far the stimulus is from the saccade goal. As shown in Figure 3B, performance was on average approximately uniform within a ±10′ window around the microsaccade goal (1.70 ± 0.18 and 1.55 ± 0.29 for 2′ and 10′, respectively; $F(4, 12) = 12.44$, $p = 0.0003$; Tukey's HSD post hoc tests, 2′ vs. 10′, $p = 0.8452$; see also Figure S4). Beyond 10′, performance decreased more steeply and dropped off more than half a unit of $d'$ at a distance of 14′ (1.70 ± 0.18 and 1.12 ± 0.17 for 2′ and 14′ away from the saccade goal; $F(4, 12) = 12.44$, $p = 0.0003$; Tukey's HSD post hoc tests, 1′ vs. 14′, $p = 0.0008$). Even if there was virtually no memory load in this task, the results align well with those obtained in the main experiment and reveal that pre-microsaccadic attention leads to perceptual benefits localized within a 10′ × 10′ region around the microsaccade goal.

## Pre-microsaccadic perceptual enhancements and microsaccade precision

With some variability across observers, microsaccades were overall characterized by a small landing error (Figure 4B). To determine whether the landing error of microsaccades had an impact on the attentional effects reported here, we analyzed performance in experiment 1 trials characterized by microsaccades landing close to the target (accurate microsaccades) vs. trials in which they landed further away (inaccurate microsaccades). Inaccurate microsaccades were defined as those with landing errors exceeding the 50$^{th}$ percentile of each individual distribution of landing errors (Figures 4C and 4D) (on average, this threshold was 8.83′ ± 2.50′). Remarkably, not only was the sensitivity higher in trials with more accurate microsaccades (Figure 4E; 2.37 ± 0.77 and 1.64 ± 0.53 for accurate and inaccurate microsaccades respectively; $t(6) = 4.36$, $p = 0.0048$) but manual reaction times also decreased in trials with more accurate microsaccades compared with trials characterized by larger landing errors (438 ± 144 and 462 ± 141 ms; $t(6) = 2.51$, $p = 0.0461$). Because distractors were displayed at nearby locations together with the target, this drop in performance could have been the result of microsaccades being aimed at the wrong stimulus. In fact, in the majority of these trials (58% ± 24%), the microsaccade landing position was closer to one of the two nearby locations than to the target location. Previous work has shown that the perceptual processing at non-saccade goals can be enhanced at the cost of accuracy or latency of saccades, i.e., a trade-off between saccade accuracy/latency and perceptual processing at non-goal locations.[49] Therefore, it is possible that the effect we observe here also reflects this trade-off; observers, rather than prioritizing the accuracy of their microsaccades, prioritized visual processing at another location. Our experimental design is not ideal to test this possibility as there are many other locations that subjects may have chosen to prioritize and performance in the incongruent trials was barely above chance. Yet, there was no statistical difference in performance between incongruent trials with inaccurate vs. inaccurate microsaccades (0.21 ± 0.32 and 0.37 ± 0.27 $d'$ for performance in incongruent trials when microsaccades were accurate and

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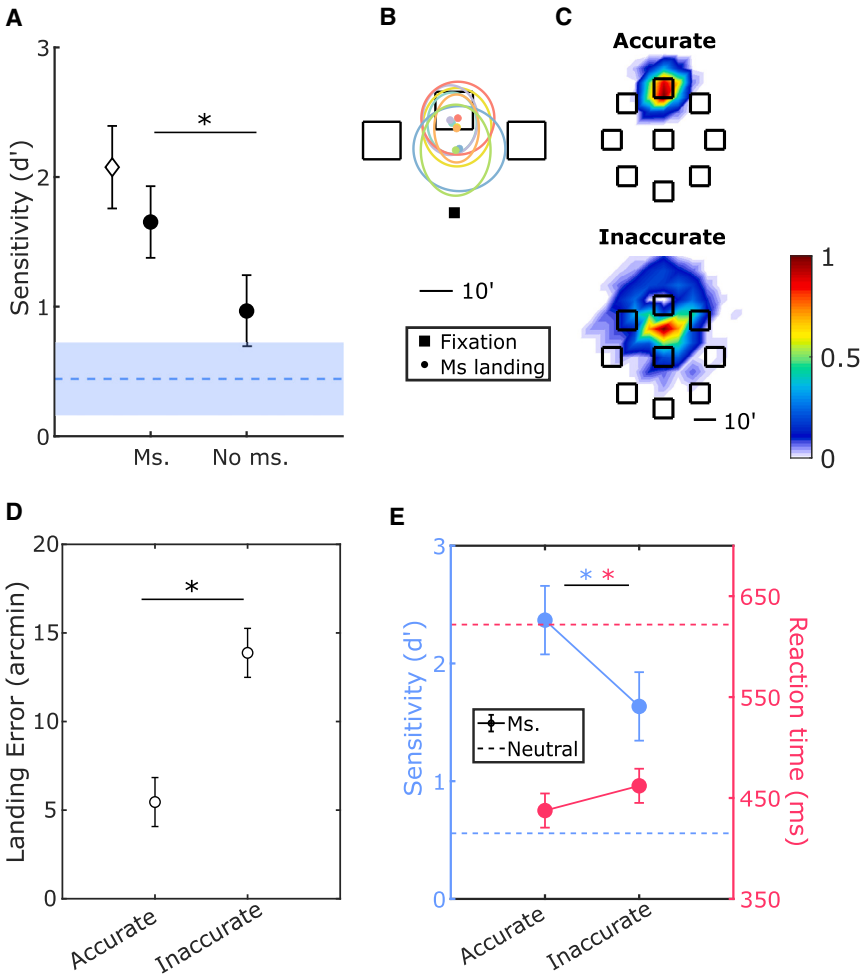


**Figure 4. The effect of microsaccade landing accuracy on performance**

(A) Average performance across observers in congruent trials, with and without microsaccades. The open diamond represents data from congruent trials with accurate microsaccades. Two observers were removed from the analysis because of too few trials in the no-microsaccade condition. Dashed lines with shaded areas represent the group mean and SEM in neutral trials. Error bars represent group means and within-subject confidence intervals among microsaccades, no microsaccades, and neutral conditions.[46] The asterisk marks a statistically significant difference ($n = 5$, $p < 0.05$, Tukey post hoc test).

(B) Microsaccade average landing positions in congruent trials with respect to their goal location (represented by the topmost box). Each color represents one single observer with its 68% confidence ellipse.

(C) Average 2D normalized microsaccade landing position distribution with respect to the goal location for accurate and inaccurate trials. Accurate and inaccurate landings were categorized based on whether the Euclidean distance between the landing position and the saccade goal location indicated by the motor cue was below or above the 50$^{th}$ percentile of the landing errors distribution for each individual observer (average microsaccade landing error in accurate and inaccurate trials: 5.46′ ± 1.52′ and 13.88′ ± 3.59′, for $t(6) = -10.54$, $p < 0.0001$).

(D) Average microsaccade landing error for accurate and inaccurate trials. Error bars represent group means and within-subject 95% confidence intervals[46] ($n = 7$).

(E) Average performance and reaction times across observers in trials with accurate/inaccurate microsaccade landing and neutral trials. Error bars represent group means and 95% within-subject confidence intervals.[46] Asterisks mark a statistically significant difference ($p < 0.05$, Tukey post hoc test). See also Figure S5.

inaccurate, respectively; $p = 0.2165$). However, it is important to note that even when the microsaccade landings were inaccurate, performance was still higher than in the neutral condition (Figure 4E; 1.64 ± 0.53 and 0.56 ± 0.27 for inaccurate and neutral conditions; $t(6) = 8.53$, $p = 0.0001$), and it was also higher than in the congruent condition without microsaccades (Figure 4A; 1.38 ± 0.34 and 0.97 ± 0.41 for inaccurate and no microsaccade conditions; $t(4) = 3.17$, $p = 0.0340$). Therefore, even if observers prioritize other locations besides the saccade goal in trials characterized by inaccurate microsaccade landings, pre-microsaccadic attention still enhances visual perception at the microsaccade goal location.

## Pre-microsaccadic perceptual modulations at the preferred locus of fixation

The preferred locus of fixation (PLF) is characterized by the highest visual acuity.[3,4] To determine whether or not sensitivity at this location changes right before microsaccade onset, we conducted a third experiment to specifically examine visual discrimination performance for stimuli presented at the PLF. This experiment was identical to experiment 1, except that the probability of the target appearing at the central vs. at a peripheral location was the same, and only the four cardinal locations and the central location were tested (even if stimuli appeared at all the nine locations). Performance at fixation was compared with performance right before the onset of microsaccades. Our results show a drop in fine spatial discrimination when stimuli are presented at the PLF during microsaccade preparation compared with fixation (Figure 5A; 0.84 ± 0.51, 1.99 ± 1.23 for pre-microsaccadic and fix. respectively; $F(2, 14) = 15.92$, $p = 0.0002$; Tukey's HSD post hoc test, $p = 0.0018$ for pre-microsaccadic vs. fix.). Interestingly, the performance at the microsaccade goal location during saccade preparation was comparable to that at the PLF in the absence of microsaccades (Figure 5A; 1.99 ± 1.23 vs. 2.24 ± 0.67; $p = 0.6264$). That is, pre-microsaccadic attention enhanced visual discrimination at the microsaccade goal to a similar degree as when the stimuli were presented at the PLF. These results are even more surprising when considering that stimuli at the PLF had a higher probability (50%) of being tested compared with any other location. If observers prioritized the location at the center of gaze to maximize performance, we would expect highest performance at the PLF, regardless of whether microsaccades were prepared or not. Nonetheless, the performance at the PLF was significantly

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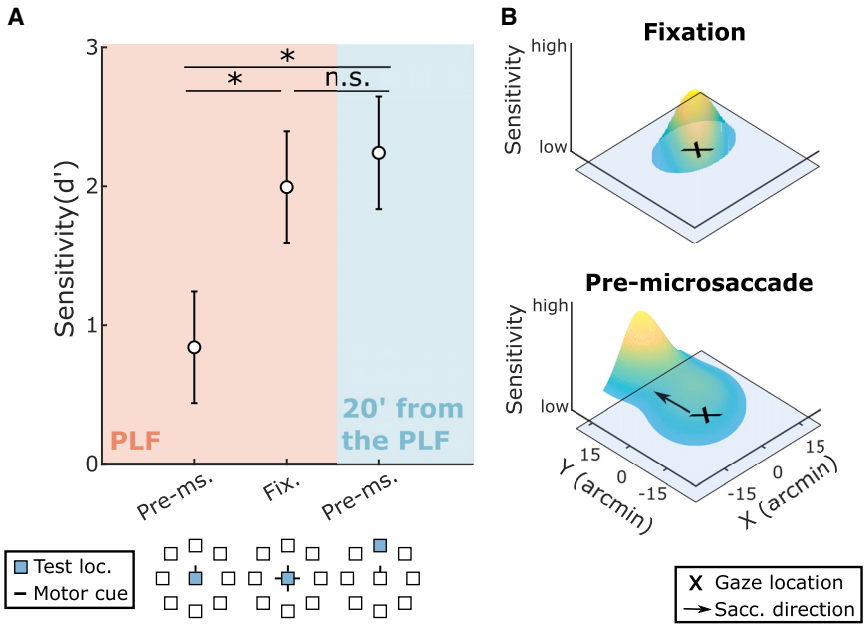


**Figure 5. Modulations of fine spatial vision before microsaccade onset at the preferred locus of fixation**

(A) Average performance at the preferred locus of fixation (PLF) in the presence (pre-microsaccadic) and in the absence (fix.) of a microsaccade (pink-shaded region) and at the saccade goal location (blue-shaded region). Error bars represent group means and within-subject 95% confidence intervals[46] (n = 8).

(B) Schematic representation of how processing resources are allocated during fixation and before the onset of a microsaccade, based on the results of this study.

impaired during microsaccade preparation compared with the fixation condition. On the other hand, performances were equally high at the PLF during fixation and at the microsaccade goal location during the preparation of the microsaccade, even though the microsaccade goal had a substantially lower probability (25%) of being tested. This further supports the idea that the effects reported here are mainly driven by pre-microsaccadic attention rather than memory selection or other task-related strategies to maximize performance. These results show that pre-microsaccadic attention not only modulates fine spatial vision at the microsaccade goal but also affects vision at the very center of gaze. It is likely that the reported drop in sensitivity at the PLF reflects a shift of processing resources from this region to the microsaccade goal location (Figure 5B).

## DISCUSSION

During brief periods of fixation, our gaze is not stationary; besides the continuous presence of ocular drift, humans perform 1–2 microsaccades per second, depending on the task.[4,10,13,15,16,53] Microsaccades are among the smallest, fastest, and most precise movements that humans are capable of executing. Once thought to be simple "flicks" of the eye, merely used to refresh the retinal image to prevent visual fading,[18,19] microsaccades are finely controlled movements[3,23] used to explore complex foveal stimuli at a finer grain.[4,13] In the past decade, the interplay between microsaccades and attention has been in the spotlight. It has been shown that the direction of microsaccades can reveal the location of the covertly attended stimuli in the visual periphery,[15,27–35] and microsaccade inhibition has been shown to correlate with temporal attention.[54] These important findings highlight the extent to which microsaccades are linked to higher-order processes. Yet, this research focused on peripheral shifts of attention at locations that are much further away from the goal location of microsaccades. Further, this has been studied in rather unnatural conditions involving prolonged sustained fixation on an impoverished foveal input. As we previously showed,[26] the interplay between microsaccades and attention is deeper and it also unfolds at the foveal scale. Understanding the effects and the spatial resolution of pre-microsaccadic attention at this scale is of paramount importance given the ubiquitous presence of microsaccades during fixation, especially when humans examine fine details.

Our findings show that the spatial resolution of pre-saccadic attention in the central fovea is in the order of 10′; i.e., the focus of attention is approximately uniform within a 10′ × 10′ window around the microsaccade target. The effects of attention completely vanished at a distance of only 16′ from this location. This effect is modulated by how close microsaccades land on their goal; smaller landing errors are associated with higher performance. Further, sensitivity at the PLF, where visual acuity is highest,[3,4] drops during microsaccade preparation to the point that fine spatial discrimination is better at the microsaccade goal location than at the very center of gaze. In this study, subjects performed instructed microsaccades toward specific locations. This is different from what happens in everyday conditions, when most of the time microsaccades occur spontaneously. Therefore, the question remains of whether the modulations reported here are also present with spontaneous microsaccades and microsaccades performed in natural viewing conditions. Addressing this question is very important for future research and has practical implications as humans perform microsaccades frequently in a variety of everyday tasks, including reading.

It is important to note that the perceptual modulation observed in this study is mainly driven by pre-microsaccadic attention rather than memory selection strategies. First, in experiment 1, the task imposed a relatively intense memory load that could have incentivized the use of these strategies. Nevertheless, the magnitude of the perceptual benefit was much higher in the trials with vs. in trials without microsaccades (including trials with failed microsaccades), even if (presumably) subjects prioritized processing at the location indicated by the initial cue in both conditions. Second, in experiment 2 in which the load of memory was virtually absent, results aligned well with those of experiment 1. In this experiment, the most effective strategy to maximize performance was to prioritize processing of whatever stimulus appeared in the cued hemifield. However, we found a

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narrow spatial modulation of the effect around the saccade goal. Third, in experiment 3, the task design incentivized prioritization of the stimuli presented at the PLF. Yet, we report a decrease in performance at that location during microsaccade preparation, while still observing a marked perceptual enhancement at the microsaccade goal location. Overall, it is possible that memory selection had an impact on our results but its influence was smaller with respect to the magnitude of the effect of pre-microsaccadic attention.

In the parafovea, the enhancement from pre-saccadic attention has been reported to extend from about 1°[55] to 2.5°[56] around the saccade target, depending on the size of the saccade and the arrangement of the saccade targets.[57] The spatial resolution of the enhanced region is much lower compared with the sub-degree resolution reported here for microsaccades, which is in the order of arcminutes. Why is the spatial resolution of pre-saccadic attention at the scale of the foveola of about 10′? We think that this is likely due to the fact that acuity seems to be approximately uniform within a 10′ region around the PLF,[58] and humans rarely make microsaccades less than 5′ in amplitude. Essentially, stimuli within this region are uniformly resolved. If, indeed, the perceptual enhancement of pre-microsaccadic attention serves as a way to preview at higher resolution the input that will fall in the 10′ region immediately surrounding the PLF, a smaller spatial focus may not be needed. On a functional basis, this resolution is adequate for most everyday tasks that demand visual acuity, such as discriminating facial expressions from a distance[13] or reading,[10] where the single resolvable details are generally larger than 10′.

Importantly, here we found that pre-msicrosaccadic attention is modulated by the precision of microsaccades. When the landing error of microsaccades was within 10′, the perceptual enhancement of the saccade target was highest; however, for larger landing errors (on average 14′), the perceptual enhancement dropped substantially. These results may appear to be different from what has been reported for larger saccades. For large saccades, the enhancement is centered around the saccade goal and it is not influenced by saccade landing error.[55,56,59] However, because in our study target and nearby distractors were separated by only 5.4′ (edge-to-edge separation), it is likely that observers were accidentally targeting the wrong stimulus, which would lead to a reduced or absent perceptual enhancement at the goal location. In fact, in trials associated with larger landing errors, observers often landed closer to the stimulus next to the saccade target. Alternatively, it is possible that the decrease in performance observed in the trials with less accurate microsaccades is a reflection of a trade-off between microsaccade accuracy/latency vs. processing of stimuli at non-goal locations.[49] Nevertheless, pre-microsaccadic perceptual enhancements were still sizable even when microsaccades were inaccurate.

Previous work on pre-saccadic attention primarily focused on the perceptual enhancement at the saccade goal location[55,59–62] without examining how saccade/microsaccade preparation influences visual perception at the very center of gaze, i.e., at the PLF. The few studies investigating this issue yielded contrasting results.[59,60,63] Some work showed an increase in performance at the fovea, as the targets were shown closer to the onset of saccades to peripheral locations as a result of foveal remapping.[59,60] However, work from Kroell and Rolfs[64] pointed out that the enhancement in visual sensitivity at the fovea during saccade preparation is restricted to visual features matching the ones of the saccade target,[64] and Hanning and Deubel[63] showed a drop in sensitivity for stimuli presented at the center of gaze before the impending saccade.[63] Here, we report a decrease in visual discrimination at the PLF during microsaccade preparation. This impairment in the ability to perceive fine spatial stimuli at the PLF before the onset of the microsaccade indicates a shift in processing resources from the PLF to the microsaccade goal location, which aligns with the results of recent work examining performance at the center of gaze during preparation of larger saccades.[63] These findings suggest that, to allocate attentional resources more efficiently, the visual system prioritizes processing of stimuli that are about to be foveated by disengaging attention from its current location and shifting it to its target location.[65]

The perceptual enhancement reported here was mainly driven by pre-microsaccadic attention; when microsaccades were not performed in the presence of a directional cue, performance in the task was substantially lower. Interestingly, however, in this latter condition performance was slightly but significantly higher compared with the neutral condition in which no directional cue was presented. There are a few possible reasons for this enhancement. First, it is possible that observers prioritized perceptual processing at the cued location over other locations to ease the memory burden imposed by the task design in experiment 1.[52] Second, because of the relatively short interval of 200 ms between the cue and the target presentation in the current study, the engagement of covert attention may be a gradual process that builds up over time, with an earlier onset[66,67] and peaks around 300 ms. Therefore, it is possible that covert attention starts to be engaged in parallel with the planning of a microsaccade. Crucially, whether this effect reflects memory selection, covert attention, or a combination of both, it only accounts for a small portion of the perceptual enhancement reported in the presence of microsaccades. In fact, the overall performance was almost 1 unit of $d'$ higher when a microsaccade was executed.

Notably, in our study the target was shown after the motor cue, and microsaccades took about 300 ms to be executed. As a result, the average time between target disappearance and microsaccade onset was approximately 200 ms. According to work from Ohl and Rolfs,[68] saccades affect visual short-term memory by facilitating sensory encoding of the saccade goal when they are performed 100–800 ms after the memory items disappear. Therefore, it is possible that the perceptual enhancement reported here also reflects the influence of microsaccades on visual short-term memory.

Humans perform microsaccades frequently in everyday life during tasks such as reading, exploring fine-detailed stimuli, or looking at objects from a distance.[3,10,13] Microsaccades can not only reshape vision by enhancing our ability to see complex foveal details at the microsaccade goal but can also alter visual perception at the center of gaze, where visual acuity is normally the highest. Together, this highly localized enhancement at the microsaccade goal and the concomitant suppression of fine spatial vision at the PLF are crucial to facilitate the processing of fine-detailed stimuli before the gaze shifts

to the object of interest. Further, our work sheds light on the highest spatial resolution of attention that can be attained at the foveal scale, revealing the striking sophistication of the human visuomotor system.

## STAR★METHODS

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## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2023.11.064.

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## AUTHOR CONTRIBUTIONS

M.P., Y.G., and N.S. designed research. Y.G. and N.S. performed research. Y.G., N.S., and M.P. analyzed data. M.P., Y.G., and A.M.C. wrote the paper.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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# STAR★METHODS

## KEY RESOURCES TABLE

| REAGENT and RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Deposited data | | |
| Original data | This paper | https://doi.org/10.17632/s82sc4mv34.1 |
| Software and algorithms | | |
| MATLAB code to process data | This paper & Mathworks | https://www.mathworks.com/ |

## RESOURCE AVAILABILITY

### Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead contact, Martina Poletti martina_poletti@urmc.rochester.edu.

### Materials availability

This study did not generate new unique reagents.

### Data and code availability

The data-set gathered during this study has been deposited to Mendeley data: https://doi.org/10.17632/s82sc4mv34.1. This study used standard, custom-built MATLAB programmed scripts that are available from the lead contact upon request.

## EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

### Human subjects

Sixteen human observers (4 males and 12 females; age range: 18–30 years) with emmetropic or corrected vision participated in the experiments. Seven observers took part in Experiment 1 (Figures 2A, 2B, and 4). Four observers took part in Experiment 2 (Figure 3). Eleven observers initially took part in Experiment 3 but three were dropped because performance was at chance level. The reported results are based on eight subjects (Figure 5A). The experiment was approved by the University of Rochester Institutional Review Boards. The experimenter reviewed and explained the material in the consent form to the participant before conducting the experiment. The form was signed only after the participant fully understood the material and voluntarily agreed to take part in the study. Consent was obtained from all participants in the study.

## METHOD DETAILS

### Apparatus

In Experiments 1 and 3, stimuli were displayed on an LCD monitor (Acer Predator XB272) at a refresh rate of 144 Hz and spatial resolution of 1920 x 1080 pixels. In Experiment 2, stimuli were displayed on an OLED monitor (Alienware AW5520QF) at a refresh rate of 120 Hz and spatial resolution of 3840 x 2160 pixels. Observers performed the task monocularly with their right eye while the left eye was patched. A dental-imprint bite bar and a headrest were used to prevent head movements. Eye movements were recorded with high precision either by means of a Generation 6 Dual Purkinje Image (DPI) eye tracker[42] (Fourward Technologies) in Experiment 1, with a 1-kHz sampling rate or by means of a custom-made digital Dual Purkinje Image (dDPI) eye tracker in Experiment 2 and 3, with a sampling rate of 340 Hz.[44] Both systems have an internal noise well below 1′ and a spatial resolution of 1′.[43,44] Stimuli were rendered by means of EyeRIS, a custom-developed system that allows flexible gaze-contingent display control.[45] This system acquires eye movement signals from the eye tracker, processes them in real-time, and updates the stimulus on the display according to the desired combination of estimated oculomotor variables.

### Data collection

Every session started with initial setup of the bite bar. For experiments conducted with the DPI eyetracker, observers were asked to rest their forehead on the headrest. For experiments conducted with the dDPI eyetracker, a magnetized helmet was used to position their head. When accurate localization of gaze position is necessary, calibration represents an important stage of the experimental procedure, performed in two phases. During the first phase, observers sequentially fixated on each of the nine points of a 3-by-3 grid, as is customary in all oculomotor experiments. In the second phase, observers refined the voltage-to-pixel or pixel-to-pixel mapping, for DPI and dDPI respectively, given by the automatic calibration. They fixated again on each of the nine points of the grid while the location of the line of sight was displayed in real-time on the screen. Observers used a joypad to correct the predicted gaze location,

shifting the real-time display to align with the grid point for each fixation, if necessary. These corrections were then incorporated into the transformation of the gaze position as well. This dual-step calibration procedure allows more accurate localization of gaze position than standard single-step procedures. The manual calibration procedure was repeated at the center of the fixation before each trial to compensate for possible drifts in the electronics as well as unpreventable head movements.

***Experiment 1 (Figures 2A, 2B, and 4)***

Observers were instructed to fixate on a central box (7.5′-by-7.5′) surrounded by 8 squares of the same size arranged in a circle with a radius of 20′. After a short period of fixation, a cue appeared for 100 ms. In congruent and incongruent trials a directional motor cue was displayed pointing to one of the four cardinal directions. Observers were instructed to shift their gaze based on the motor cue direction as soon as it appeared. In neutral trials, a non-directional cue pointing in all four directions appeared surrounding the central square, instructing observers to maintain their fixation at the center. As soon as the cue disappeared, high-acuity stimuli, lines tiled 45° either to the left or right, were presented for 100 ms simultaneously within each square. 600 ms after the stimuli offset a response cue was presented and observers were instructed to report the orientation of the stimulus previously presented at that location. In congruent/incongruent trials, the saccade cue indicated the same/different location as the response cue. Congruent condition had a probability of $\approx 10-20\%$ of occurring. All other incongruent locations had an equal probability of $\approx 10-11\%$ of being tested. Performance in the neutral condition was above chance level (61% ± 5%) in five (within-subject Z-test for proportions, $P < 0.0008$) out of seven observers.

***Experiment 2 (Figure 3A)***

Observers were instructed to fixate on a central marker (5′×5′) surrounded by two squares, signaling the microsaccade goal location 20′ to the right and to the left of the marker. Observers were instructed to shift their gaze as soon as possible based on the direction of a motor cue. After a variable blank interval (100 to 260 ms), two high-acuity stimuli, bars tiled ±45°, were presented for 50 ms simultaneously to the right and to the left of the central fixation maker. Observers were instructed to report the orientation of the stimulus presented on the side indicated by the initial motor cue. Stimuli randomly appeared at the same eccentricity (20′) from the fixation marker but varied in distance between 0′ to 20′ from the saccade goal location.

***Experiment 3 (Figure 5A)***

Experiment 3 was identical to Experiment 1 except that the target had the same probability of being presented at the center and at another peripheral location in the array and only the four peripheral cardinal locations were tested besides the central location.

## QUANTIFICATION AND STATISTICAL ANALYSIS

### Analysis of oculomotor data

Recorded eye movements were segmented into drift and saccades. Classification of eye movements was performed automatically and then validated by trained laboratory personnel. Trials were discarded if large saccades occurred at anytime between the saccade cue onset and target offset and/or gaze position drifted more than 10′ away from the central marker during this time. Trials in which no microsaccade was performed 450 ms after target onset were categorized as no microsaccade trials.

Saccades with an amplitude of less than 30′ were defined as microsaccades. In the neutral condition, to ensure that observers maintained their gaze at the center, trials with microsaccades anytime between the saccade cue and response cue onset were discarded.

### Analysis of performance

Statistical comparisons between different conditions across observers were conducted using two-way ANOVA (subject x condition) followed by Tukey post hoc tests in MATLAB. Comparisons between any two conditions were examined by means of paired two-tailed t-tests. On average, performance was evaluated over 100 trials per trial type per observer. Performance was expressed as a measure of the sensitivity index, $d'$, based on observers' performance in the visual discrimination task.[69]