Vision Research 211 (2023) 108277

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

An eye for detail: Eye movements and attention at the foveal scale

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ABSTRACT

Human vision relies on a tiny region of the retina, the 1-deg foveola, to achieve high spatial resolution. Foveal vision is of paramount importance in daily activities, yet its study is challenging, as eye movements incessantly displace stimuli across this region. Here I will review work that, building on recent advances in eye-tracking and gaze-contingent display, examines how attention and eye movements operate at the foveal level. This research highlights how exploration of fine spatial detail unfolds following visuomotor strategies reminiscent of those occurring at larger scales. It shows that, together with highly precise control of attention, this motor activity is linked to non–homogenous processing within the foveola and selectively modulates sensitivity both in space and time. Overall, the picture emerges of a highly dynamic foveal perception in which fine spatial vision, rather than simply being the result of placing a stimulus at the center of gaze, is the result of a finely tuned and orchestrated synergy of motor, cognitive, and attentional processes.

1. Fixational eye movements: A deeper link between oculomotor behavior and vision

High-resolution vision is restricted to the 1-degree region of the retina known as the foveola. This region is anatomically different from the rest of the retina, it is free from capillaries and rods, cones are most densely packed, and connect to midget bipolar cells and midget ganglion cells through a private line (Kolb, 2007). Because visual acuity and other visual functions gradually deteriorate as we move away from the foveola, humans rely on a tight link between perception and action to compensate for these limitations. Rapid gaze shifts (saccades) occur 2–3 times every second, and bring objects of interest at the center of gaze where they can be viewed at high resolution. Notably, the coupling of visual functions and saccades is not only limited to the active sampling of the visual scene, something that has been extensively documented since the original work from Yarbus in the sixties (Yarbus, 1967), but it extends to the way saccades alter the retinal input (Boi, Poletti, Victor, & Rucci, 1998; Mostofi et al., 2020) (see Rolfs et al. (2022) for a review on the coupling between sensory processing and eye movements). Interestingly, however, in the periods between saccades the eye is not stationary, but it continues to move even when the attended stimulus is already foveated (Fig. 1*A*,*B*). Hence, the term fixation itself is misleading as the retinal input is far from being fixed. Fixational eye movements generate a substantial amount of motion that would be immediately visible if it had resulted from the motion of objects in the scene (Poletti & Rucci, 2016; Steinman, 1976; Rolfs, 2009; Collewijn & Kowler, 2008). Over a fixation period of a few seconds the eye can span an area as large as the foveola (Cherici, Kuang, Poletti, & Rucci, 2012). The presence of these small eye movements suggests a deeper coupling between visual functions and oculomotor activity that extends to periods of fixation.

Fixational eye movements come in different varieties. Primarily we distinguish between microsaccades and ocular drift (Fig. 1*A*,*B*). Microsaccades are small and rapid gaze shifts. They are among the fastest, most precise and smallest movements that humans are capable of. Microsaccades are typically defined based on amplitude thresholds. However, since they are part of a continuum with saccades (Otero-Millan, Macknik, Langston, & Martinez-Conde, 2013; Hafed & Krauzlis, 2012; Zuber, Stark, & Cook, 1965), their definition is somewhat arbitrary. Different studies have used different thresholds, ranging from 0.2^o (Cunitz & Steinman, 1969), to 2° (Martinez-Conde, Macknik, Troncoso, & Dyar, 2006) (see Collewijn & Kowler, 2008 and Poletti & Rucci, 2016 on this issue). Here we adopt a definition based on anatomical and physiological considerations, and define microsaccades as the saccades smaller than the radius of the foveola ($<0.5^o$), the rod and capillary-free high acuity region of the fovea (Curcio, Sloan, Kalina, & Hendrickson, 1990; Rossi et al., 2010). Saccades in this amplitude range yield more than 50% [1] overlap in the pre and the post-saccadic retinal input to the foveola.

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[1] Calculated based on the area of the overlapping region between two circles of identical radius (representing the 1 deg foveal field) separated by an amount proportional to the amplitude of microsaccades.

https://doi.org/10.1016/j.visres.2023.108277
Received 28 March 2023; Received in revised form 8 June 2023; Accepted 8 June 2023
Available online 27 June 2023

In the periods in between microsaccades the eye moves continually in a slower and jittery way, a motion that resembles a random walk, often referred to as ocular drift (Ditchburn, 1973; Cornsweet, 1956; Cherici et al., 2012; Fiorentini & Ercoles, 1966; Skavenski, Hansen, Steinman, & Winterson, 1979; Poletti, Aytekin, & Rucci, 2015; Epelboim & Kowler, 1993). The presence of these eye movements has intrigued scientists for decades. However, it was not until the 1970s and the 1980s that these eye movements could be recorded with sufficiently high resolution, and answers regarding their role in visual perception could be addressed (Skavenski et al., 1979).

2. Beyond visual fading, the contribution of microsaccades to fine spatial vision

Initially, when microsaccades were first examined more rigorously, the dominant view posited that their primary function was that of preventing image fading during fixation (Ditchburn, Fender, & Mayne, 1959). Because stimuli that do not move on the retina fade over time (Ditchburn & Ginsborg, 1952; Riggs & Ratliff, 1952; Yarbus, 1967), microsaccades were proposed as a retinal refreshing mechanism (Ditchburn et al., 1959). In the early 2000 this view gained further support (Martinez-Conde et al., 2006; McCamy et al., 2012). However, this issue has remained controversial (Cornsweet, 1956; Gerrits & Vendrik, 1970; Nachmias, 1961; Kowler & Steinman, 1980b; Steinman, 2003; Collewijn & Kowler, 2008; Poletti & Rucci, 2010; Kagan, 2012). Under normal viewing conditions the duration of a typical fixation period is less than half a second, in many instances too short to induce fading (McCamy, Macknik, & Martinez-Conde, 2014), and upon saccade landing the retina is exposed to a strong visual transient enhancing the power of the stimulus over a large range of spatial frequencies (Mostofi et al., 2020). Further, the retinal motion introduced by ocular drift on its own has been shown to be sufficient to maintain visibility (McCamy et al., 2014), and under conditions eliciting visual fading, the rate of microsaccades systematically decreases (Poletti & Rucci, 2010). It is also important to consider that, normally, additional retinal motion is introduced by head and body instability (Skavenski et al., 1979; Poletti et al., 2015; Aytekin et al., 2014), to the point that the visual system most times is faced with the task of reducing retinal motion within a reasonable range rather than introducing motion to refresh a fading image (Poletti et al., 2015). Finally, most studies examined the role of microsaccades in preventing visual fading in highly unnatural condition; humans rarely stare at a blank screen for several seconds or minutes while stimuli are presented in the visual periphery. Microsaccades, like big saccades and blinks, can undoubtedly refresh the retinal image, but that is unlikely their primary function during normal conditions when humans view complex scenes and the stimulus at the center of gaze is often rich in detail. What is then the main function of microsaccades in vision? It seemed like the jury was still out. To address this question, as long advocated by Steinman and colleagues (Steinman, 1995; Steinman, 2003; Herst, Epelboim, & Steinman, 2001), fixational eye movements need to be studied in more natural settings.

A few studies examining microsaccades during fine spatial vision tasks concluded that microsaccades were a nuisance for fine spatial vision and in these condition they needed to be suppressed (Winterson & Collewijn, 1976; Bridgeman & Palca, 1980) or that they made no difference to performance (Kowler & Steinman, 1977; Kowler & Steinman, 1979; Kowler & Steinman, 1980a). Crucially, even when using high-precision eyetracking many studies are limited by the accuracy of the eyetracking method in localizing the line of sight; one thing is to be able to detect even the smallest microsaccade, another is to know with high accuracy where the microsaccade moves the line of sight on the scene. To that end, gaze localization accuracy should be in the order of arcminutes, but most times it is in the order of one degree (Holmqvist et al., 2011) and it is severely impacted by loose head stabilization and, in most commercial video eyetrackers, by changes of pupil size, making it impossible to know where microsaccades shift the center of gaze over a stimulus (Choe, Blake, & Lee, 2016; Wyatt, 2010; Holmqvist & Blignaut, 2020; Bedell & Stevenson, 2013; Drewes, Zhu, Hu, & Hu, 2014; Wildenmann & Schaeffel, 2013). This constitutes a major limitation in the study of fixational eye movements; imagine studying the functions of large saccades without knowing where they move the gaze on the visual scene, the only information available being their rate, amplitude and direction. In fact, it is only when higher accuracy in gaze localization is possible that we can truly appreciate the contribution of microsaccades to visual perception.

In a series of recent studies using a high-precision Dual Purkinje Image eyetracker (Crane & Steele, 1985; Ko, Snodderly, & Poletti, 2016; Wu et al., 2023) coupled with custom-made system for gaze contingent display control allowing for more accurate localization of the line of sight (Santini, Redner, Iovin, & Rucci, 2007), we showed that microsaccades are frequent and minutely controlled in fine visuomotor tasks (Fig. 2 *A* –*D*). While subjects performed a virtual threading of the needle task on a monitor display, microsaccades of 10–15 arcminutes were used to precisely relocate gaze between the eye of the needle and the thread even if both thread and eye of the needle always laid within the central 1 deg foveola (Ko, Poletti, & Rucci, 2010) (Fig. 2 *A*,*B*). Such a refined level of control over microsaccades is another indication that microsaccades do not simply represent a mechanism to counteract visual fading as that level of precision would not be necessary for a mere refreshing mechanism. But why such a refined level of control over

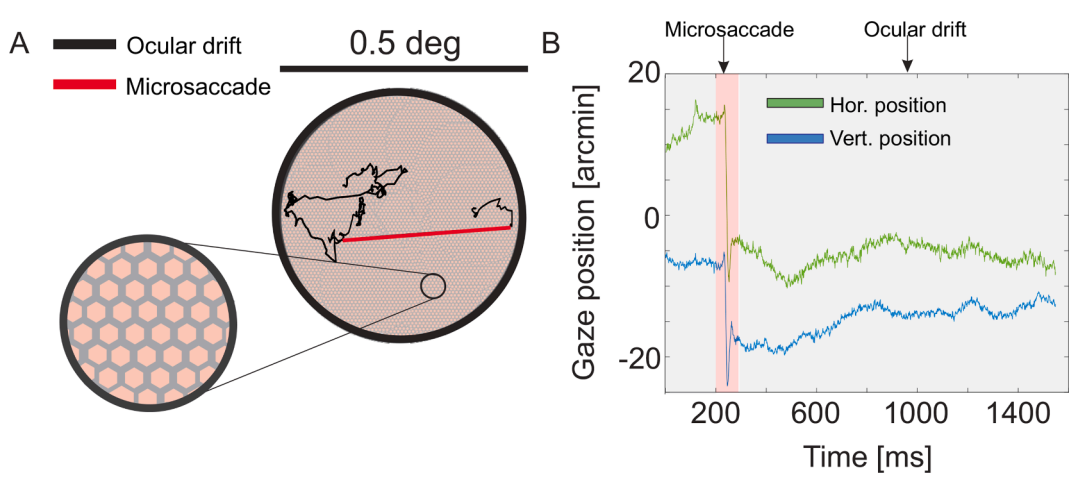

Fig. 1. Fixational eye movements. A, incessant small eye movements during fixation normally displace the retinal image over many photoreceptor. An example trace is shown relative to a sketch of the photoreceptor mosaic in the central fovea drawn to scale. **B**, examples of fixational eye movements.

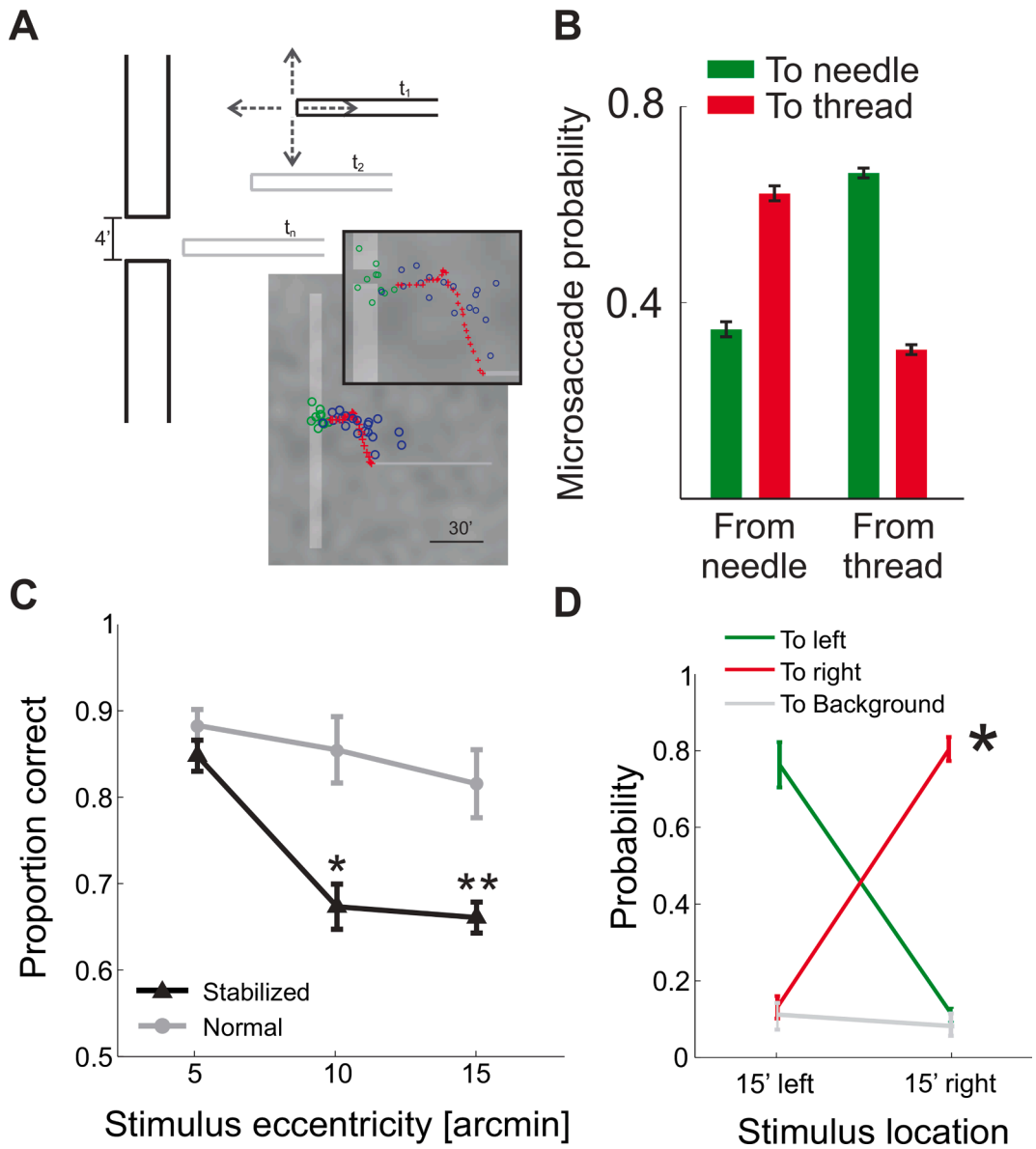

Fig. 2. Microsaccades in fine visuospatial tasks. A, an example of spatial distributions of in-between microsaccades fixations during a threading of the needle task in a typical trial. Blue and green circles represent fixations on the thread and on the eye of the needle, respectively. The red crosses mark the trajectory followed by the thread, which moved at a constant pace and its vertical position was adjusted by the subject. Insert, higher magnification of the center of the display. **B**, average probabilities (N = 6) of microsaccades landing on the thread and the needle based on their starting location. Data refer to saccades smaller than 20 arcmin. **C**, Average subject performance (N = 4) as a function of the stimulus eccentricity under retinal stabilization and under normal viewing. In each condition, asterisks mark statistically significant differences with respect to the proportions of correct responses at 50 (∗p <0.05; ∗∗p < 0.005; two-tailed paired t test). **D**, proportions of microsaccades landing on one of the two stimuli presented 15 arcminutes to the left or the right of the center of gaze and on the background region during the two periods of grating presentation. Microsaccades were more likely to relocate the preferred retinal locus of fixation on the stimulus currently displaying the grating than anywhere else. Asterisks mark significant differences between the probabilities of landing in a given region of the image in the two temporal intervals ($p < 0.01$; two-tailed paired t test). Error bars represent SEM. Figures adapted from Ko et al., 2010 (*A –B*), and Poletti et al., 2013 (*C –D*).

microsaccades is needed at this scale where acuity is highest? A later study helped addressing this open question.

To further examine the contribution of microsaccades to fine spatial vision in a follow-up study subjects were asked to perform a fine spatial discrimination task. Gratings were presented within two nearby narrow apertures a few arcminutes in size. Stimuli were displayed sequentially first on the left and then on the right aperture, and were maintained within the central fovea, but their offset from the central fixation point was systematical changed of just tiny amounts from the center of gaze. Subjects reported whether or not the two gratings were tilted in the same direction (Poletti, Listorti, & Rucci, 2013). To eliminate the influence of fixational eye movements in one condition stimuli were maintained at a fixed eccentricity on the foveola throughout the course of the trial by means of retinal stabilization. In another condition, stimuli were viewed in the presence of the physiological retinal motion caused by fixational eye movements. While performance under retinal stabilization declined at the larger eccentricities tested within the central fovea, performance under normal vision varied little with eccentricity (Fig. 2 *C*). The drop in performance under retinal stabilization could not be attributed to visual fading; the foveal presentation of above threshold stimuli, their sudden onset and offset and their short duration (<1 s) ensured that visual fading did not occur. Additionally, a similar drop in performance was seen under normal viewing conditions in trials without microsaccades even when ocular drift maintained the stimulus in motion on the retina.

A closer examination of the oculomotor behavior under normal viewing conditions showed that subjects used microsaccades to precisely relocate the preferred locus of fixation on the fine spatial stimuli (Fig. 2 *D*). In fact, when microsaccades did not land precisely on the stimuli performance dropped, further supporting the idea that performance drop under retinal stabilization was not due to visual fading. Ultimately, the results of this study show that fine spatial vision is not uniform across the central fovea but drops sharply with minute displacements from a preferred retinal locus of fixation. Microsaccades precisely shift this preferred locus repositioning the stimulus on the retina to enable its examination at a finer level of detail (Poletti et al., 2013).

Importantly, the results of these studies not only provided further support to the idea that microsaccades are controlled, and proposed a new role for microsaccades in vision, but they also contributed to the realization that microsaccades are a key ingredient if we want to unravel the mechanisms underlying fine spatial vision in the central fovea.

3. Microsaccades and visual exploration of foveal stimuli

In the studies described above stimuli either moved on the display or were flashed at different locations and were the only salient items presented to the subject, hence microsaccades may have been purely driven in a reflexive manner by bottom-up compensatory mechanisms aimed at maintaining the preferred locus of fixation on these stimuli. This raises the question of whether microsaccades can also be guided top-down and be actively used in the exploration of complex foveal stimuli based on the task requirements. Human faces are ideal stimuli to address this question. It is well established that the specific oculomotor strategy for examining a face is driven top-down and varies with the task (Schurgin et al., 2014; Kanan, Bseiso, Ray, Hsiao, & Cottrell, 2015; Mehoudar, Arizpe, Baker, & Yovel, 2014; Blais, Jack, Scheepers, Fiset, & Caldara, 2008; Peterson & Eckstein, 2013). Humans are also familiar with viewing faces from a range of distances. While the face of a person at a distance of a few meters covers several degrees of visual angle, it covers only 1 deg of visual angle when viewed from a distance of many meters, as it happens when sitting a few rows away from the actors at the theatre. In this latter condition we are still capable of discerning facial expressions. Shelchkova et al. (Shelchkova, Tang, & Poletti, 2019) showed that in these conditions humans do not simply fixate on the target but they use microsaccades between 10 and 20 arcminutes to actively explore faces as they do at a larger scale using saccades. In one task participants were asked to judge whether a ≈ 1 deg face was looking straight at them, and in another task to determine whether the face was smiling at them (Fig. 3*A*,*B*). Despite the small size of the stimulus and the fact that the object was already foveated and ideally placed within the foveola at the beginning of each trial, subjects visually explored the face with microsaccades, and the specific scanning strategy used depended on the task performed; when judging facial expression microsaccades mostly landed on the mouth and nose and almost never landed on the eyes, however, when subjects judged gaze direction, this pattern flipped, indicating that microsaccades in natural viewing conditions are actively driven by top-down factors (Fig. 3*C*,*D*). Furthermore, we showed that idiosyncrasies in the scanning behavior across subjects are preserved across scales, subjects who kept fixation on the nose when judging facial expression larger faces, did so also when viewing faces at the foveal scale (Shelchkova et al., 2019). Therefore, the details of the stimuli at the center of gaze are explored using visual scanning strategies that are strikingly similar to those used when exploring larger scenes.

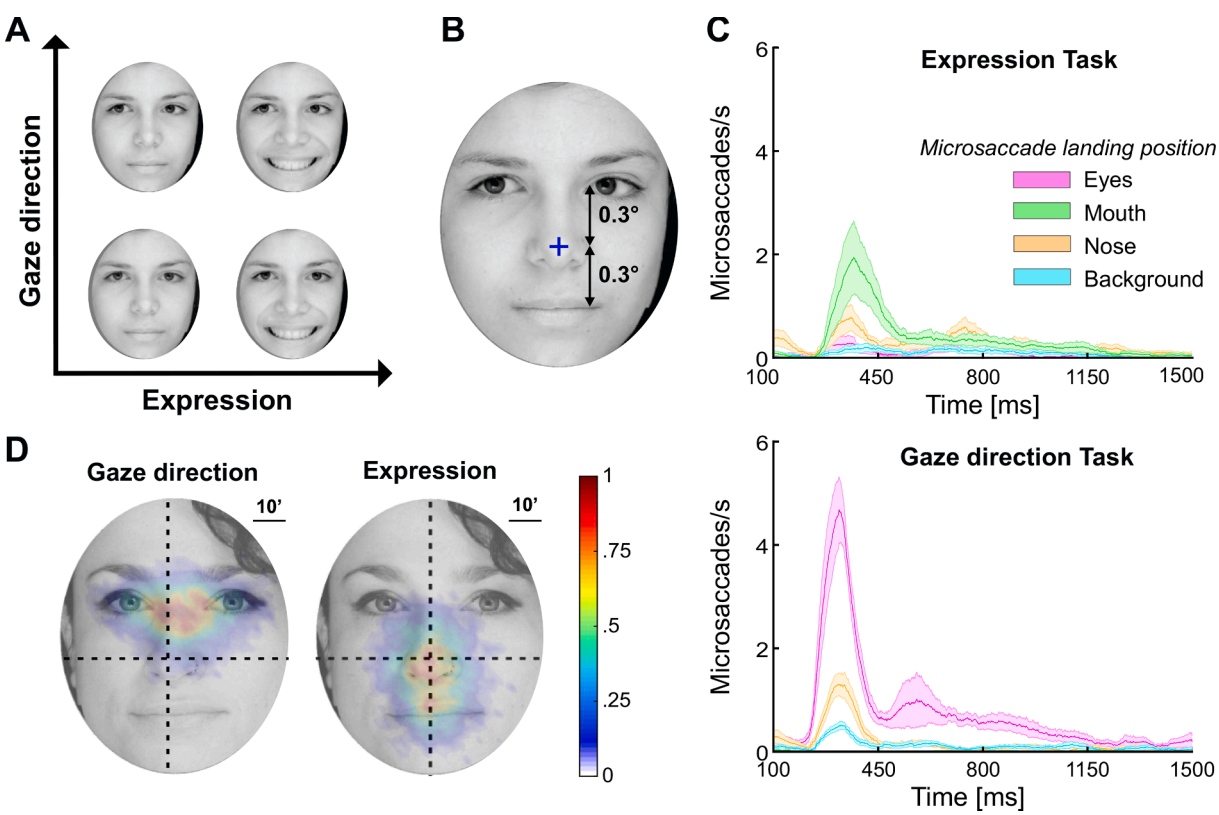

Fig. 3. Microsaccades during visual exploration at the foveal scale. A, face stimuli were generated by changing gaze direction and shape of the mouth. The same face was presented in four different versions: gaze looking straight or looking away and smiling or neutral expression. In the gaze direction task, subjects judged gaze direction, and in the expression task they judged whether or not the face was smiling. **B**, the distance between the eyes/mouth and the initial fixation location (blue cross) was the same. The face covered 1.46^o of visual angle in height. **C**, average probability of microsaccade landing position in the two tasks (N = 10). Data have been filtered using a running average with a 100-ms window. Shaded regions are SEM. **D**, average 2D normalized gaze distribution probability in the gaze direction and in the expression tasks. Figures adapted from Shelchkova et al., 2019.

Another example of how microsaccades contribute to visual exploration of fine details is illustrated in Intoy and Rucci (Intoy & Rucci, 2020). Microsaccades were measured while subjects looked at a 20/20 eye chart line. Results showed that microsaccades as small as 10 arcminutes precisely relocated the preferred locus of fixation from one optotype to the next. This pattern of microsaccades was very different from the pattern of microsaccades recorded during sustained fixation on a marker. Again, high accuracy in localizing the line of sight was crucial in these studies to reveal the role played by microsaccades and the level of finesse that the visuomotor system is capable of.

The fact that microsaccades can be finely tuned and controlled, as well as driven by the goal of the task, raised the question of whether they are voluntary eye movements. They are, in fact, differently from large saccades, often referred to as involuntary. This is a question that has interested vision scientists since the sixties, and back then a few studies already showed that even the smallest microsaccade can be performed voluntarily and that humans can suppress microsaccades on demand (Steinman, Cunitz, Timberlake, & Herman, 1967; Haddad & Steinman, 1973). Following up on that work there is now clear evidence that microsaccades are under voluntary control. We recently showed that subjects can perform microsaccades of different sizes precisely aimed at a target when instructed to (Poletti, Intoy, & Rucci, 2020) (see also Fig. 5*D*), and that humans are capable of performing memory guided microsaccades (Willeke et al., 2019). Additionally, it is now well established that microsaccades are generated by the same neural substrate controlling saccades (Hafed, Goffart, & Krauzlis, 2009; Krauzlis, Goffart, & Hafed, 2017; Hafed, Chen, Tian, Baumann, & Zhang, 2021), and they show the same adaptability as larger saccades (Havermann, Cherici, Rucci, & Lappe, 2014). Therefore, when subjects are not forced to maintain fixation on a marker, a task that only occurs in laboratory conditions, microsaccades are not involuntary, uncontrolled movements, but rather voluntary and finely controlled. Ultimately microsaccades are no different than saccades, they just operate on a different scale; while saccades are used to explore the scene at a larger scale and shift the fovea on potentially interesting and relevant stimuli, microsaccade serve a different purpose, allowing for finer examination of the foveated stimulus.

4. Controlling attention at the foveal scale

It is well established that there is a tight link between eye movements and attention (Kowler, Anderson, Dosher, & Blaser, 1995), hence, the fine control of microsaccades inevitably raises the question of whether attention can be controlled with a similar precision at the scale of the foveola. The idea that the focus of attention is constrained by the fovea has strong roots within the classical view of attention as the "mind's eye movement" (Dover, 1890). In this view, "foveation and focus of attention usually coincide, and perception can be enhanced by focusing attention as well as by foveating" (Fernandez-Duque & Johnson, 1999). This view was reinforced by findings suggesting that the attentional spotlight is approximately 1 deg in size, about the size of the foveola (Eriksen & Hoffman, 1972) (see Johnston & Dark (1986) for a review), and that all stimuli within a circular region of 1 deg benefit equally from attention (Juola, Crouch, & Cocklin, 1987). A different view was proposed by Nakayama and Mackeben (Nakayama & Mackeben, 1989) who reported that after a localized cue was presented within the foveola the ability to find a target changes depending on the cue-target interval following the same trend over time independently of stimulus size and eccentricity suggesting that attention may be focused on a specific section of the central fovea. However, it was not clear if there was a cost in performance associated to the other uncued foveal location or how performance would compare to a neutral condition in which attention was not engaged. Later on it was reported that attentional tracking of moving objects is no longer possible when they subtend an area smaller than 1 degree, suggesting a 1 degree limit in the resolution of attention (Intriligator & Cavanagh, 2001). Importantly, none of these studies controlled for fixational eye movements, in particular for potential confounding effects of microsaccades, and the uncertainty in gaze localization was larger than the size of the fovea even when eyetracking was used, hence, it was impossible to control the exact position on the cue and target stimuli with respect to the center of gaze, something that is crucial when manipulating attention at this scale.

A fine control of attention within the foveola has important implications, most importantly, it would contribute to enhance humans' ability to discriminate detail and to guide visual exploration of complex foveal stimuli. To probe the control of attention at the foveal scale Poletti, Rucci, and Carrasco (2017), using a high-precision eyetracking and retinal stabilization, tested observers in a miniature version of a typical spatial cueing task (Posner, 1980). All stimuli were reduced in size to fit within the 1-deg foveola, that is, the distance between the cued and un-cued location was of only 20 arcminues. Results showed that once fixational eye movements are controlled for and trials with microsaccades discarded, covert endogenous attention can be selectively shifted of as little as 20 arcminutes across the foveola enhancing fine spatial discrimination and reducing reaction times for stimuli presented at the selected attended locations (Poletti et al., 2017) (Fig. 4*A*). This selective enhancement was accompanied by a drop in performance at the unattended foveal location. Crucially, another implication of this study was that attention can be allocated independently from microsaccades execution both within the foveola and in the visual periphery; the effect of attention was shown to be present independently from the execution of microsaccades.

This fine control of attention is not only limited to voluntary endogenous attention but it extends to exogenous attention (Zhang, Shelchkova, Ezzo, & Poletti, 2021). Foveally localized exogenous cues lead to fast and transient enhancements of visual acuity at selected foveal locations (Fig. 4*B*), later followed by a reverse pattern, reminiscent of the inhibition of return phenomenon, characterized by an enhancement at the other initially un-attended location in the foveola. Altogether these findings show that covert shifts of attention are not only useful to enhance low-resolution vision at peripheral locations, but also to improve fine spatial vision at selected locations where the observer is already looking. It has been argued that an important function of covert attention is to attenuate gaps in visual function between the fovea and the periphery (Anton-Erxleben & Carrasco, 2013). Because lack of homogeneity in fine spatial vision has been reported in the foveola (Poletti et al., 2013; Intoy & Rucci, 2020), these results suggest that attentional deployment may serve a similar balancing function within the foveola, by tempering uneven performance at nearby retinal locations. Furthermore, covert attention at this scale may also help alleviate the processing challenges posed by crowded visual stimuli typical of natural scenes. Crowding has, indeed, been shown to occur even at the foveal scale leading to a reduction of acuity (Coates, Levi, Touch, & Sabesan, 2018).

5. The interplay of attention and microsaccades at the foveal scale

The link between microsaccades and attention has been in the spotlight for more than two decades. Research has shown that the direction of microsaccade can reveal the location of the attended stimuli in the visual periphery (Liu, Nobre, & van Ede, 2022; Meyberg, Sinn, Engbert, & Sommer, 2017; Hafed & Clark, 2002; Yuval-Greenberg, Merriam, & Heeger, 2014; Yu, Herman, Katz, & Krauzlis, 2022; Lowet et al., 2018; Hafed, 2013; Engbert & Kliegl, 2003; Laubrock, Kliegl, Rolfs, & Engbert, 2010; Pastukhov & Braun, 2010). Notably, the focus of this research has been on examining peripheral shifts of attention at locations that are much further away from the target location of microsaccades, and this has been studied in rather unnatural conditions involving prolonged sustained fixation on an impoverished foveal input. However, the foveal input is normally complex and rich in detail, and it is often relevant for the task being preformed. Therefore, by studying the

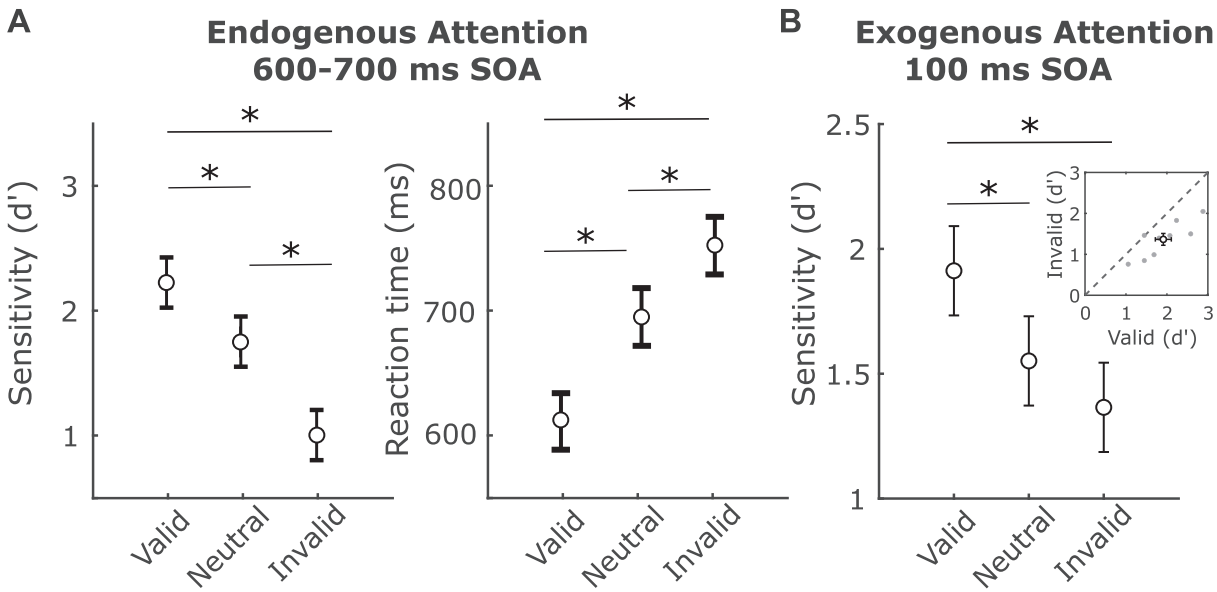

Fig. 4. Fine spatial attention in the foveola. **A**, endogenous attention. Accuracy (d') and reaction times, for different trial types across observers (N = 5). Differences between valid and invalid trials were statistically significant for all individuals. **B**, exogenous attention. Accuracy (d') at a stimulus onset asynchrony of 100 ms (N = 9). Single subjects performances are shown in the inset. $*P < 0.05$ (Tukey HSD post hoc tests). Error bars are 95% CI. Figures adapted from Poletti et al., 2017 (A) and Zhang et al., 2021 (B).

link between attention and microsaccades in this way we may be missing others, and likely more important, aspects of this interplay.

It is known that the act of programming a saccade leads to an obligatory shift of attention to the saccade target, even before the eyes have begun to move (Hoffman & Subramaniam, 1995; Kowler et al., 1995; Deubel & Schneider, 1996). Although attention and saccadic eye movements are heavily interdependent (Jonikaitis & Moore, 2019), recent research lends support to the notion that pre-saccadic attention is

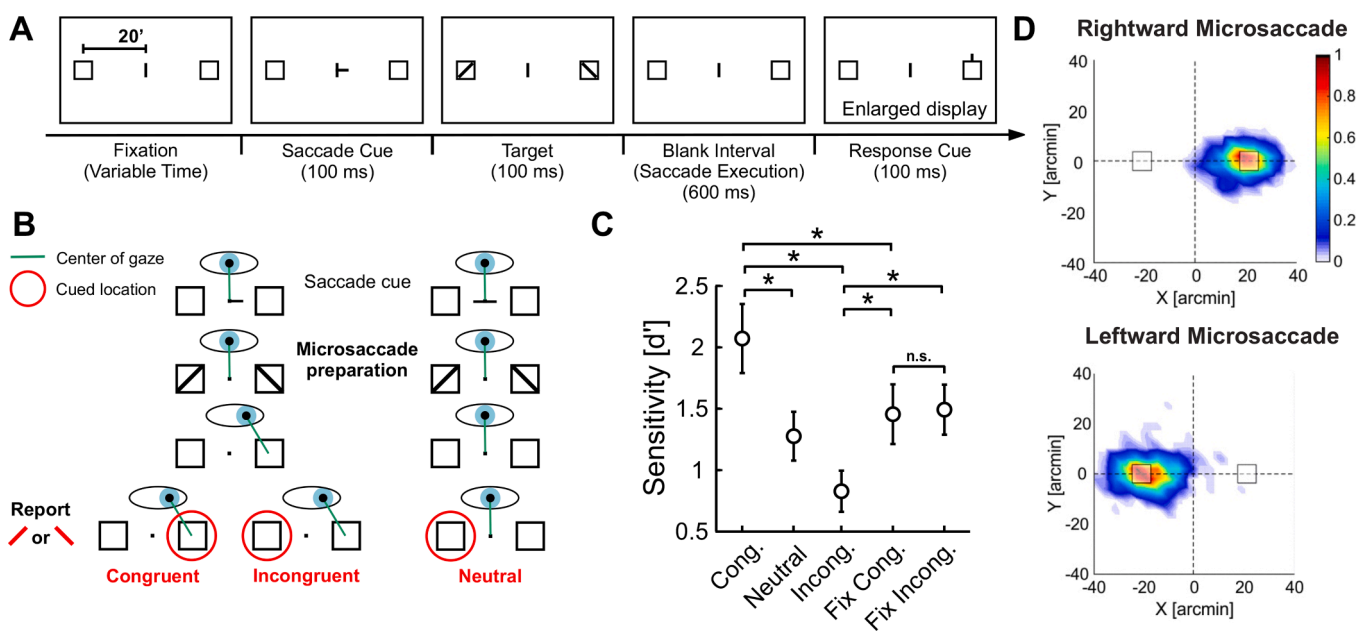

Fig. 5. The interplay of attention and microsaccades at the foveal scale. **A**, subjects maintain fixation on a central marker surrounded by two squares (5 × 5 arcminutes in size) 20 arcminutes away. After a brief period of fixation, a central saccade cue appears, instructing the subject to shift the gaze as soon as possible to one of the two squares with a microsaccade. Immediately after the saccade signal, two stimuli, bars tilted $\pm 45^{o}$, 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**, average (N = 6) accuracy (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). **D**, 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. Error bars are SEM. $*P < 0.05$, Tukey's post hoc test. Figures adapted from Shelchkova and Poletti, 2020.

controlled by processes different from those controlling covert attention (Li, Pan, & Carrasco, 2021b; Li, Hanning, & Carrasco, 2021a). Pre-saccadic attention prioritizes processing and enhances visual perception of the saccade target (Li, Pan, & Carrasco, 2016; Ohl, Kuper, & Rolfs, 2017; Li et al., 2021b). This mechanism is important because it prepares the visual system to process the stimulus that will fall at the center of gaze upon saccade landing. Crucially, this mechanism has been shown to operate also at the foveal scale. Our ability to perceive foveal details drastically changes right before the onset of microsaccades (Shelchkova & Poletti, 2020). Subjects were asked to discriminate the orientation of a fine spatial stimulus briefly presented before the onset of a microsaccade. The stimulus could be presented at the target location of the microsaccade or at the opposite location, *i.e.*, just 20 arcminutes to the right or to the left of the preferred locus of fixation (Fig. 5*A*,*B*,*D*). Results showed that 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 (Fig. 5*C*). This effect was not present in the absence of microsaccades and its strength increased as the stimulus was presented closer to the onset time of the microsaccade. These findings not only show that the interplay between microsaccades and attention extends to the foveal scale with a surprisingly fine level of spatial resolution, but they also indicate that foveal vision is being modulated in space and time during fixation when microsaccades occur. Therefore, the benefits of microsaccades for foveal vision are not restricted to the spatial relocations that microsaccades bring about, but they are also associated to pre-microsaccadic attention.

Importantly, vision is modulated also during microsaccades, in particular it has been reported that the ability to detect highly localized luminance changes across the fovea is suppressed during microsaccades (Intoy, Mostofi, & Rucci, 2021). The extent and dynamics of microsaccadic perceptual suppression vary with eccentricity within the foveola; suppression is stronger and faster in the most central portion, where sensitivity is generally higher, and selectively rebounds at the onset of a new fixation. This mechanism can be particularly useful during active examination of fine detail in the central fovea (Intoy et al., 2021).

6. Microsaccades in everyday tasks

It is critical not just to investigate microsaccades utilizing richer and more complex foveal stimuli, but also to understand their role in everyday tasks. One activity that humans engage in daily is reading. Oculomotor behavior, in particular saccades, has been widely characterized and studied during reading (Rayner, 1998; Rayner et al., 2009). However, there is a lack of studies examining fixational eye movements, and in particular microsaccades during reading. Morrison and Rayner (1981) have shown that the amplitude of saccades scales with the size of

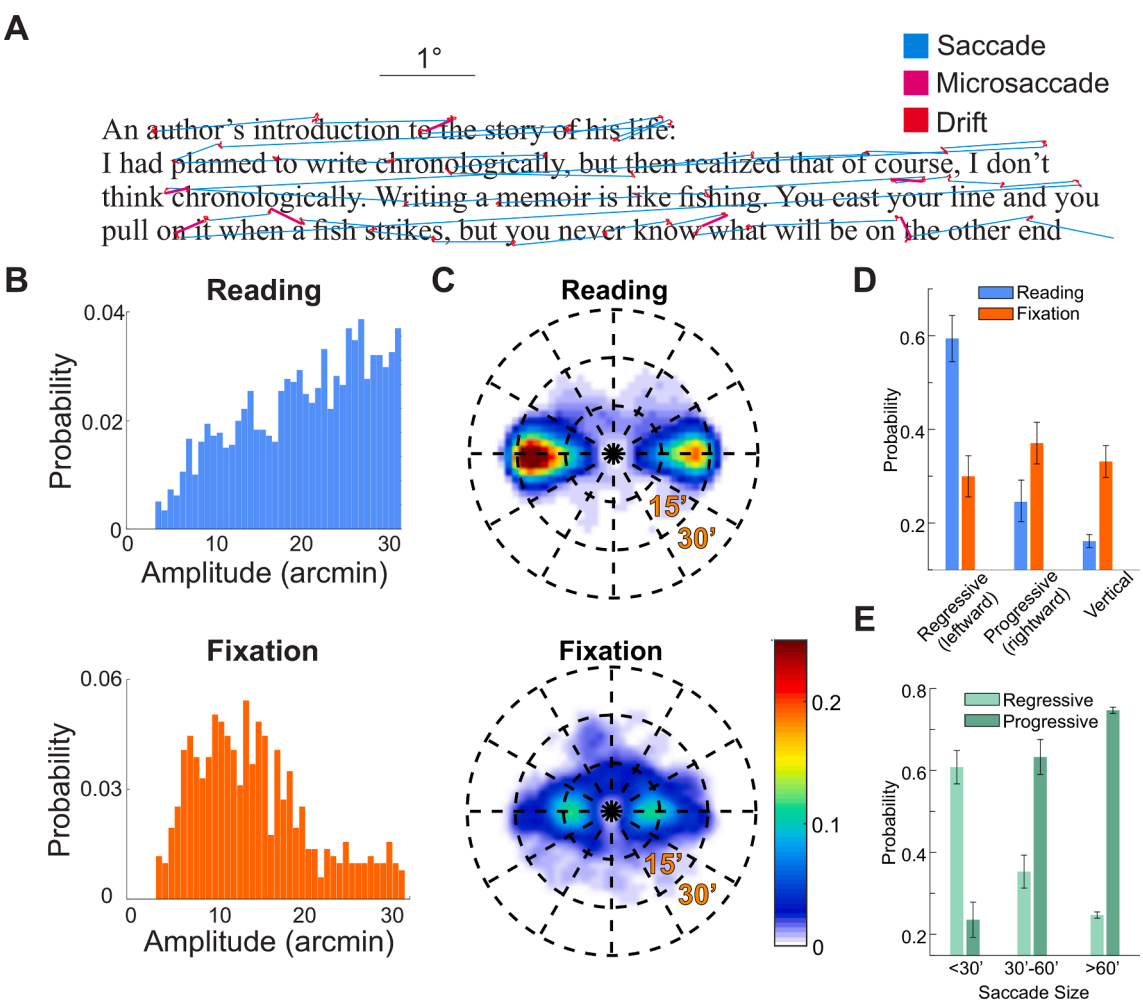

Fig. 6. Microsaccades during everyday tasks. A, an example of eye movements during reading. The lines of text are an excerpt from one of the paragraphs used in the study. Different types of eye movements are color-coded. **B**, probability distribution of microsaccade amplitudes during reading and sustained fixation across all the tested subjects (N = 6). **C**, average 2D polar histograms of microsaccades direction and amplitude during reading and sustained fixation. **D**, average probability of progressive (rightward), regressive (leftward) and vertical (up and downward) microsaccades in reading and fixation. **E**, average probability of regressive and progressive saccades during reading as a function of saccade amplitude. Error bars represent SEM. Figures adapted from Bowers and Poletti, 2017.

the characters in the text. It has also been shown that microsaccades normally occur during reading pauses whose duration is longer than normal (Cunitz & Steinman, 1969). By using high-resolution eye-tracking and precise gaze localization, we showed that microsaccades are relatively frequent during reading (Fig. 6*A*) Bowers and Poletti (2017). Further, we reported that microsaccade characteristics during reading differ from those measured during sustained fixation: microsaccades are larger in size and primarily leftwards during reading (Fig. 6*B-E*), *i.e.* they move the line of sight backward on the text, a tendency also reported by Kowler and Anton (Kowler & Anton, 1987). Based on these results we proposed that during reading microsaccades serve two important functions: (1) a corrective function, by moving the gaze regressively within longer words when the preceding saccade lands too far toward the end of these words, and (2) an exploratory function, by shifting the gaze on adjacent words to gain additional information before the execution of the next saccade. Thus, microsaccades may benefit reading by enhancing the visibility of nearby words. Microsaccades have also been shown to be sensitive to the lingusitic structure (Yablonski, Polat, Bonneh, & Ben-Shachar, 2017). Ultimately these findings highlight the importance of examining fine oculomotor behavior in reading and understanding if and how it is altered in individuals with reading difficulties (Rima & Schmid, 2021).

In between saccades and microsaccades; control and contributions of ocular drift to fine spatial vision

In between saccades and microsaccades the eye continues to move as a result of ocular drift, the incessant jitter of the eye that resembles a random walk and appears to move the gaze erratically (Steinman & Collewijn, 1980; Cherici et al., 2012; Poletti, Listorti, & Rucci, 2010; Rucci et al., 2015; Nachmias, 1959; Burak, Rokni, Meister, & Sompolinsky, 2010; Engbert, Mergenthaler, Sinn, & Pikovsky, 2011; Kuang, Poletti, Victor, & Rucci, 2012; Intoy & Rucci, 2020). During drift periods each eye follows its own trajectory almost independent from that of the other eye (Poletti et al., 2015; Ditchburn & Ginsborg, 1953; Krauskopf, Cornsweet, & Riggs, 1956; Krauskopf et al., 1960). Not surprisingly the predominant view portrays drift as some type of random motion over which the oculomotor system has no control. However, to reliably measure this eye movement, drift is studied in head-fixed conditions; normally, the head of the observer is immobilized by means of a bite bar and/or a head rest. This is in stark contrast to what happens under normal viewing conditions when the motion of the retinal image during fixation results from both fixational head and eye movements (Skavenski et al., 1979; Poletti et al., 2015; Aytekin et al., 2014). It is therefore, important to examine drift under head-free conditions.

Poletti et al. (2015) reanalyzed data collected by Steinamn and

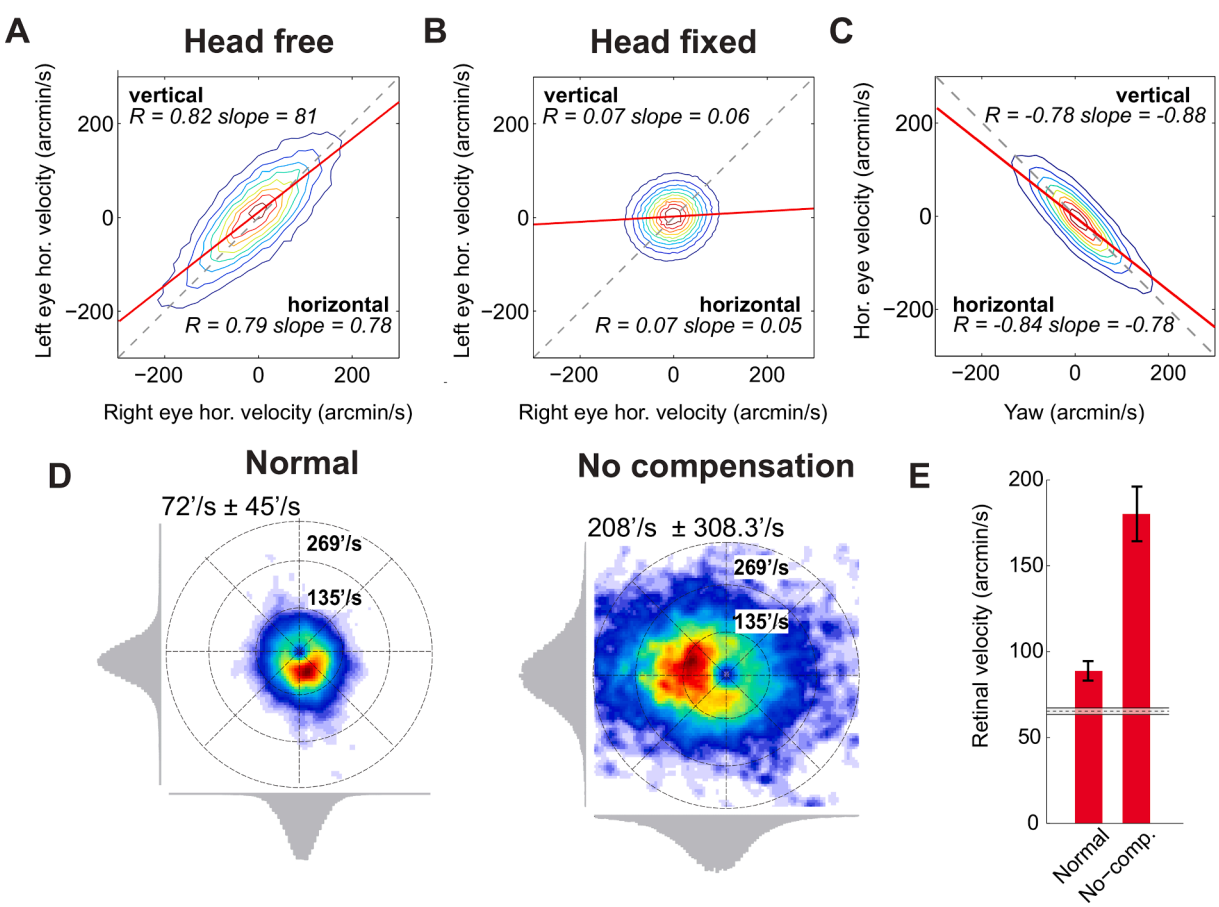

Fig. 7. Ocular drift during head-free viewing. A-B, joint probability distributions for the instantaneous horizontal velocities of ocular drift in the two eyes. Colored lines represent iso-probability contours. Similar results were obtained for the vertical component of motion. In the head fixed condition (*B*) the subject's head was firmly immobilized by a bite bar and a headrest. **C**, comparison between the velocities of head and eye rotations. The horizontal and vertical components of ocular drift velocity are plotted as a function of the angular speeds of head yaw and pitch, respectively. In all panels, the solid and dashed lines represent the linear regression and the 45° diagonal, respectively. Average correlation and slope of the linear regression are reported in each panel for both the vertical and horizontal component of motion. Data represent averages across four observers. **D**, examples of probability distributions of the velocity of the fixated target on the retina. Head-eye compensation was disrupted by decoupling head and eye traces. **E**, average speeds of the retinal projection of the fixated target for the normal and the no-compensation condition. For comparison, the dashed line shows the average retinal speed measured in standard experiments with head immobilization, when subjects freely observed natural scenes. Error bars and the shaded region represent one SD. Figures adapted from Poletti et al., 2015.

colleagues (Epelboim et al., 1997) with the Maryland Revolving Field Monitor (MRFM), a custom device specifically designed to give precise measurements without requiring immobilization of the head. We examined head and eye behavior during steady fixation when eye speed was below 4 deg/s (average speed below 2 deg/s). In contrast with what happens when the head is fixed, during head-free fixation the motion of the two eyes is highly correlated (Poletti et al., 2015) (Fig. 7*A*,*B*). This happens because there is a strong anticorrelation in the pattern of fixational eye and head movements (Fig. 7*C*). Because ocular drift not only corrected for previous head movements but also frequently anticipated them, suggesting a joint control of fixational head and eye movements, it is unclear whether this behavior is governed by the same mechanisms controlling VOR and OKN operating at a much finer scale, or if it is the outcome of a different mechanism. By artificially decoupling eye and head movements during fixation we showed that this fine-scale compensatory mechanism is of paramount importance for vision, as its absence would result in excessive retinal speeds, a condition dysfunctional for visual acuity (Poletti et al., 2015) (Fig. 7*D*,*E*). Therefore, ocular drift is not simply random motion, fixational head and eye movement work together during fixation to maintain the amount of retinal motion within an ideal range. Further supporting the idea that drift is far from being a random motion of the eye, a recent study showed that the visuomotor system has access to ultra-fine extraretinal knowledge of drift motion and is capable of using this knowledge for inferring fine spatial relationships (Zhao, Ahissar, Victor, & Rucci, 2023)

Still, even in the presence of this compensatory mechanism, humans are exposed to a significant amount of motion on the retina (Kuang et al., 2012; Skavenski et al., 1979; Ratnam, Domdei, Harmening, & Roorda, 2017; Anderson, Ratnam, Roorda, & Olshausen, 2020; Intoy & Rucci, 2020). Further, it has been shown that this drift-related motion drives robust activity of V1 neurons (Snodderly, Kagan, & Gur, 2001; Kagan, Gur, & Snodderly, 2008) (see Snodderly (2016) for a review). This raises fundamental questions on the mechanisms underlying the establishment of fine spatial representations and how the visual system avoids the perceptual blur that one would expect from the smearing of the stimulus on the retina (Barlow, 1952; Burak et al., 2010; Anderson et al., 2020; Packer & Williams, 1992). On the other hand, it has been argued for over a century that drift motion may actually be beneficial to visual acuity by *structuring*—rather than just *refreshing*—neural activity (Hering, 1899; Arend, 1973; Averill & Weymouth, 1925; Marshall & Talbot, 1942; Steinman & Levinson, 1990; Ahissar & Arieli, 2001), an hypothesis originally formulated by Hering (Hering, 1899) and later refined into the so-called dynamic theories of visual acuity (Averill & Weymouth, 1925; Marshall & Talbot, 1942; Arend, 1973). In support of this view

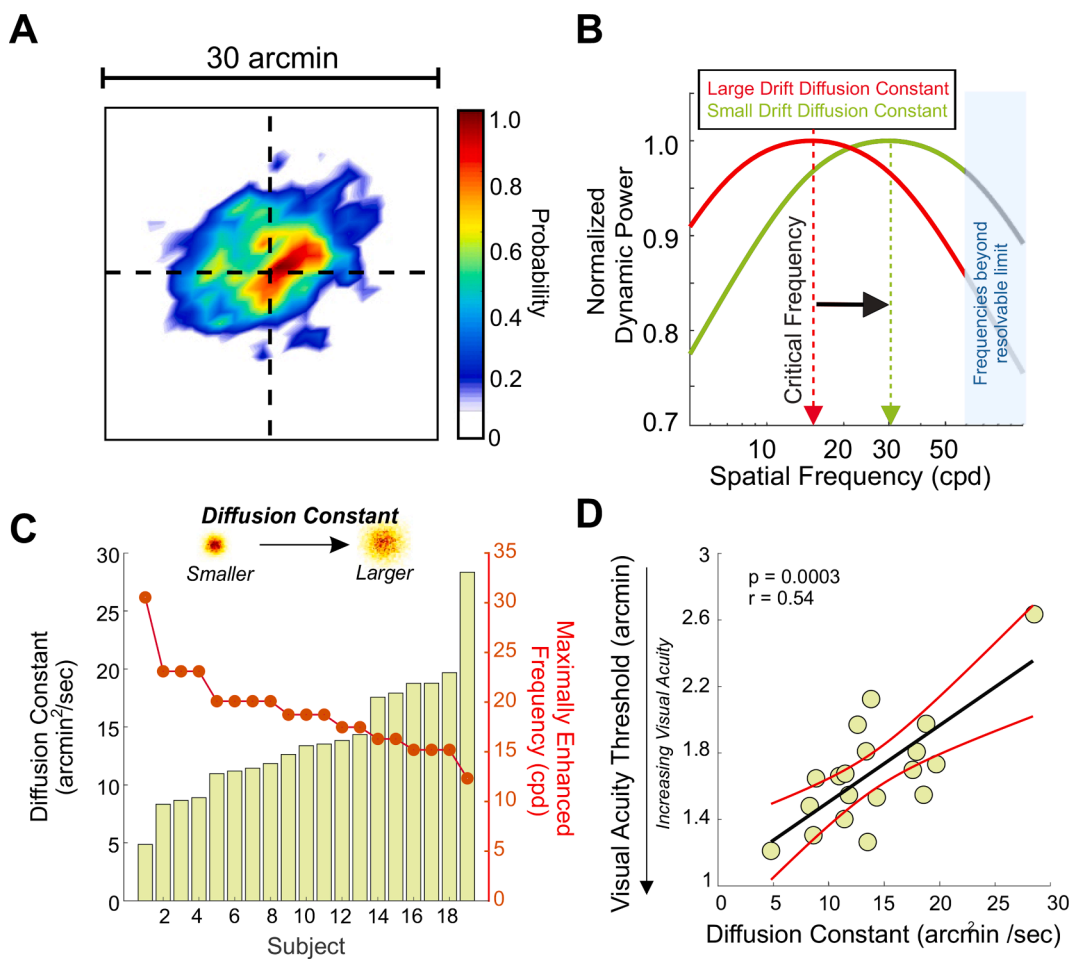

Fig. 8. Oucular drift and visual acuity. A, normalized 2D probability distributions of gaze position during stimulus presentation for a typical subject. **B**, average amplitudes of the luminance fluctuations resulting from drift motion characterized by a different diffusion constant during viewing of gratings at individual spatial frequencies. Each curve represents the signal effective in driving retinal ganglion cells, estimated as the total power released by drift at nonzero temporal frequencies within the bandwidth of neuronal sensitivity. Note that, rather than being constant across spatial frequencies, this signal is strongest within a frequency band that varies with the amount of drift. The shaded blue region marks frequencies beyond human sensitivity. **C**, individual drift diffusion constants and corresponding critical frequencies (red dots). The illustrations on top represent theoretical 2D distributions of gaze position (red colors indicate higher densities) for smaller and larger diffusion constants. **D**, visual acuity thresholds as a function of drift diffusion constant in the task. Each point represents an individual subject (N = 19). Error bars are 95% confidence intervals of the regression line. Figures in part adapted fromClark et al. (2022).

recent studies have shown that fine spatial vision is specifically impaired in the absence of the retinal image motion resulting from ocular drift (Rucci, Iovin, Poletti, & Santini, 2007; Ratnam et al., 2017; Intoy & Rucci, 2020; Agaoglu, Sheehy, Tiruveedhula, Roorda, & Chung, 2018). Mounting evidence now indicates that fixational retinal motion plays a fundamental role in visual acuity. It has been shown that drift can be modulated by the task (Intoy & Rucci, 2020; Shelchkova et al., 2019; Lin, Intoy, Clark, Rucci, & Victor, 2023) and the viewed stimulus (Malevich, Buonocore, & Hafed, 2020), and it has been observed that the way drift transforms spatial patterns into a spatiotemporal flow on the retina implements a crucial information-processing step tuned to the characteristics of the natural visual world (Rucci et al., 2015). This transformation discards redundant information and enhances neural responses to luminance discontinuities, processes long argued to be important goals of early visual processing (Attneave, 1954; Barlow, 1961; Olveczky, Baccus, & Meister, 2003; Ahissar & Arieli, 2001; Rucci, Edelman, & Wray, 2000), which is expected given that neurons in the retina and the early visual system are relatively insensitive to an unchanging input (Purpura, Tranchina, Kaplan, & Shapley, 1990).

The retinal motion introduced by drift (Fig. 8*A*) (or by the interplay of drift and fixational head motion) is ideal for visual acuity (Intoy & Rucci, 2020; Rucci et al., 2007), and the link between drift and acuity is so strong that acuity can be predicted based on the pattern of ocular drift (Clark, Intoy, Rucci, & Poletti, 2022). Interestingly, there is considerable variability in the amount of drift across individuals (Fig. 8*C*). Drift diffusion constant, a measure quantifying how rapidly the line of sight tends to move away from its current location, varies of a factor of four across observers (Clark et al., 2022). These individual differences profoundly affect the structure of spatiotemporal signals to the retina; the spectral distribution of the resulting luminance modulations strongly correlates with individual visual acuity (Fig. 8*B*). Further, at the single subject level, trials characterized by drift with larger vs. smaller diffusion constant are associated with lower performance in an acuity task, suggesting that the amount of ocular drift actively modulates visual acuity (Clark et al., 2022). As a result, in healthy emmetropes, acuity can be predicted from the motor behavior elicited by a simple fixation task, without directly measuring it (Clark et al., 2022) (Fig. 8*D*). Overall these studies indicate that oculomotor behavior is a crucial component necessary to fully understand the mechanisms underlying visual acuity and the factors leading to individual differences in acuity.

7. Conclusive remarks

The research reviewed here contributes to show that vision is an intrinsically active process, even during the short periods of fixation, and the visuomotor system has a remarkable level of oculomotor control even over the smallest eye movements. Albeit in different ways, both drift and microsaccades contribute to fine spatial vision. Together with highly precise control of attention, microsaccades are linked to non–homogeneous processing within the foveola and contribute to fine spatial vision modulating sensitivity across the foveola both in space and time. Drift, on the other hand, modulates the retinal input in a way that is optimal for visual acuity enhancing high spatial frequencies. Fixational eye movements and attention at the foveal scale are optimized to perform a finer grain examination of the foveal input. Therefore, fine spatial vision is not the mere consequence of placing a stimulus at the center of gaze, it is rather an active process and the outcome of a synergy of motor, cognitive, and attentional processes, all finely tuned and dynamically orchestrated.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgments

NIH grant R01EY029788-01 and the Sloan Research Fellowship to M.P.

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