Behavioral/Cognitive

Spatial and Temporal Factors Influencing Fixational Saccades

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Much research has focused on how perceptual, cognitive, and attentional processes modulate microsaccades, the small rapid gaze shifts that humans perform when attempting to maintain steady gaze on a point. Yet the reasons why these fixational saccades occur in the first place have remained unclear. Long-standing theories have argued for either spatial (i.e., gaze centering) or temporal mechanisms (i.e., a periodical release process). However, this debate has never been resolved, primarily because of uncertainty in determining where the observer looks. Whereas modern eye-trackers enable detection of small eye movements, accurate localization of the line of sight remains challenging. Here, rather than indirectly inferring gaze position from oculomotor activity, we used a gaze-contingent procedure to directly estimate the perceived center of the visual field, a method that has been previously shown to effectively reduce uncertainty. Our results from subjects of both sexes show that the generation of fixational saccades depends on the interaction of spatial and temporal factors. Fixational saccades are remarkably accurate in correcting for fixation errors, even when gaze is minimally displaced. However, fixational saccades also occur when gaze is centered, but their latency increases as the fixation error decreases. These results suggest that fixational saccades serve an important corrective function when needed, but they can only be avoided for a limited period of time when fixation is already accurate.

Key words: attention; eye movements; fixation; microsaccade; oculomotor control; saccade

Significance Statement

It is unclear why humans perform small rapid gaze shifts (microsaccades) while attempting to maintain steady gaze on a point. Building upon recent advances in eye-tracking and gaze-contingent display control, here we show that normal fixation requires the interplay between two sophisticated processes: the generation of very accurate targeted microsaccades and the selective suppression or delaying of unnecessary ones. These results advance knowledge on the visuomotor strategy by which humans maintain steady gaze and raise questions about how the interplay between these two processes is altered in conditions of impaired fixation.

Introduction

Humans rely on rapid gaze shifts, known as saccades, to explore visual scenes. These abrupt eye movements relocate the line of sight every few hundreds of milliseconds, allowing visual inspection by the foveola, the central 1° region of the retina that holds the highest acuity. While saccades primarily move gaze toward new regions of the scene, minute saccades, known as microsaccades, also occur when the attended object is already within the foveola (Rolfs, 2009; Kowler, 2011; Rucci and Poletti, 2015). Indeed, saccades <30′, which result in >50% overlap between the pre- and post-saccadic images within the foveola, occur frequently during examination of high-acuity detail (Shelchkova et al., 2019; Intoy et al., 2021) and in crowded visual scenes (Poletti, 2023; Prahalad and Coates, 2024).

Under normal viewing conditions, microsaccades yield various perceptual benefits, including precise centering of the stimulus (Ko et al., 2010; Poletti et al., 2013), attentional enhancements (Hafed and Clark, 2002; Engbert and Kliegl, 2003; Poletti, 2023), particularly at the center of gaze (Intoy et al., 2021), as well as temporal transients that facilitate visual processing (Ditchburn, 1973; Martinez-Conde et al., 2006; Mostofi et al., 2020). Interestingly, however, tiny saccades also occur when observers are just asked to maintain steady fixation on a marker without additional visual stimuli and/or tasks (Fiorentini and Ercoles, 1966; Steinman et al., 1973). In the presence of such impoverished conditions, the

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aforementioned perceptual benefits seem less relevant, and it remains unclear why humans continue to execute saccades under these conditions (Fig. 1*A*,*B*). In the following, we will refer to the microsaccades performed while maintaining sustained fixation on a marker as *fixational saccades*.

Two proposals for explaining the occurrence of fixational saccades have long been debated. The first hypothesis relies on spatial factors and goes back to Cornsweet (1956), who proposed that these saccades aim to correct for spatial offsets in the desired fixation location caused by ocular drift, the incessant intersaccadic motion of the eye. This hypothesis, which assumes ocular drift to be incapable of maintaining accurate fixation by itself, is supported by the observation that the rate of fixational saccades decreases under retinal stabilization, when ocular drift no longer causes the fixation marker to move away from the center of gaze (Cornsweet, 1956; Poletti and Rucci, 2010). The second hypothesis relies on temporal factors and goes back to Nachmias (1961), who argued that fixational saccades are an unavoidable component of the strategy adopted by an oculomotor system designed to frequently shift gaze when confronted with the unnatural task of maintaining prolonged fixation. In support of this view are the observations that ocular drift actually acts as a form of

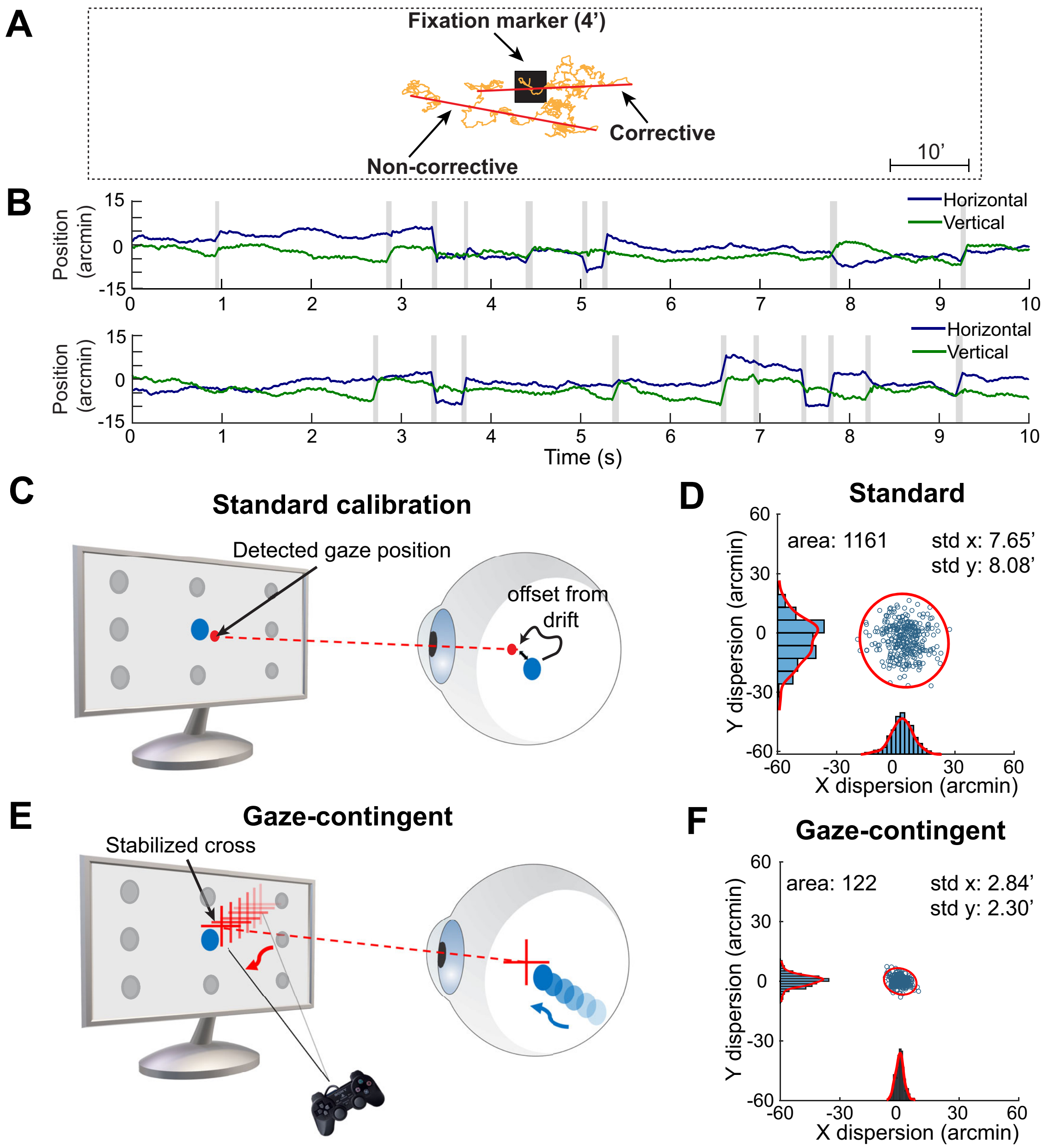

Figure 1. Fixational saccades and gaze localization. ***A***, Small saccades occur during attempted steady fixation. Subjects were instructed to fixate on a 4′ × 4′ white marker presented on a uniform black background. Fixational saccades were classified as corrective or non-corrective (i.e., error-producing) depending on whether they moved the line of sight closer to or farther from the fixation marker. ***B***, Example of gaze position in a trial. The gray bars mark the fixational saccades. ***C–D***, Uncertainty in estimating the center of gaze following standard calibration procedures. ***C***, A standard calibration estimates the line of sight by asking observers to fixate on points at known locations. ***D***, Variability in the gaze position estimated following repeated calibrations on a 9-point grid. Each data point represents the mean gaze position estimated while fixating on a marker. Values in *D* report the standard deviation on each axis and the 95% confidence interval of the resulting region of uncertainty (in arcmin^2). ***E–F***, Benefits of a gaze-contingent refinement of the perceived center of gaze. ***E***, Subjects used a joypad to correct the position of the line of sight, which was displayed in real-time based on the outcome of the 9-point calibration. Corrections where then incorporated into the mapping transformation. ***F***, This procedure substantially improves the precision of gaze localization.

slow control (Steinman et al., 1973; Epelboim and Kowler, 1993; Kowler, 2011; Intoy and Rucci, 2020; Malevich et al., 2020; Lin et al., 2023) and Nachmias' claim that the duration of the interval in between successive fixational saccades tends to be a more reliable predictor of microsaccade occurrence than the fixation error (Nachmias, 1959).

A major difficulty for elucidating the factors involved in the generation of fixational saccades is posed by the need to accurately localize the line of sight. Examination of the possible influence of fixation errors requires pinpointing the center of gaze, i.e., determining the point in the scene that projects onto the center of the preferred fixation locus on the retina. Unfortunately, whereas state-of-the-art eye-trackers enable detection of very small eye movements, accurately mapping the location of the line of sight in the scene remains difficult. Gaze localization is typically achieved via calibration procedures that measure the average signals provided by the eye-tracker while fixating at known points in the scene (Fig. 1*C*). However, multiple factors, including the incessant presence of fixational eye movements and inaccuracies in mapping the eye-tracker output signals into visual angles, contribute to create a region of uncertainty that can easily be as large as the foveola itself. An example is provided in Figure 1*D*, where each data point represents the mean gaze position measured while fixating at the center of the display resulting from a separate repetition of a standard 9-point calibration procedure. Note the dispersion of measurements on both axes, resulting in a considerable region of uncertainty.

To circumvent these challenges, in this study, we examined fixation errors relative to the *perceived center of gaze*. That is, rather than attempting to indirectly estimate the line of sight from the fixational behavior, we directly asked observers to pinpoint their perceived fixation location in the scene (Fig. 1*E*). This was achieved via a gaze-contingent procedure that continually displayed the currently estimated center of gaze and iteratively incorporated the subject's feedback to refine the estimate. We have previously shown that this procedure yields highly consistent results, greatly reducing uncertainty in gaze localization over standard methods (Ko et al., 2010; Poletti and Rucci, 2016). This improvement is shown in the example of Figure 1*F*, in which the gaze-contingent refinement was performed after each repetition of the 9-point calibration in Figure 1*D*. Note that variability decreased by approximately a factor of 3 on each axis following this procedure, about an order of magnitude in two-dimensional space.

Using this approach, in this study, we revisited the contribution of spatial and temporal factors in the generation of fixational saccades by examining how these movements shift the perceptual center of gaze. We show that both classical hypotheses are correct: fixational saccades serve a spatially corrective function when needed, and they are remarkably accurate in correcting for fixation errors. However, fixational saccades also occur when the line of sight is already correctly centered, a counterproductive fixational behavior that appears to originate from limitations in the extent of the temporal window by which saccades can be avoided.

Methods

Subjects

Six observers (three females) with normal, non-corrected vision participated in the study. With the exception of one of the authors, all participants were naive about the purposes of the experiment and were compensated for participating. All subjects possessed uncorrected 20/20 vision, tested by a standard Snellen eye-chart. They were all experienced subjects, meaning that they had prior experience with psychophysical experiments requiring the maintenance of prolonged fixation. Informed consent was obtained from all participants, and the study followed the procedures approved by the Institutional Review Boards at the University of Rochester and Boston University.

Stimuli and apparatus

Subjects maintained fixation on a white 4′ square marker displayed at maximum contrast (14.16 cd/m^2) for periods of 10 s. To ensure precise control of both the task and visual stimulation, the fixation marker was presented in isolation over a uniformly black background (0.003 cd/m^2) in an otherwise dark room. The fixation marker was displayed right in front of the subject, at the center of a fast-phosphor CRT monitor (a 20″ Iiyama HM204DT) at a resolution of 1024×768 pixels and a vertical refresh rate of 200 Hz. Subjects were kept at a fixed distance of 123 cm from the monitor by means of a dental-imprint bite bar and a head-rest so that each pixel covered approximately 1′ in visual angle.

The movements of the right eye were measured by means of a Generation 6 Dual Purkinje Image (DPI) eye-tracker (Fourward Technologies). The internal noise of this system is about 20″ (Crane and Steele, 1985; Ko et al., 2016), enabling a spatial resolution of approximately 1′ (Stevenson and Roorda, 2005). Stimuli were observed monocularly, while the left eye was patched. The analog voltages representing oculomotor signals were first low-pass filtered by a fifth-order Butterworth filter with a 3 dB cutoff frequency at 500 Hz. A high cutoff frequency works well with the DPI eye-tracker, as the signal from inter-saccadic eye motion is over an order of magnitude above the noise level at the relatively low temporal frequencies where most power is concentrated (Ko et al., 2016). Data were then sampled at 1 kHz and saved in digital format.

Procedure

Data from each subject were collected in four experimental sessions conducted on separate days. Each session lasted approximately 1 h and consisted of several blocks of 20 consecutive experimental trials, which also included conditions not presented in this study. Each block of trials lasted for 10–15 mins, with a considerable fraction of time spent on preliminary adjustments to ensure that the subject was comfortably positioned in the apparatus and the eye-tracker well tuned to track the Purkinje images. A calibration procedure then followed to convert the voltages given by the eye-tracker into degrees of visual angle, as described in detail below. These preparatory steps were performed while the room was illuminated by a desk lamp, which was then turned off during data collection, so that the fixation marker was the sole visible stimulus. Breaks were taken in between blocks of trials, when the lights of the room were again turned on. As a consequence, subjects were never constrained in the apparatus for >15 mins consecutively and were minimally dark-adapted. Participants did not spontaneously report experiencing autokinesis, although they were not specifically tested for this effect.

A gaze-contingent calibration was conducted to achieve accurate localization of the perceived center of gaze. As described in previous articles (Ko et al., 2010; Poletti et al., 2013; Poletti and Rucci, 2016), this procedure involved two sequential steps. In the first phase, subjects fixated sequentially on each of the 9 points of a 3×3 grid, a standard practice in eye-tracking experiments. The grid points were spaced 3.38° apart along both the horizontal and vertical axes. These measurements were used to establish an initial mapping between the eye-tracker's output voltages and corresponding visual angles via a bilinear transformation. A bilinear function is sufficient for accurate mapping, given the high linearity of the DPI eye-tracker in the central operating region (Crane and Steele, 1985; Wu et al., 2023).

This initial mapping was then refined in the second phase of the calibration, when the estimated location of the line of sight was displayed on the monitor in real-time by means of a red cross (16′ wide; 3 cd/m^2). In this phase, subjects fixated again on each of the points of the grid and used a joypad to correct the position of the estimated center of gaze at each location. These corrections were incorporated into the voltage-to-pixel transformation. The gaze-contingent refinement was repeated at the center of the display before each experimental trial to correct for possible small movements of the subjects and drifts in the apparatus. This approach considerably reduces uncertainty in gaze localization (Fig. 1*D–F*) and has been at the foundation of several previous studies on the perceptual functions of eye movements (Poletti and Rucci, 2016; Poletti, 2023).

Data analysis

Only trials with uninterrupted eye-tracking, in which both first and fourth Purkinje images were continually visible, were selected for data analysis. Periods of blinks were automatically detected by the DPI eye-tracker and removed from data analysis. The resulting dataset included an average of ∼5 mins of maintained fixation from each subject.

Oculomotor traces were segmented into complementary periods of drift and saccades. Eye movements were classified automatically and verified through visual inspection. Gaze shifts exceeding 3′ in amplitude and exhibiting peak velocities >3°/s were identified as saccades. The use of a minimum displacement threshold effectively rejects false alarms and excludes very small movements that keep the line of sight centered on the fixation marker. Consecutive events closer than 15 ms were merged together into a single saccade, a method that automatically excluded the post-saccadic overshoots that may result from the movement of the lens and the dampening of the eye-tracker (Deubel and Bridgeman, 1995; Stevenson and Roorda, 2005). Periods that were not classified as saccades were automatically labeled as drifts, the slow motion of the eye in between saccades.

Saccade amplitude was defined as the modulus of the vector connecting the two locations at which eye speed became greater (saccade onset) and lower (saccade offset) than 2°/s. In this study, we do not set an arbitrary amplitude to distinguish between saccades and microsaccades; all saccade movements were analyzed together irrespective of their amplitudes and indicated as fixational saccades. Pairs of successive saccades were labeled as potential square wave jerks based on the conjunction of three criteria: angular direction of the two saccades within ±10°, amplitude difference <40%, and intersaccadic interval <200 ms.

To determine how saccades move gaze, we examined the position of the perceived center of gaze (the line of sight) relative to the fixation marker. Given the small amplitude of the eye movements examined in this study, we defined the *fixation distance* as the Euclidean distance between the line of sight and the center of fixation marker. For each saccade, we compared the fixation distance at the onset and offset of the movement. Saccades were labeled as corrective or error-producing (non-corrective) depending on whether they decreased or increased the fixation distance. In Figure 5*A,B*, to measure saccade accuracy, we computed the difference between the initial and final position of the line of sight separately on the horizontal and vertical axes. Saccade precision in Figure 5*C,D* is measured by the standard deviation of the saccade endpoints.

To evaluate the robustness of our results, we applied the same analysis criteria to two additional fixation datasets obtained from separate experiments. The first dataset, from Cherici et al. (2012), included recordings from 14 subjects instructed to maintain precise fixation on a white marker presented over a uniform black background for 5 s. The second dataset, from Shelchkova et al. (2019), comprised data from 10 subjects who fixated for 1.5 s on a black marker displayed against a uniform gray background. The results are presented in Figure 4*D–F*.

Results

We investigated the characteristics of fixational saccades during a simple sustained fixation task. Subjects were instructed to maintain gaze on a small (4′) white square (the fixation marker), presented at maximum contrast for 10 s. The marker was positioned directly in front of the observer at the center of a uniformly dark background. To minimize potential visual or oculomotor distractions, no other stimuli were visible during the trial.

Consistent with previous findings (Cherici et al., 2012; Clark et al., 2022), observers varied in the precision with which they maintained fixation. As illustrated in Figure 2*A*, individual gaze distributions showed that some observers attempted to maintain fixation near the exact center of the marker, while others displayed small but systematic biases. Nonetheless, all subjects maintained accurate fixation, keeping the marker consistently within the foveola despite incessant eye movements.

Saccades occurred frequently, and their characteristics were similar to those of previous studies (Fig. 2*B–D*; Collewijn and Kowler, 2008; Cherici et al., 2012; Thaler et al., 2013; Scholes and Roach, 2015). Across observers, the mean ± standard deviation of the saccade rate was 1.3 ± 0.75 saccades/s, ranging individually from a minimum of 0.53 to a maximum of 2.23 saccades/s and resulting in a median intersaccadic interval of 435 ± 130 ms. Most saccades were horizontal (Fig. 2*D*) and <30′, with only a small percentage (<7%) exceeding 1°. The mean individual saccade amplitude ranged from 6′ to 36′, yielding an average of 19′ ± 13′ across observers.

Building on our capability of accurately localizing the perceived center of gaze, we analyzed when fixational saccades are generated and how they shift the line of sight. To assess the influence of spatial offsets, we first examined saccade occurrence as a function of the fixation distance—the distance between the gaze position and the center of the fixation marker—at the time of saccade onset. The cumulative frequency plot in Figure 2*E* shows that the majority of fixational saccades (on average 60% ± 3% across observers, ranging from 33% to 78%) were initiated when the fixation distance was <7.5′. Notably, this tendency to trigger saccades even when gaze is already near the marker persists after accounting for the gaze displacements caused by ocular drifts preceding each saccade: approximately 30% of fixational saccades occurred following drift epochs during which the fixation distance never exceeded 7.5′, and over 10% followed periods in which gaze remained continuously on the marker. This finding that fixational saccades occur when there is little or no fixation distance relative to the perceived center of gaze already excludes the possibility that saccades are solely caused by the spatial displacement relative to the intended fixation location.

To further examine when fixational saccades are triggered, Figure 2*F* plots the same data from Figure 2*E* after dividing the saccade counts by the bin areas, so to estimate the probability distribution of saccade occurrence as a function of the fixation distance (black circles in Figure 2*F*). Note that saccade probability closely mirrors the probability of gaze position (the red squares in Fig. 2*F*). That is, the region with the highest probability of saccade occurrence corresponds to where gaze tends to dwell most frequently. To take time into account, Figure 2*G* shows the rate of fixational saccades, computed by normalizing the saccade occurrence distribution by the distribution of time spent at each distance from the fixation marker (the two curves in Fig. 2*F*). Figure 2*G* shows that the saccade rate increases substantially with greater fixation distance. The mean saccade rate was 1.1 saccades/s when the center of gaze was within a distance of 5′ from the fixation marker. It increased by a factor of 5, up to 5.6 saccades/s when the fixation distance was between 20′ and 25′. Thus, the spatial offset between the gaze position and the fixation marker also plays an important role in eliciting fixational saccades.

To determine how the fixation distance influences saccades, we classified each saccade as either corrective or non-corrective based on whether it moved gaze closer to or farther from the fixation marker, respectively (Fig. 1*A*). Corrective saccades were slightly more frequent than non-corrective ones in five out of six observers, yielding a mean corrective-to-non-corrective ratio of 1.18. Interestingly, these two saccade types exhibited distinct characteristics: non-corrective saccades had slightly larger amplitudes (Fig. 3*A*) and were preceded by considerably longer intersaccadic intervals—more than twice as long—compared to

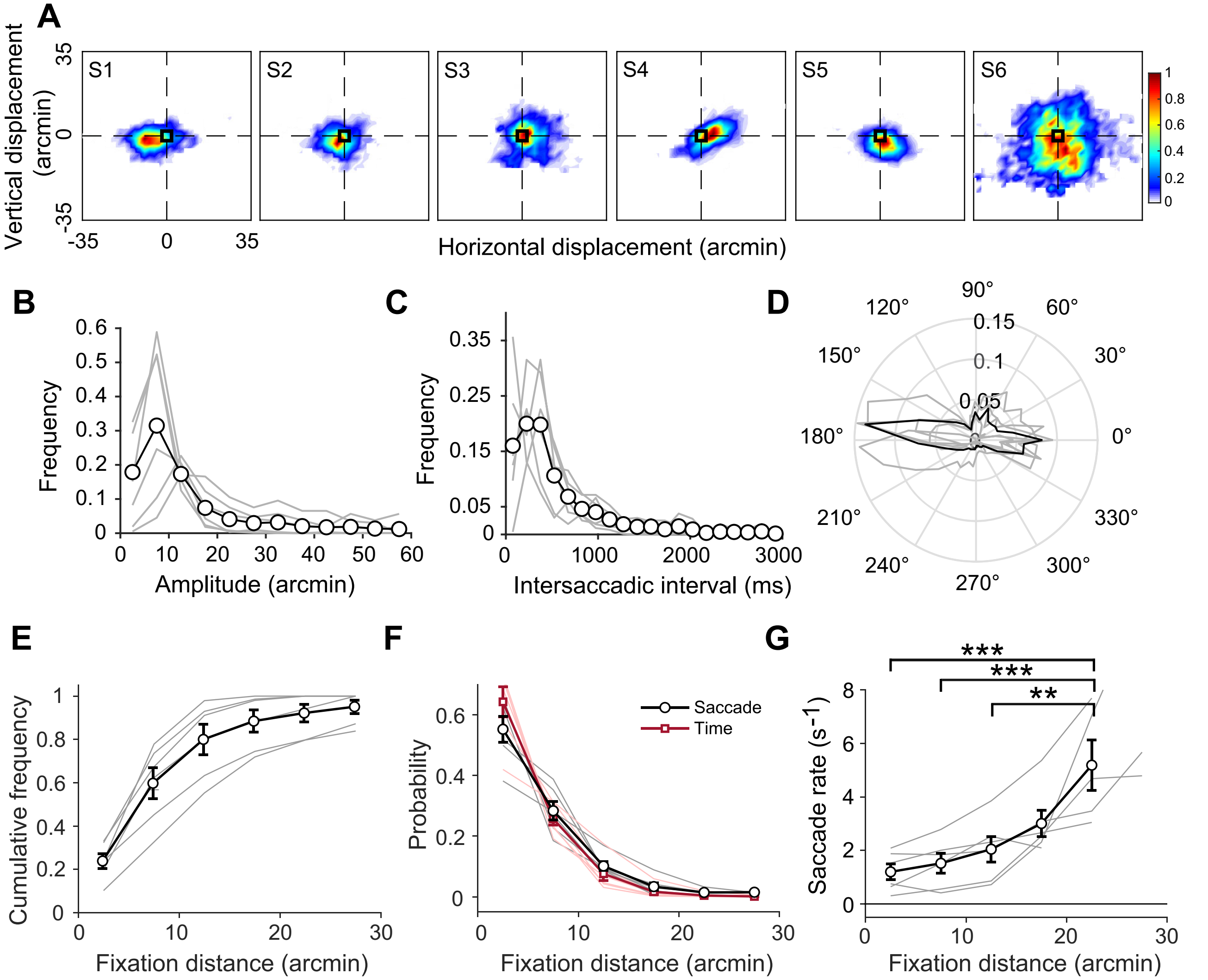

Figure 2. Characteristics of fixational eye movements. ***A***, Normalized two-dimensional probability distributions of gaze position. Each panel shows the data of an individual observer. The central black rectangle in each graph represents the fixation marker. ***B–D***, Probability distributions of (***B***) saccade amplitude, (***C***) intersaccadic interval, and (***D***) saccade direction. ***E–G***, Saccade occurrence as a function of gaze position: (***E***) cumulative frequency; (***F***) saccade probability (circles) and fixation time (squares); and (***G***) saccade rate. Data represent averages across the $N = 6$ observers ± one standard error. Gray (and pink) lines are data from individual subjects. The abscissa marks the fixation distance at the time of saccade onset. In ***G***, all rates differ from zero (horizontal gray line; $p = 0.03$, one-sample Wilcoxon sign-rank tests). Stars mark significant differences across distances (**$p < 0.01$, ***$p < 0.001$; one-way ANOVA with post hoc comparison tests).

corrective saccades (Fig. 3*B*). Moreover, the rate of these two saccade types varied differently with fixation distance (Fig. 3*C*). The rate of corrective saccades increased with increasing fixation distance, suggesting that these saccades were generated to re-center gaze [$F(4, 28) = 10.62$, $p = 10^{-5}$; one-way ANOVA]. In contrast, the rate of non-corrective saccades remained relatively constant, with no statistically significant differences across fixation distances [$F(4, 28) = 1.92$, $p = 0.14$; one-way ANOVA]. These findings indicate that the overall increase in saccade rate with fixation distance (Fig. 2*G*) is primarily driven by corrective saccades, which not only make up a larger proportion of the total saccade pool at greater distances (Fig. 3*D*) but also occur with shorter intersaccadic intervals (Fig. 3*C*).

This difference is further examined in Figure 3*D*, which shows the probability that a saccade occurring at a given fixation distance is either corrective or non-corrective. To provide a reference baseline, the gray curve in Figure 3*D* shows the probability of performing one of the two types of saccade by chance based on the population of saccade amplitudes and directions measured for each individual. As shown by these data, the probability that a saccade is corrective increases with the fixation distance at a rate that far exceeds what would be expected by chance, already reaching statistical significance at a fixation distance of 7.5′ ($t = 2.12$, $p = 0.04$, one-tailed paired *t*-test). These data suggest two components in the production of fixational saccades: (a) a spatial mechanism that repositions the line of sight to ensure accurate fixation; and (b) a temporal mechanism that modulates the frequency of saccade generation with fixation distance.

To more thoroughly evaluate the contributions of spatial and temporal factors to the generation of fixational saccades, we estimated the probability of saccade occurrence as a joint function of fixation distance and the time elapsed since the previous saccade (the pre-saccadic interval). A two-way ANOVA indicated that both factors significantly influenced saccade probability [pre-saccadic interval: $F(5, 150) = 12.78$, $p = 10^{-14}$; fixation distance: $F(4, 150) = 22.08$, $p = 10^{-10}$] with a significant interaction between them [$F(20, 150) = 1.74$, $p = 0.03$].

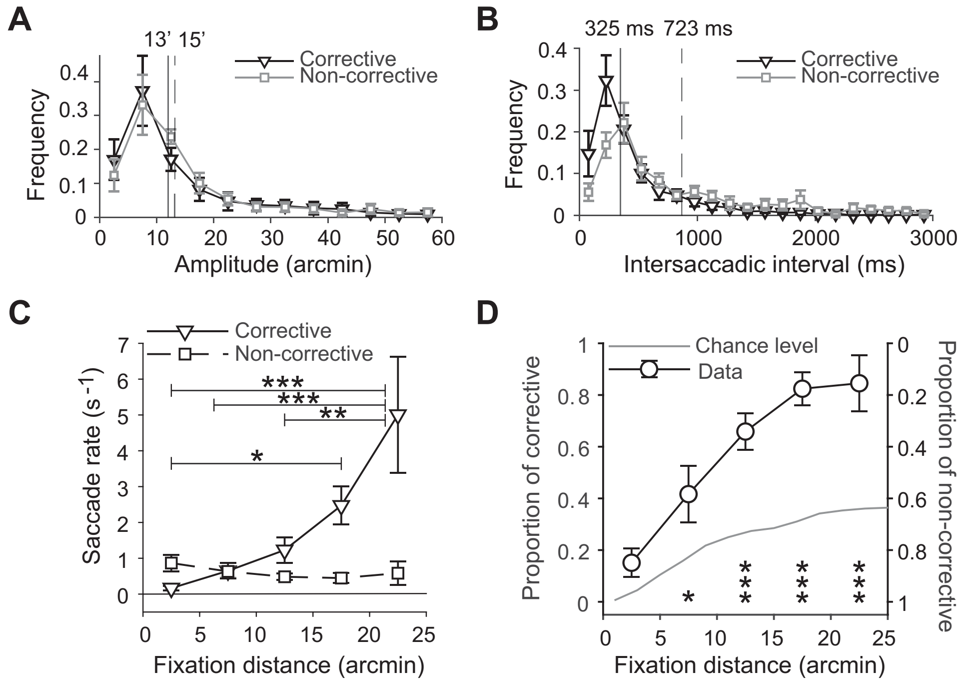

Figure 3. Corrective and non-corrective saccades. ***A–B***, Average probability distributions of (***A***) saccade amplitudes and (***B***) intersaccadic intervals for saccades that reduce or increase the fixation distance (corrective and non-corrective saccades, respectively). Note that non-corrective saccades tend to have longer intervals, shifting their probability distribution to the right. Vertical lines mark the average of the medians across observers. ***C***, Mean rates of corrective and non-corrective saccades as a function of the fixation distance at the time of saccade onset. Stars mark statistically significant differences across distances (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$; one-way ANOVA with post hoc comparison tests). ***D***, Proportions of corrective and non-corrective saccades as a function of the fixation distance. The gray line represents the average chance-level probability of a corrective saccade across observers. For each observer, the chance-level probability was estimated by simulating the same number of saccades, with each saccade direction and angle being randomly chosen from the recorded saccade pool. Stars mark statistical significance against chance (*$p = 0.04$; ***$p = 10^{-4}$; paired *t*-tests). In all panels, data points are averages across $N = 6$ observers. Error bars represent ±1 SEM.

This interaction between the fixation distance and the pre-saccadic interval is emphasized in Figure 4*A*, which shows the probability distributions of pre-saccadic intervals (the ordinate) for saccades that started at various fixation distances (the abscissa). It is clear from these data that the distribution of pre-saccadic intervals varies systematically with the fixation distance at which a saccade originates. Saccades initiated from relatively large fixation distances are typically preceded by short fixation durations, yielding a relatively narrow distribution. For instance, the mean pre-saccadic interval for saccades starting at a fixation distance >20′ is only 118 ms. The data in Figure 3*C–D* indicate that these saccades are predominantly corrective, an observation confirmed by the distribution for corrective saccades only, shown in Figure 4*B*. In contrast, saccades originating when gaze is already close to the fixation marker are preceded by longer and more broadly distributed fixation durations. The mean pre-saccadic interval for saccades starting within 5′ of the marker is 448 ms, and these saccades are mostly non-corrective, as shown by Figure 4*C*.

These effects were not restricted to the tightly controlled conditions of our experiments, where a fixation marker was presented in isolation, without other visual stimuli. The bottom row of Figure 4 compares pre-saccadic intervals for saccades originating at small and large fixation distances (the bottom and top 10th percentiles of the distributions) across three viewing conditions: complete darkness with a white marker (Fig. 4*D*; same data as in the top row), a white marker on a black background with ambient room lighting and visible monitor edges (Fig. 4*E*; data from Cherici et al., 2012), and a black marker on a uniform gray background (Fig. 4*F*; data from Shelchkova et al., 2019). Although the absolute duration values varied slightly between conditions, all three exhibited similar spatiotemporal dependencies. Saccades originating farther from the target consistently showed significantly shorter pre-saccadic intervals, indicating that these space-time interactions are part of the general strategy by which observers maintain fixation.

Given that the fraction of corrective saccade grows rapidly as gaze moves away from the fixation marker, we examined how effectively saccades correct for spatial offsets in gaze positions during fixation. To quantify accuracy, we compared the saccade displacement to the fixation distance at the saccade starting position. Figure 5*A,B* show the outcome of this comparison on the horizontal and vertical axis, respectively. In both panels, a perfectly accurate saccade would generate a displacement equal to its fixation distance, resulting in a point aligned on the 45° diagonal. These data demonstrate that fixational saccades are quite effective in correcting for spatial errors. Accuracy was remarkable on the horizontal axis, where the average saccade amplitude was almost identical to the fixation distance. On the vertical axis, a systematic undershoot was visible so that fixational saccades corrected for about 20% to 50% of the displacement.

While fixational saccades are on average very accurate, like all small saccades (Poletti et al., 2020), they tend not to be as precise. Figure 5*C,D* show the dispersion of saccade landing positions on the two axes. Each data point represent the standard deviation in the gaze position at the end of a saccade estimated for all saccade starting at a given displacement and averaged across subjects. The precision of fixational saccades varied little with the fixation distance from the marker. Interestingly, despite their lower accuracy, fixational saccades were more precise on the vertical axis, perhaps a consequence of the fact that most saccades were primarily horizontal (Fig. 2*D*). On both axes, precision varied little as a function of the starting position of the saccade, suggesting an approximately fixed level of uncertainty in the execution of such small saccades.

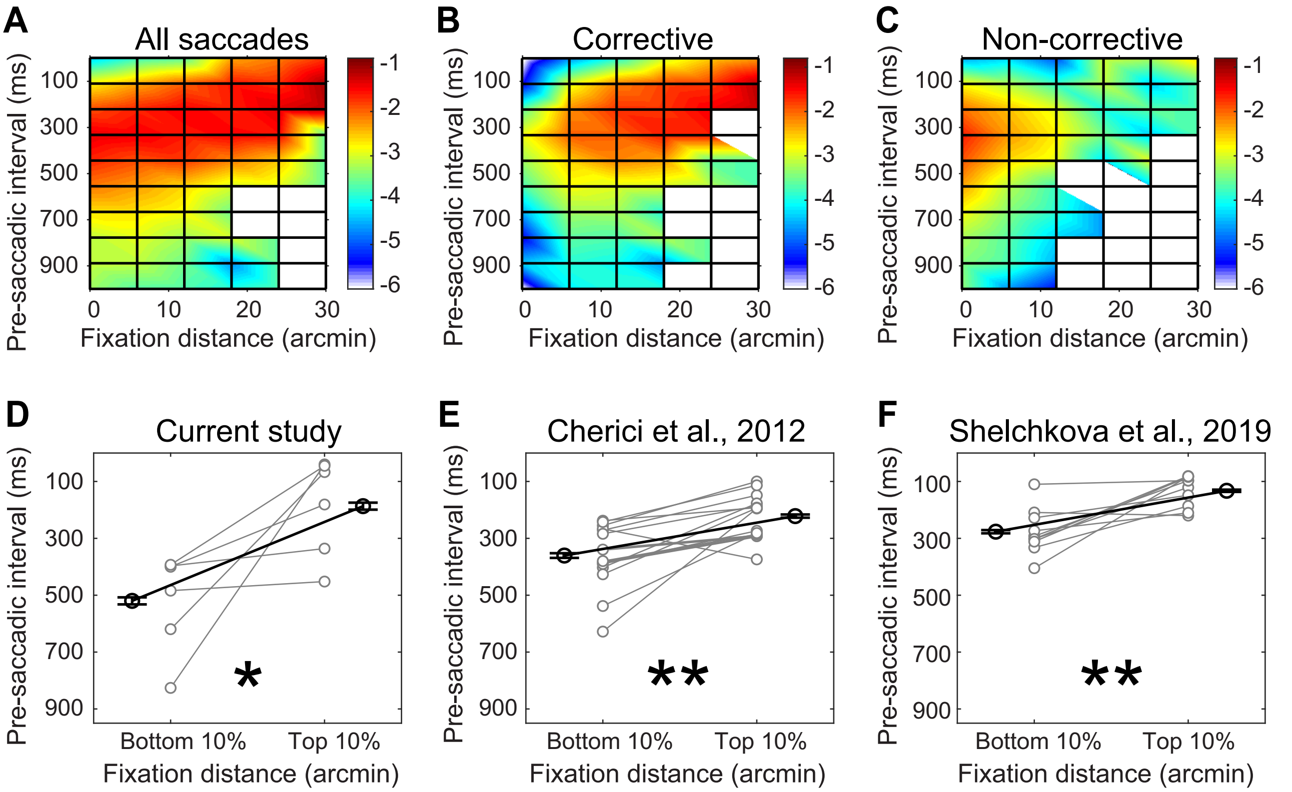

Figure 4. Space-time dependence of fixational saccades. ***A–C***, Probability distributions of pre-saccadic intervals (ordinate) for saccades starting at various fixation distances (abscissa). Panel ***A*** includes all saccades, while ***B*** and ***C*** show the distributions for corrective and non-corrective saccades, respectively. Data in all panels are pooled across $N = 6$ observers and shown on a log scale over the [0.002–0.45] probability range. ***D–F***, Median pre-saccadic intervals for saccades generated close and far from the fixation marker (bottom and top 10th percentiles). The three panels show data for: (***D***) an isolated white marker on a black background (this study; $t = 2.78$, $^{*}p = 0.04$, two-tailed paired *t*-test); (***E***) a white marker on a black background with visible monitor edges (data from Cherici et al., 2012; $t = 4.17$, $^{**}p = 0.001$, two-tailed paired *t*-test); and (***F***) a black marker on a gray background (data from Shelchkova et al., 2019; $t = 4.30$, $^{**}p = 0.002$, two-tailed paired *t*-test). Black lines with circles in panel ***D–F*** are averages across observers. Error bars represent ±1 SEM. Gray lines are data from individual observers.

Having established that fixational saccades tend to serve a corrective function when the line of sight deviates from the marker, we further examined the temporal relationship between successive oculomotor events. Figure 6 shows how the probabilities of maintaining fixation and of initiating either type of saccade evolve following corrective and non-corrective saccades that land at various distances from the marker. Regardless of landing accuracy, corrective saccades are consistently followed by a prolonged post-saccadic fixation interval. On average, it takes approximately 600 ms before the probability of initiating a new saccade surpasses that of maintaining fixation. However, the nature of the subsequent saccade—corrective or non-corrective—depends on the accuracy of the preceding one. When a corrective saccade lands close to the marker (Fig. 6*A*), the probability of initiating another saccade increases gradually and is predominantly associated with non-corrective saccades. In contrast, when a corrective saccade lands farther from the marker (Fig. 6*C*), the probability of triggering another corrective saccade rises more rapidly than that of initiating a non-corrective one.

Distinct dynamics are observed following non-corrective saccades (Fig. 6, middle row). In this case, regardless of the landing distance, the probability of initiating a subsequent saccade increases rapidly, reaching chance level in under 400 ms. This rise is driven primarily by corrective saccades, whose probability increases markedly faster than that of non-corrective ones. These differences in saccade dynamics were highly consistent across individual subjects, as summarized in Figure 6, bottom row. All participants exhibited significantly longer post-saccadic intervals following corrective saccades compared to non-corrective ones (Fig. 6*G*). Likewise, in all subjects, the rate of change in the probability of subsequent saccade types varied systematically with the accuracy and nature (corrective or non-corrective) of the previous saccade (Fig. 6*H*). These patterns indicate that observers tend to rapidly correct saccades that increase the fixation error and maintain prolonged fixation after successful corrections.

Discussion

Vision science experiments often require subjects to maintain strict and prolonged fixation on a visual marker. Under these conditions, frequent saccades are observed in both humans and non-human primates, even in the absence of other tasks or stimuli. Why saccades occur during sustained fixation has long been a subject of debate. Our study shows that, as long speculated (Cornsweet, 1956; Nachmias, 1959), both temporal and spatial factors contribute to the dynamics of fixational saccades. When fixation is not accurate, these saccades serve an important corrective function by accurately bringing the line of sight closer to the intended fixation location. Saccades, however, often also increase the fixation error, as they continue to occur even when fixation is already accurate. In such cases, the pre-saccadic interval increases considerably.

A long-standing idea for explaining the existence of fixational saccades is that they help centering gaze by correcting for small spatial displacements in the intended position of the fixation marker (Cornsweet, 1956; Fiorentini and Ercoles, 1966).

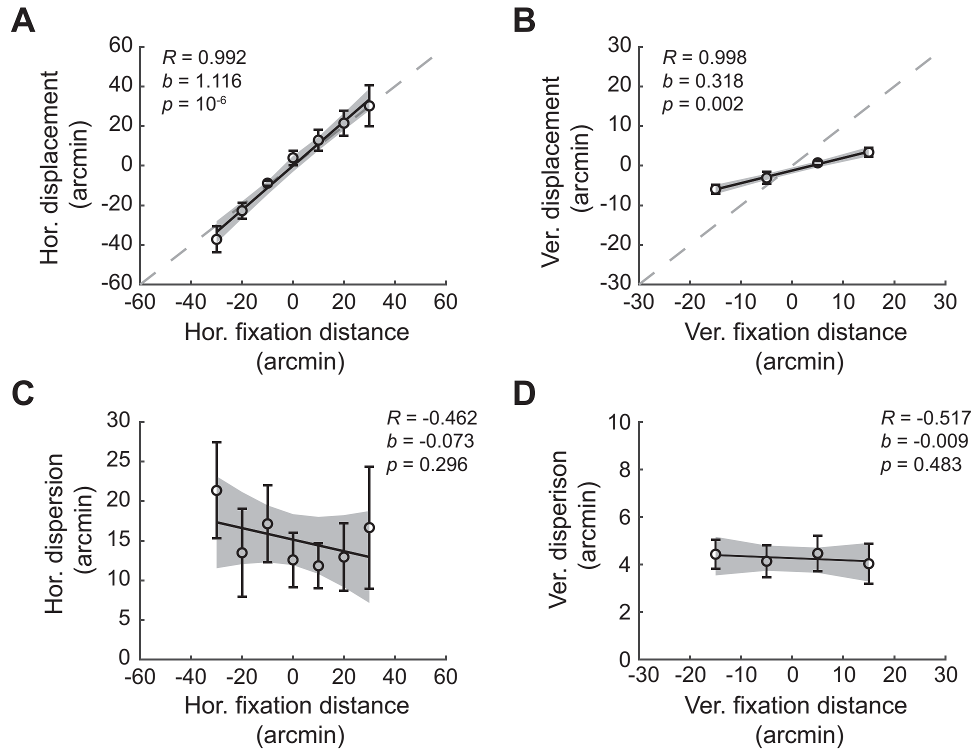

Figure 5. Accuracy and precision of fixational saccades. ***A–B***, Accuracy. Gaze displacements resulting from fixational saccades as a function of their starting position relative to the fixation marker (the fixation distance; abscissa). Each panel shows data on one of the two Cartesian axes. The dashed gray line marks the ideal saccade displacement for fully correcting the fixation error. ***C–D***, Precision. Standard deviation in the distributions of landing positions for saccades starting at various distances from the fixation marker. Separate panels show data for the horizontal and vertical axes. In all panels, data points and errorbars represent averages across observers ±1 SEM. Linear regressions (black lines) and their 95% confidence intervals (shaded regions) are also shown, with correlation coefficient (*R*), slope (*b*), and probability values (*p*) reported in each panel.

However, previous studies that investigated this proposal have provided mixed results (Nachmias, 1959; Krauskopf et al., 1960; Boyce, 1967; Kowler, 1991; Engbert and Kliegl, 2004; Rolfs, 2009). This is not too surprising if one considers that estimation of the fixation error requires accurate localization of the line of sight, a major challenge in eye-tracking, with errors that can easily exceed the width of the foveola (Hornof and Halverson, 2002; Zhang and Hornof, 2011). Traditionally, estimation of the center of gaze has relied on the distributions of gaze position assumed during maintained fixation at known locations. A similar approach has been more recently used in retinal imaging studies, where the preferred retinal locus of fixation is estimated from the corresponding spatial distribution covered on the retina by the fixation marker (Kilpeläinen et al., 2021; Reiniger and Harmening, 2021). However, gaze and retinal distributions are often oddly shaped (Cherici et al., 2012; Bowers et al., 2021), and they are affected by the very presence of fixational saccades, adding uncertainty to the estimate.

To circumvent these issues, rather than indirectly estimating the center of gaze from oculomotor behavior, here we directly asked the observer to pinpoint the perceived position of their center of gaze. This procedure substantially sharpens the distribution of gaze positions, thus reducing uncertainty in gaze localization. Using this approach, our data show that fixational saccade are extremely accurate in correcting for spatial offsets in the perceived gaze position. This effect is particularly pronounced on the horizontal axis, the displacement direction of the majority of fixational saccades. While on average very accurate, fixational saccades are not always precise, as the dispersion of landing positions remains approximately constant with the starting fixation distance. These findings closely match the accuracy and precision of small voluntary saccades toward targets at various distances measured with similar methods (Poletti et al., 2020).

While the fixation distance plays an important role in triggering saccades, it is clearly not the only contributor. The simple observation that the majority of fixational saccades occurs when gaze is already very close to the intended fixation location reveals the presence of non-spatial factors. It has long been suggested that a periodic temporal mechanism may be involved in the generation of fixational saccades (Nachmias, 1959; Bosman et al., 2009). Our findings support a role of temporal factors, but also exclude a simple oscillatory mechanism. This happens because the average intersaccadic interval systematically decreases with increasing distance between the center of gaze and the fixation marker: while saccades promptly compensate for spatial offsets, they can only be avoided for a limited period of time when already fixating accurately. Thus, as emphasized by Figure 4*A*, the occurrence of fixational saccades heavily relies on the interaction between the fixation distance and the time elapsed since the previous saccade.

This interaction between spatial and temporal factors, specifically the longer intersaccadic interval preceding non-corrective saccades, may appear to conflict with previous experimental observations. Engbert and Kliegl (2004) examined how saccades affect the distance traveled by gaze as a function of time relative to the displacement caused by fixational drift alone. They found that fixational saccades increase the spatial displacement over a time window of tens of milliseconds and decrease it over hundreds of milliseconds. Our study differs from these previous

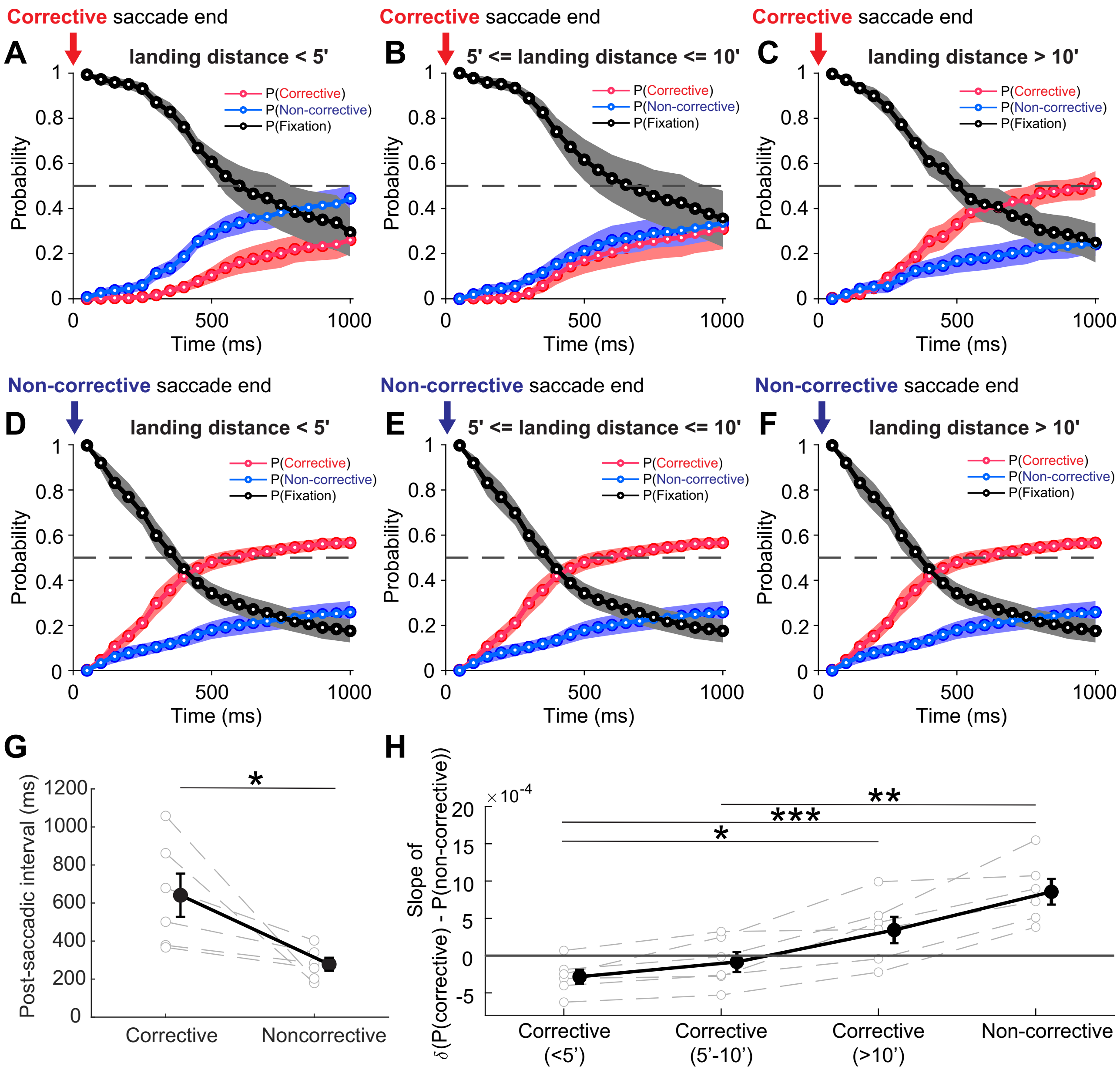

Figure 6. Post-saccade dynamics. ***A–F***, Temporal evolutions of the probabilities of three complementary oculomotor events following either a corrective (top row) or a non-corrective saccade (middle row). Time zero represents the landing time of the saccade. The three curves in each panel mark the probabilities of maintaining fixation (black curve), initiating a corrective saccade (red curve), and initiating a non-corrective saccade (blue curve). In each row, separate panels illustrate the dynamics following saccades that landed at different distances from the center of the fixation marker. Data represent averages across observers. Shaded regions mark ±1 SEM. ***G***, Comparison of the post-saccadic intervals following corrective and non-corrective saccades. Data represent the duration of the period in which the probability of maintaining fixation exceeds that of initiating a subsequent saccade ($t = 3.12$, $*p = 0.01$, unpaired t-test). ***H***, Comparison of growth rates in the probabilities of corrective and non-corrective follow up saccades. Data points represent the difference between the temporal derivatives of the two saccade probabilities (red and blue curves in ***A***–***F***), averaged over the interval from saccade end to the time at which the probability of maintaining fixation drops to chance level. The probability of executing a corrective saccade increases more rapidly following either a non-corrective saccade or an inaccurate corrective saccade ($*p = 0.04$, $**p = 0.001$, $***p = 0.0002$, One-way ANOVA with post hoc comparison tests). In both ***G*** and ***H*** data represent averages across observers. Error bars mark ±1 SEM. Gray circles and thin lines represent data from individual observers.

analyzes for consideration of the absolute position of gaze, rather than the relative displacement. The results reported here are, in fact, fully compatible with this previous report, as saccades contribute to maintain fixation, therefore decreasing the displacement over long temporal scales, while moving gaze faster than drifts, therefore increasing the traveled distance over short time windows. Our study goes beyond the previous literature by mapping the absolute error at which fixational saccades occur, determining how they shift gaze relative to the perceived center of fixation, and clarifying the roles of spatial and temporal factors.

Since fixational saccades both cause and correct for fixation errors, an interesting question is whether part of our results could be explained by possible saccadic intrusions. In particular, the corrective saccades that rapidly occur at larger displacements are reminiscent of the return saccades in square wave jerks, pairs of horizontal saccades in which the first saccade moves the eye away from the intended fixation point while the second one brings gaze back onto the target following a short interval (Sharpe et al., 1982; Abadi and Gowen, 2004). In our study, on average about 55% of the non-corrective saccades performed while accurately fixating on the marker were followed by corrective saccades. When square wave jerks were identified using the standard flagging criteria of opposite direction, similar amplitude, and brief intersaccadic interval (see Methods), they accounted for <4% of the total number of saccades, and results were practically unaffected by removing these events from data analysis. Still, even if the parameters of saccade pairs in our data differ from those commonly used for square wave jerks, the probability of following up with a corrective saccade increases and the intersaccadic interval decreases as a non-corrective saccade brings gaze farther away from the marker. Thus, our data are consistent with the proposal that pairs of self-correcting saccades are part of the strategy by which also healthy observers maintain fixation (Otero-Millan et al., 2011).

While our study focused specifically on the interaction between spatial offsets and temporal lags, it is well established that other factors also contribute to the generation of fixational saccades. For example, both the experimental instructions provided to participants (Steinman et al., 1967) and the properties of the fixation marker (Thaler et al., 2013) influence the rate of fixational saccades. These influences raise the question of how generalizable our results are. In our experiments, we intentionally used a small fixation marker to allow for precise quantification of fixation errors. However, the data presented in Figure 4*D–F*, obtained using a larger fixation marker (11×11 arcmin, nearly an order of magnitude larger in area) and visible backgrounds exhibit similar spatiotemporal dependencies, suggesting that our results generalize across different viewing conditions.

When maintaining fixation is not the sole task—as is often the case in vision science experiments—attentional and cognitive processes also contribute. Under such conditions, many studies have examined how fixational saccades are modulated by factors such as the appearance of a new stimulus (Steinman, 1965; Rolfs et al., 2008; McCamy et al., 2013), its visibility (Ditchburn, 1973; Martinez-Conde et al., 2006; Hsieh and Tse, 2009; Poletti and Rucci, 2010), and the allocation of attention (Hafed and Clark, 2002; Engbert and Kliegl, 2003; Palmieri et al., 2023; Guzhang et al., 2024). Sustained fixation, however, occurs rarely outside the laboratory. Under more natural viewing conditions, when fixation is not experimentally enforced, microsaccades behave similarly to larger saccades: they support fine-scale exploration within the foveal region by centering the preferred fixation locus on details of interest, even when the entire stimulus already falls within the foveola (Ko et al., 2010; Shelchkova et al., 2019; Intoy and Rucci, 2020; Poletti, 2023). Under these conditions, microsaccades are likely influenced by many of the same factors that govern the generation of larger saccades.

The results of this study raise the hypothesis that the production of fixational saccades is driven by the interplay of two complementary processes: a corrective process that redirects gaze toward the intended position when fixation is inaccurate, and a temporal process that eventually triggers fixational saccades even when gaze is already close to the intended location. Multiple sensorimotor regions along the descending pathway from the frontal eye field to the brain stem are known to be involved in the generation of fixational saccades (Hafed et al., 2009; Hafed, 2011; Godlove and Schall, 2016; Krauzlis et al., 2017; Schall et al., 2017; Schall and Paré, 2021). Within this network, several mechanisms could account for our findings. For example, the longer intersaccadic intervals observed when the line of sight is close to the fixation marker may reflect both an active suppression of non-corrective saccades and/or the delayed reaching of a triggering threshold in the saccade initiation pathway. Neurophysiological investigations with precise gaze localization are needed to investigate these possibilities and elucidate the neural mechanisms underlying our findings.

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