Modulations of foveal vision associated with microsaccade preparation

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It is known that attention shifts prior to a saccade to start processing the saccade target before it lands in the foveola, the high-resolution region of the retina. Yet, once the target is foveated, microsaccades, tiny saccades maintaining the fixated object within the fovea, continue to occur. What is the link between these eye movements and attention? There is growing evidence that these eye movements are associated with covert shifts of attention in the visual periphery, when the attended stimuli are presented far from the center of gaze. Yet, microsaccades are primarily used to explore complex foveal stimuli and to optimize fine spatial vision in the foveola, suggesting that the influences of microsaccades on attention may predominantly impact vision at this scale. To address this question we tracked gaze position with high precision and briefly presented high-acuity stimuli at predefined foveal locations right before microsaccade execution. Our results show that visual discrimination changes prior to microsaccade onset. An enhancement occurs at the microsaccade target location. This modulation is highly selective and it is coupled with a drastic impairment at the opposite foveal location, just a few arcminutes away. This effect is strongest when stimuli are presented closer to the eye movement onset time. These findings reveal that the link between attention and microsaccades is deeper than previously thought, exerting its strongest effects within the foveola. As a result, during fixation, foveal vision is constantly being reshaped both in space and in time with the occurrence of microsaccades.

high-acuity vision | eye movements | attention

Saccades bring objects of interest into the foveola, the 1° retinal region where visual resolution is highest. It is well established that extrafoveal visual perception is modulated in correspondence with saccade preparation (1, 2). This modulation appears to depend on fast presaccadic shifts of attention (1, 3). Even before the eye starts to move, peripheral vision is enhanced (4–8), and sensory tuning is reshaped at the saccade target location; the gain of high spatial frequencies increases (9, 10), and orientation tuning narrows (5, 9). These changes occur only briefly, from approximately 60 to 100 ms before the onset of a saccade (4, 5, 9–13), and have a profound influence on visual perception, as humans perform saccades every few hundred milliseconds.

What are the benefits of this sensory tuning of the visual input? Because high-acuity vision is limited to the small 1° foveal region, one obvious advantage of this mechanism is that the low-resolution presaccadic input is briefly enhanced and sharpened before it lands on the high-resolution fovea (9, 10). This effectively offers a glimpse of what is going to fall at the center of gaze after the saccade (14). In addition, presaccadic attention is also believed to play a role in maintaining spatial stability across saccades (6, 9, 15–17) and in keeping track of the attended objects across saccades (6, 13, 18).

However, saccades are not only made to reorient the fovea. Tiny saccades, less than 0.5° in size, known as microsaccades, occur at a relatively high rate (19), once the object of interested is foveated. In the presence of naturally rich foveal stimuli, these miniature saccades are precisely controlled. They shift the fixated object within the foveola (20, 21) to enable task-driven exploration of the foveal stimulus following similar strategies to larger saccades (22). Recent findings have shown the existence of premicrosaccadic changes of visual perception at locations much farther away from the retinal location targeted by the microsaccade (23). Other findings revealed the presence of a link between microsaccade preparation and peripheral processing at the neural level (24); microsaccade preparation leads to a neural enhancement of stimuli that are presented at an eccentric location congruent with the microsaccade direction. Current evidence, therefore, suggests that the effects associated with microsaccade preparation are primarily exerted in the visual periphery.

While the perceptual consequences of microsaccades have been examined only with stimuli very far from their landing positions, recent research has shown that covert attention, independently of microsaccades, can be selectively deployed within the foveola to retinal locations that are less than 20 arcmin away from the preferred locus of fixation (25). This finding raises the possibility that premicrosaccadic shifts of attention can selectively modulate visual perception within the foveola itself, rather than just at more peripheral locations. If present, these modulations could play a crucial role in reducing nonuniformities in foveal vision (21) and facilitate visual discrimination of foveal stimuli away from the preferred locus of fixation.

Significance

A tight relationship exists between eye movements and attention. Attention briefly shifts ahead of saccade execution, contributing to the processing of the saccade target before it lands in the high-resolution fovea. Yet, once the target is foveated, microsaccades, tiny saccades maintaining the fixated object within the foveal boundaries, continue to occur. The link between attention and microsaccades has been less investigated. Using high-precision eyetracking we examined whether and how foveal vision is affected by microsaccade preparation. Our findings show that during fixation foveal vision is modulated in a peculiar way both in space and in time. Right before microsaccade onset a surprisingly selective enhancement of high-acuity vision occurs at its target location.

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Data deposition: The data necessary to generate all of the figures (containing data) in the main text and the matlab scripts used to produce these figures have been deposited in the Open Science Framework repository (https://osf.io/hvjy7/).

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Addressing these issues is important to better understand the oculomotor contribution to foveal vision, as well as the spatiotemporal dynamics of visual perception during fixation. Here we investigate whether and how visual acuity at selected foveal locations changes before the onset of microsaccades.

Results

To investigate whether premicrosaccadic attentional shifts modulate visual perception in the foveola we recorded eye movements at high resolution while subjects performed a fine spatial vision task. Subjects were asked to discriminate the orientation of a high-acuity stimulus briefly presented before the onset of a microsaccade (Fig. 1 *A*–*C*). They were instructed to fixate on a marker and shift their gaze as soon as a saccade cue appeared at the marker position indicating where to look. Based on the direction of this signal, gaze was shifted toward one of two foveal locations only 20′ away. Microsaccades had to be performed to precisely shift gaze. Soon after the saccade signal, while the microsaccade was being prepared, two high-acuity stimuli were briefly presented, one at each location. After the gaze shifted, a response cue appeared, and subjects reported the orientation of the stimulus that was previously presented at that location.

Because of the way the experiment was designed, microsaccades performed in a trial could either land at the position indicated by the response cue (congruent trials) or land at the opposite location (incongruent trials). The experiment also included a neutral condition. In this condition, the saccade signal was not presented, and subjects maintained fixation without performing a microsaccade (Fig. 1*B*). Congruent, incongruent, and neutral trials had the same probability of occurring in the task; i.e., the saccade cue was independent of the response cue location.

Shifting the gaze in minute amounts on command may not be as simple as executing a saccade toward a peripheral target. Early work has shown that humans are capable of generating microsaccades as small as 3′ in response to small steps of a fixation marker (26). However, there are no previous reports documenting the accuracy of these small eye movements when produced voluntarily in response to a central cue. Therefore, we first ensured that subjects were capable of precisely shifting their gaze to the nearby stimuli based on the saccade cue. To this end, we examined the average landing error of microsaccades, i.e., the distance between the microsaccade landing position and the stimulus location as indicated by the saccade cue. Fig. 2*A* and *SI Appendix*, Fig. S1 show the average two-dimensional (2D) distribution of microsaccade landing positions for trials in which the saccade cue pointed to the left and to the right location, respectively. The average SD of the landing error was $6.4' \pm 1.8'$ and $4.1' \pm 1.2'$ on the x and y axes for leftward microsaccades and $6.2' \pm 1.7'$ and $3.5' \pm 1'$ on the x and y axes for rightward microsaccades (the average landing location was $-18' \pm 3.8'$ on x, $-0.1' \pm 1.7'$ on y and $17.9' \pm 2.2'$ on x, $0.6' \pm 1.4'$ on y for leftward and rightward microsaccades, respectively). Although with some variability (*SI Appendix*, Fig. S1), all subjects were able to shift their gaze with remarkable precision based on the direction indicated by the cue.

Executing precise microsaccades was not the only task requirement. Microsaccades also had to be performed in a timely manner soon after the presentation of the saccade signal. It is known that microsaccades are characterized by longer latencies compared to saccades (27). Depending on the task, latencies of microsaccades can be up to 200 ms slower than those of saccades (28, 29). In our task, the average latency of microsaccades, measured as the time between the saccade signal onset and the onset of the microsaccade, was 457 ± 112 ms (Fig. 2*B* and *SI Appendix*, Fig. S2). These values are larger than those reported in the literature, most likely because microsaccades in this task were elicited by a central cue rather than by a stimulus presented at a given foveal eccentricity or by a step of the fixation marker. Furthermore, the central fixation marker was not turned off, but remained visible throughout the trial, further delaying the gaze shift (30). To ensure that microsaccades were performed in a timely manner, we selected only the trials with the faster microsaccade latencies for our main analysis. This selection was based on each subject's latency distribution (*SI Appendix*, Fig. S2;

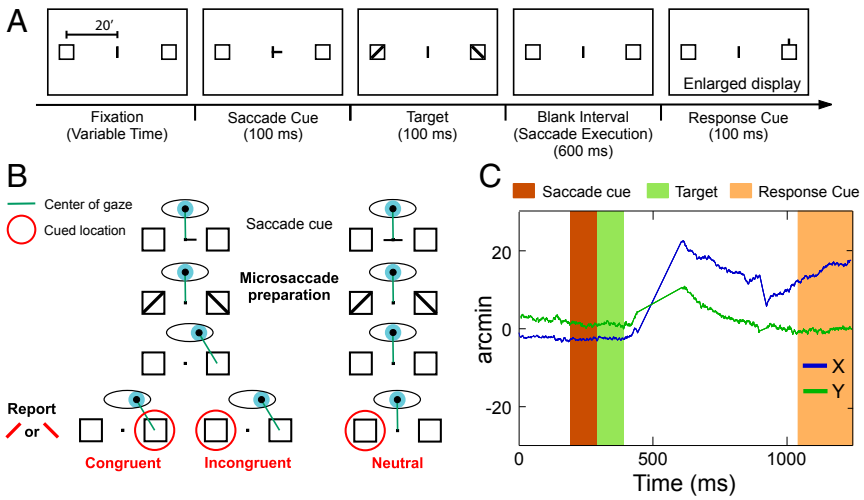

Fig. 1. Methods. (*A*) Experimental protocol. Subjects maintain fixation on a central marker surrounded by two squares (5′ × 5′ in size) 20′ away. After a brief period of fixation, a central saccade cue appears, instructing the subject to shift the gaze as soon as possible to one of the two squares. Immediately after the saccade signal, two stimuli, bars tilted ±45°, are briefly presented (100 ms), one in each square. After a blank interval (600 ms), a response cue appears. Subjects are instructed to report the orientation of the stimulus previously presented at the cued location. The direction of the saccade cue is not predictive of the response cue location. (*B*) Microsaccades are prepared during the brief interval between the saccade cue onset and the target offset and are executed right after the target is turned off. In congruent trials, microsaccades land on the previously cued location. In incongruent trials, microsaccades land on the opposite side of the cued location. In neutral trials, the saccade cue is replaced by central arrows pointing in both directions, and subjects maintain fixation throughout the trial. All types of trials had the same probability of occurrence. (*C*) An example of a typical eye movement trace during the course of a trial.

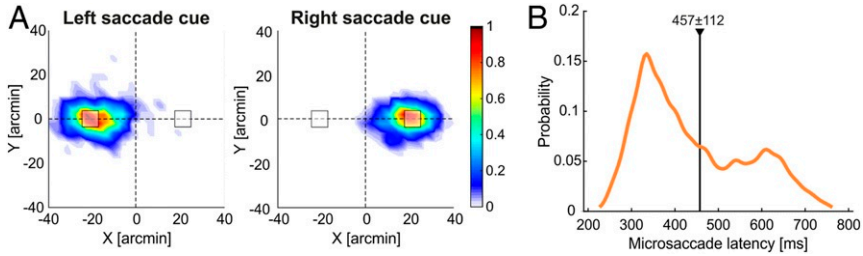

Fig. 2. Microsaccades in the task. (*A*) Average 2D normalized microsaccade landing position distribution probability for trials in which the saccade cue pointed to the left and to the right, respectively. White shaded squares, drawn to scale, represent the location where the stimuli appeared. (*B*) Average microsaccade latency distribution. The black solid line marks the average of the distribution.

z scores for each participant: −0.7, −0.4, −0.6, 0.8, −0.8, 1.7). In these selected trials microsaccade latency was on average 384 ± 105 ms.

Our data show that the ability to discriminate the orientation of high-acuity stimuli, measured as d', was enhanced in congruent trials compared to incongruent and neutral trials (2.07 ± 0.69, 0.83 ± 0.41, and 1.28 ± 0.49 for congruent, incongruent, and neutral trials, respectively, ANOVA F(4,20) = 9.88, $P < 0.0001$; Tukey's honest significance (HSD) post hoc tests, congruent vs. incongruent, $P < 0.0001$; congruent vs. neutral, $P = 0.006$; neutral vs. incongruent, $P = 0.21$; Fig. 3 *A* and *B* and *SI Appendix*, Fig. S3). Preparing a microsaccade had the immediate effect of selectively enhancing fine spatial vision at its target location. On the contrary, fine spatial vision at the opposite foveal location was substantially impaired. These results show that processing of the microsaccade target starts well ahead of the microsaccade execution.

Not only was performance lower in the incongruent trials; manual response reaction times were also longer (309 ±118 ms, 437 ±133 ms, and 338 ±100 ms, for congruent, incongruent, and neutral trials, respectively, ANOVA F(4,20) = 9.9, $P < 0.001$; Tukey's HSD post hoc tests, congruent vs. incongruent, $P < 0.0001$; congruent vs. neutral, $P = 0.8$; neutral vs. incongruent, $P = 0.004$; Fig. 3*C*). Such a difference in reaction times was not driven by the trial selection criteria. Crucially, this finding shows that the higher performance in congruent trials was not the result of speed–accuracy tradeoff; i.e., longer reaction times did not increase discrimination accuracy, further supporting the idea that microsaccade preparation was responsible for the main effect reported here. The slowing down of processing times in incongruent trials also highlights the importance of reducing the impact of distractors. Saccade targets are generally not viewed in isolation; in natural conditions they are embedded in a complex visual environment where several distractors are present. Therefore, slowing down the processing of stimuli other than the saccade target likely has the effect of further increasing sensitivity to the saccade goal, and it may be instrumental in improving the precision and accuracy of microsaccades. This could be particularly important for microsaccades directed toward fine spatial stimuli, when even a small error in amplitude may result in the saccade target falling outside the small preferred locus of fixation where sensitivity is highest.

The results reported here are not due to changes of gaze position in the interval preceding the onset of the stimuli. Because of their temporal dynamics, microsaccades normally occurred after the stimuli presentation. Furthermore, we selected only trials in which no microsaccade occurred before the saccade cue. Still, gaze position during fixation may shift many arcminutes away from the central marker due to ocular drift. Therefore, to ensure that stimuli were always displayed at similar retinal eccentricities in all conditions we selected only trials in which the distance of gaze from the central fixation marker remained below $10'$ (arcminutes) until the offset of the high-acuity stimuli. In the trials selected for data analysis the average retinal distance between the center of gaze and the fixation marker was similar in all conditions ($-0.5' \pm 1.1'$, $-0.5' \pm 1'$, and $-0.4' \pm 0.8'$ for congruent, incongruent, and neutral trials, respectively; Fig. 4) and for both leftward and rightward saccade signals (*SI Appendix*, Fig. S4). Since, during stimulus presentation, retinal stimulation was comparable across trials, conditions differed in the oculomotor behavior only after the stimulus offset, whether or not a microsaccade occurred (neutral vs. congruent and incongruent trials) and whether or not it landed at the location indicated by the response cue (congruent vs. incongruent trials).

Endogenous covert attention requires at least 300 ms to be deployed (31–34). In the present protocol, the interval between

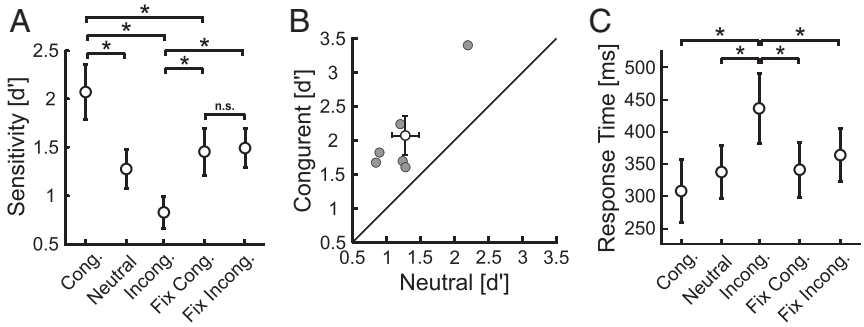

Fig. 3. Perceptual effects of microsaccade preparation. (*A*) Average ($N = 6$) sensitivity (d') in different trial types. Performance is also shown for trials in which a saccade cue was presented but subjects did not perform a microsaccade (fixation congruent/incongruent). (*B*) Performance in neutral trials plotted against performance in congruent trials. The white data point and error bars represent group mean and SEM. The gray circles represent single-subject data. (*C*) Average manual response times. Error bars are SEM. Asterisks mark a statistically significant difference (*$P < 0.05$, Tukey's post hoc test).

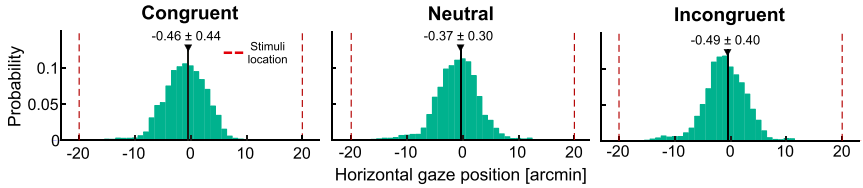

Fig. 4. Gaze position during stimuli presentation. Shown is average distribution of horizontal gaze position when stimuli were displayed in the three conditions tested. Red dashed lines indicate the locations of the stimuli. Solid lines represent the average of the distributions.

the onset of the saccade cue and stimuli offset was of only 200 ms, suggesting that covert voluntary attention was not responsible for the reported effect. To determine whether these spatially selective modulations of foveal vision were caused by microsaccade preparation rather than covert shifts of attention, we examined subjects' performance in the congruent and incongruent trials in which microsaccades did not occur. Our findings show that on average, the difference in performance ($\Delta d'$) between these two types of trials was minimal and statistically not different from zero in the absence of microsaccades (1.46 ± 0.6 and 1.49 ± 0.5 for congruent and incongruent trials, respectively; $P = 0.87$, Tukey's HSD post hoc test, Fig. 3*A*). *SI Appendix*, Fig. S3 shows that this null effect was the result of some observers exhibiting a higher and others a lower performance in the congruent compared to the incongruent trials. For the two observers showing a higher performance in the congruent condition, the size of the effect was about half of that when a microsaccade was executed. A residual effect in the absence of microsaccades may reflect either an early influence of covert attention or a planned and then aborted microsaccade. On the other hand, a lower performance in congruent compared to incongruent trials for other subjects may be the result of an active suppression of microsaccades, as in most of these trials subjects were explicitly instructed to maintain fixation. Therefore, the difference between congruent and incongruent trials seen in the task was primarily the consequence of microsaccade preparation.

The reported changes in visual perception preceding microsaccade execution were also modulated by the onset time of the microsaccade. If microsaccades with longer latencies were included in the analysis, a stronger effect was observed when the target appeared 233 ± 72 ms before the onset of the microsaccade; the intensity of the effect then progressively decreased as the temporal interval between the target onset and the microsaccade onset increased (1.2 ± 0.42, 0.52 ± 0.4, shortest vs. longest delay; $P = 0.02$, Tukey's post hoc test; Fig. 5). Although individual differences were present, all subjects showed the same trend (*SI Appendix*, Fig. S5). These results indicate that closer to the onset time of a microsaccade, the modulation of visual perception within the foveola is stronger.

Discussion

In this study we examined modulations of visual perception within the foveola during the time of microsaccade preparation. This was possible due to high-precision eye tracking and a gaze-contingent display system allowing for accurate gaze localization, capabilities that are beyond what can be achieved with standard eye-tracking techniques. Our findings reveal that during fixation, visual perception at the foveal scale is constantly being reshaped in a spatially selective way before the onset of microsaccades. More specifically, microsaccade preparation leads to an enhancement of fine spatial vision at the microsaccade target location, as well as a concomitant reduction of fine spatial vision at the nontargeted location, even if these locations are just a few arcminutes away from each other. This effect is strongest up to about 200 ms before the onset of the microsaccade and decreases with time. Although at a different spatial and temporal scale, these findings echo what happens in the visual periphery during saccade preparation (4). Notably, these findings are not what we would expect based on the current evidence, according to which the effects of microsaccade execution/preparation are associated with peripheral modulations of sensitivity/neural activity and peripheral allocation of covert attention (23, 24). Differently, here we show that, in the presence of complex foveal stimuli, a condition more akin to natural viewing, there are significant perceptual consequences of microsaccades at the foveal scale.

The outcome of our study prompts the question, what is the function of such a refined premicrosaccadic attention mechanism? One possibility is that it connects pre- and postmicrosaccadic percepts, in a similar way to how presaccadic attention operates at a larger scale. Presaccadic attention is, indeed, believed to act as a bridge between the lower-resolution presaccadic and the high-resolution postsaccadic stimulation (9, 10, 14). At the foveal scale, the differences between the pre- and postmicrosaccadic stimulation are not as drastic as between the fovea and the visual periphery. Yet, fine pattern vision is not uniform across the foveola and it begins to deteriorate already 10′ away from the preferred locus of fixation (21). Hence, enhancing visual discrimination at the microsaccade target location may effectively render the percept at that location more homogenous with the percept at the preferred locus of fixation.

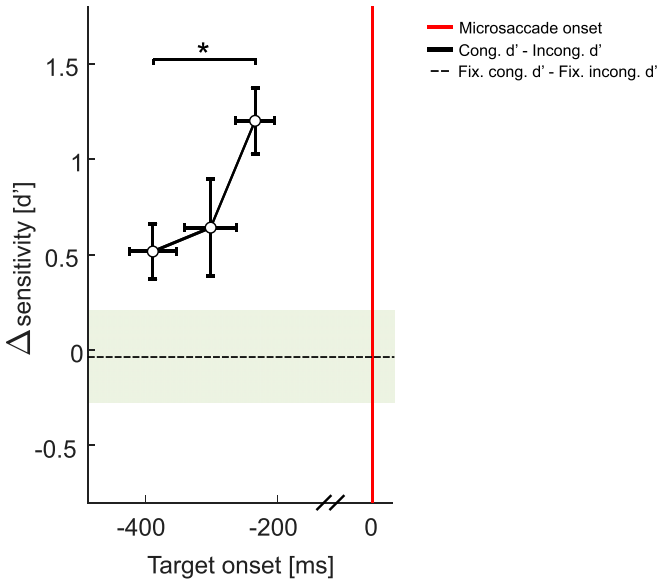

Fig. 5. Temporal course of the effect. Shown is the difference in performance between congruent and incongruent trials ($\Delta d'$) as a function of time relative to saccade onset (red line). Dashed lines indicate the average difference between fixation congruent and incongruent trials in which no microsaccades were performed. Error bars are SEM. The asterisk marks a statistically significant difference (*$P < 0.05$, Tukey's post hoc test).

Another function of this premicrosaccadic mechanism may be that of aiding the maintenance of visual stability during periods of fixation. Generally, the need for visual stability is associated with saccades shifting the retinal input of large amounts. Although microsaccades may not produce noticeable shifts in the visual stimulation across the entire visual field, they cause major changes of the visual input in the foveola. Still, the human percept during fixation is that of a seamless and stable foveal stimulus. How stability at this scale is maintained when the eye drifts is a matter of debate (35, 36). However, it is likely that microsaccades have an associated corollary discharge signal (37, 38), which can be used to update foveal spatial representations according to the upcoming eye movement.

This research also shows that microsaccades benefit vision not only by spatially relocating the preferred locus of fixation on the detail of interest (21), but also by selectively modulating foveal vision during their preparation time. Overall, these two effects together lead to a >300-ms time frame in which the percept at the location of interest is viewed at the highest possible resolution. This can be crucial when exploring foveal stimuli and visual detail (22), especially when considering that the visual system may experience a general drop in visual sensitivity across the foveola during the time a microsaccade is being executed (39).

Importantly, the benefits of premicrosaccadic shifts of attention are associated not only with an enhanced visual perception at the attended foveal locations, but also with a reduction of sensitivity to distractors at other foveal locations. This could be particularly crucial when dealing with a crowded foveal input, which happens often when we examine a visual scene from a distance. This is similar to what happens when covert attention is focused at a specific location within the foveola; perceptual benefits at the attended location are accompanied by impairments at the nonattended locations (25).

Interestingly, the reported effects of presaccadic attention are generally limited to ≈100 ms before the saccade onset. In contrast, here we found that, for microsaccades, the temporal dynamics of this effect extend to a longer period before the onset of the microsaccade, with smaller effects seen as early as 400 ms before the microsaccade onset (Fig. 5). This longer time frame is, at least in part, the result of the slower microsaccade latencies; normal saccadic latencies range between 150 and 200 ms (27), whereas microsaccade reaction times are significantly longer (25). Depending on the size of the microsaccade, latency can be up to 350 ms or longer. Notably, not only are saccadic latencies longer at this scale, but also detection reaction time is longer for stimuli appearing in the foveola than in the parafovea (25). Therefore, this different time frame may simply reflect the longer processing times characterizing foveal vision not only at the cortical level, but also at the retinal stage (40).

Finally, this study raises an important issue: The perceptual effects, as well as the neural dynamics, induced by microsaccade execution and preparation have been, for the majority, studied using peripheral stimuli and a deprived foveal input, generally consisting of a fixation marker. In normal conditions, however, foveal stimulation is rich in detail, and one of the main functions of microsaccades is that of enabling visual exploration of the foveal input (22). It is, therefore, crucial to examine the neural and perceptual correlates of microsaccades in the presence of a more complex foveal stimulus. This is a difficult problem to address, as it requires the ability to track eye movements at high resolution with fine spatial accuracy, limit visual stimulation to specific foveal locations, and/or selectively record from neurons coding the foveal input. Our findings show that in this context, microsaccades are associated with spatially selective modulations of the foveal visual field. Naturally, this observation leads to the question of what happens when both peripheral and foveal stimuli relevant for the task are present at the same time. Are microsaccades and their associated perceptual effects limited to the peripheral or the foveal input or both? Further research is needed to address this question.

In sum, our study shows how visual perception is selectively modulated across the foveola and how these modulations are time locked with the onset of microsaccades. Vision across the foveola is not uniform; it constantly changes in space and time over the short duration of a fixation period in relation with microsaccade preparation. These changes not only are spatially selective, characterized by a remarkably fine spatial resolution, but also follow a specific time course, which seems to operate on a different temporal scale than for larger saccades.

Methods

Observers. A total of six emmetropic human observers (five females and one male), all naive about the purpose of the study, participated in the experiment (age range 18 to 29 y). The full study protocol was approved by the Boston University Charles River Campus Institutional Review Board and informed consent was obtained from all participants following procedures approved by this board.

Stimuli and Apparatus. Stimuli were displayed on a fast-phosphor CRT monitor (Iyama HM204DT) at a vertical refresh rate of 85 Hz and spatial resolution of 2,048 × 1,536 pixels (1 pixel = 0.53′). Observers performed the task monocularly with their right eye while the left eye was patched. A dental-imprint bite bar and a headrest prevented head movements. The movements of the right eye were measured by a Generation 6 Dual Purkinje Image (DPI) eye tracker (Fourward Technologies), a system with an internal noise of 20 arcsec and a spatial resolution of 1 arcmin. Vertical and horizontal eye positions were sampled at 1 kHz and recorded for subsequent analysis. Stimuli were rendered by EyeRIS, a custom developed system based on a digital signal processor, which allows flexible gaze-contingent display control. 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.

Procedural and Experimental Tasks. Every session started with preliminary setup operations that lasted a few minutes. The subject was positioned optimally and comfortably in the apparatus. Afterward, a calibration procedure was performed in two phases. In the first phase, subjects sequentially fixated on each of the nine points of a 3 × 3 grid, as is customary in oculomotor experiments. These points were located 90 pixels apart on the horizontal and vertical axes. In the second phase, subjects confirmed or refined the voltage-to-pixel mapping given by the automatic calibration. In this phase, they fixated again on each of the nine points of the grid while the location of the line of sight estimated on the basis of the automatic calibration was displayed in real time on the screen. Subjects used a joypad to correct the predicted gaze location, if necessary. These corrections were then incorporated into the voltage-to-pixel transformation. This dual-step calibration allows a more accurate localization of gaze position than standard single-step procedures, improving 2D localization of the line of sight by approximately one order of magnitude. The manual calibration procedure was repeated for the central position before each trial to compensate for possible drifts in the electronics as well as microscopic head movements that may occur even on a bite bar. Subjects were instructed to fixate on a marker located between two 5′ × 5′ boxes at the center of the display. After an initial fixation period, a horizontal line would appear from the fixation marker, pointing to the left or the right. Subjects shifted their gaze on the box indicated by this signal. If the horizontal line bisected the fixation marker, subjects were instructed to maintain their gaze on the marker and these were categorized as neutral trials. As soon as the saccade signal was turned off, high-acuity stimuli, 7′ × 1′ bars, tilted 45° to the right or to the left, were presented one in each box simultaneously for 100 ms. The contrast of these stimuli, ranging from black to a neutral gray, was adjusted to achieve 75% performance on neutral trials. Six hundred milliseconds after the stimuli offset, a vertical line, a response cue, would appear above one of the two boxes. Subjects were asked to report the orientation of the stimulus previously presented in that box by pressing a button on a remote controller within a 4-s time period following the response cue presentation. Trials in which subjects successfully shifted their gaze in the direction of the saccade cue were labeled congruent if the saccade signal

direction and the response cue direction matched and incongruent if they did not match.

Data Analysis. Recorded eye movement traces were segmented into separate periods of drift and saccades. Classification of eye movements was performed automatically and then validated by trained laboratory personnel with extensive experience in classifying eye movements. Periods of blinks were automatically detected by the DPI eye tracker and removed from data analysis. Only trials with optimal, uninterrupted tracking, in which the fourth Purkinje image was never eclipsed by the pupil margin, were selected for data analysis. Eye movements with minimal amplitude of 3′ and a peak velocity higher than 3°/s were selected as saccadic events. Saccades with an amplitude of less than 0.5° (30′) were defined as microsaccades. Consecutive events closer than 15 ms were merged together into a single saccade to automatically exclude postsaccadic overshoots. Saccade amplitude was defined as the vector connecting the point where the speed of the gaze shift grew greater than 3°/s (saccade onset) and the point where it became less than 3°/s (saccade offset). Periods that were not classified as saccades or blinks were labeled as drifts. Trials with blinks/loss of tracks (0.2%) were discarded. Only congruent and incongruent trials in which only one microsaccade occurred in the interval between target offset and response cue onset were used for analysis. In all conditions, trials with microsaccades occurring in an 80-ms period preceding the saccade signal onset were discarded. Comparisons between conditions across observers were tested using d' tests. On average, performance was evaluated over more than 400 trials per observer. d' was used as a measure of the sensitivity index based on subjects' performance in the visual discrimination task (41).

Data Availability. The data necessary to generate all of the figures (containing data) in the main text and the matlab scripts used to produce these figures have been deposited in the Open Science Framework repository (https://osf.io/hvjy7/).

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