Control and Functions of Fixational Eye Movements

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Abstract

Humans and other species explore a visual scene by making rapid eye movements (saccades) two to three times every second. Although the eyes may appear immobile in the brief intervals between saccades, microscopic (fixational) eye movements are always present, even when an observer is attending to a single point. These movements occur during the very periods in which visual information is acquired and processed, and their functions have long been debated. Recent technical advances in controlling retinal stimulation during normal oculomotor activity have shed new light on the visual contributions of fixational eye movements and the degree to which these movements can be controlled. The emerging body of evidence, reviewed in this article, indicates that fixational eye movements are important components of the strategy by which the visual system processes fine spatial details; they enable both precise positioning of the stimulus on the retina and encoding of spatial information into the joint space–time domain.

VISION AND EYE MOVEMENTS

Vision is an active process. Humans collect visual information from a remarkably broad field of view, covering an angle larger than 180 deg. Monitoring such a wide area, however, comes at a cost: A variety of visual functions, including acuity, are not uniform throughout the visual field; rather, they progressively deteriorate with increasing distance from a small central region that is approximately the size of the full moon in the sky (Weymouth et al. 1928, Jacobs 1979, Legge & Kersten 1987, Hansen et al. 2009, Nandy & Tjan 2012). This small central region is the portion of the visual field that projects onto the foveola, the tiny area of the retina in which rod receptors are absent and cones are most densely packed. Thus, to efficiently examine a visual scene, humans must move their eyes. They must be capable of both redirecting the high-acuity foveola toward interesting locations in the scene and keeping it focused on moving objects.

Rapid gaze shifts (saccades) normally occur two to three times every second (**Figure 1*a***). Visual information is acquired, and the targets for successive saccades selected, in the brief fixation intervals in between these movements, effectively establishing a tight loop between perception and action. The fixational sequence enabled by saccades is only the most evident aspect of a deep sensory–motor coupling (Kowler 2011). Close examination of gaze position reveals the presence of incessant microscopic eye movements during fixation (**Figure 1*b***). Although we are normally not

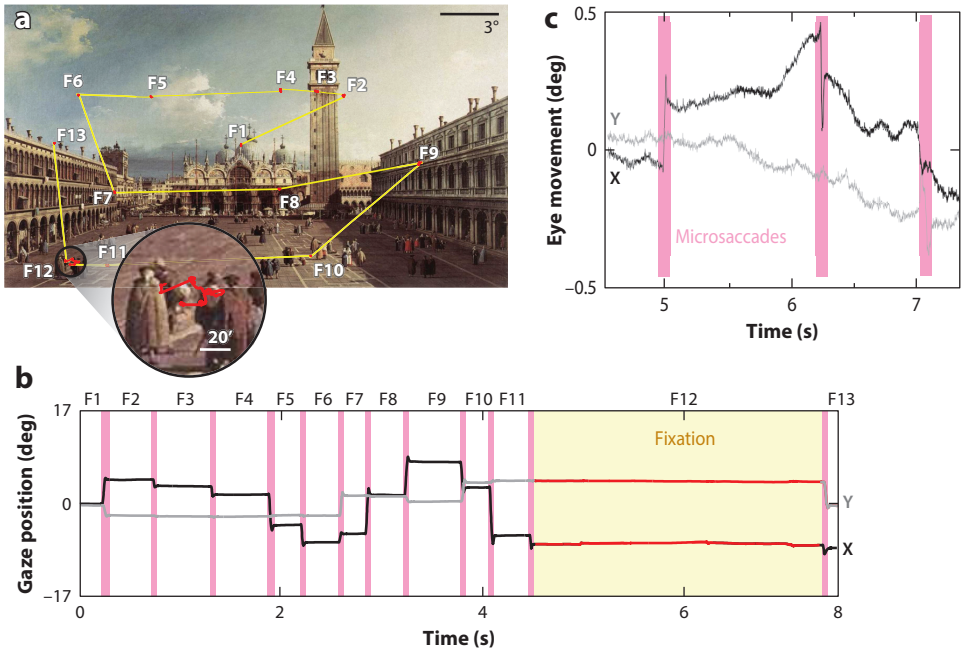

Figure 1

Normal eye movements. (*a*) As an observer explores a scene, saccades (*yellow lines*) separate brief periods of fixation, in which visual information is acquired (F1–F13; *red dots*). As shown in the enlargement, small eye movements continually occur during fixation. (*b*) Horizontal and vertical traces of the oculomotor sequence in panel *a*. Magenta bars indicate saccades. Microscopic saccades, called microsaccades, are barely visible in this graph, owing to its large scale. (*c*) Traces of the eye movements present during one fixation (F12; *circle* in panel *a* and *yellow region* in panel *b*). Data represent horizontal and vertical deviations from the mean eye positions. The eye wanders along a seemingly random trajectory (ocular drift), occasionally interrupted by microsaccades (*magenta bars*).

aware of these movements, they yield speeds of retinal motion that would be visible immediately if they had originated from objects in the scene rather than from our own eyes.

The study of fixational eye movements is often considered an area of specialty for oculomotor researchers. These movements are commonly regarded as a nuisance by experimentalists, rarely taken into account in the explanation of experimental results, and generally ignored by theories of visual functions. Yet they have been observed in a wide variety of species, including the owl, a predator believed to not move its eyes (Pritchard & Heron 1960, Skavenski et al. 1975, Collewijn & Van Der Mark 1972, Greschner et al. 2002, Steinbach 2004). Furthermore, fixational eye movements can be regarded as the ultimate token of behavior necessary to enable normal vision: Percepts tend to fade away when retinal image motion is eliminated, whereas visual functions appear normal when fixational instability is the only source of input modulation (Ditchburn & Ginsborg 1952, Riggs & Ratliff 1952, Tulunay-Keesey 1982). Thus, fixational eye movements are sufficient for enabling vision of stationary scenes, but how they do so remains unknown. Given the temporal integration windows of neurons, it also remains unclear how the visual system establishes fine spatial representations (Burak et al. 2010) and how it avoids perceptual blurring of the image (Packer & Williams 1992) despite the incessant presence of these movements.

Although traditionally regarded as a simple means to refresh neural activity and prevent perceptual fading, a plethora of mounting evidence indicates that fixational eye movements play a more central role in vision. These movements are now known to modulate neural responses in various cortical areas (Martinez-Conde et al. 2000, Snodderly et al. 2001, Kagan et al. 2008, Hafed et al. 2009, Herrington et al. 2009, Hohl & Lisberger 2011), and multiple findings support the idea that they contribute not only to the acquisition of visual information but also to its processing (Ahissar & Arieli 2001, Rucci 2008, Rolfs 2009). In this article, we summarize the main characteristics of fixational eye movements (see the section titled "Types of Fixational Eye Movements") and review some recent findings within this emerging body of evidence. We focus first on smooth intersaccadic movements (see the section titled "Visual Functions of Intersaccadic Fixational Movements") and then on microscopic saccades (see the section titled "Visual Functions of Microsaccades").

TYPES OF FIXATIONAL EYE MOVEMENTS

Although multiple indirect observations have long provided evidence that the eyes are always in motion, the first direct measurements of microscopic eye movements only became possible in the middle of last century, when eye-tracking methods with sufficient resolution were first developed (Ratliff & Riggs 1950, Barlow 1952, Ditchburn & Ginsborg 1953). These recordings have revealed the existence of a rich and diverse oculomotor activity (**Figure 1*b***).

Fixational eye movements are traditionally subdivided into three categories (Kowler 2011), with a tiny jitter (tremor) superimposed to an apparently erratic slow motion (ocular drift), occasionally interrupted by small saccades (microsaccades). But classification becomes challenging for the movements with the smallest amplitudes, and the boundaries between categories are not as clear as one may assume, particularly that between drift and tremor. For this reason, this article often uses the term ocular drift (or, for brevity, drift) to refer to the intersaccadic motion of the eye in general, without attempting to subdivide this motion into separate categories. The following subsections summarize the general characteristics of fixational eye movements.

Intersaccadic Movements

As shown in **Figure 1*c***, the eyes move in a smooth but jittery way during the periods in between the abrupt gaze shifts caused by saccades. A slow meandering motion and a smaller superimposed

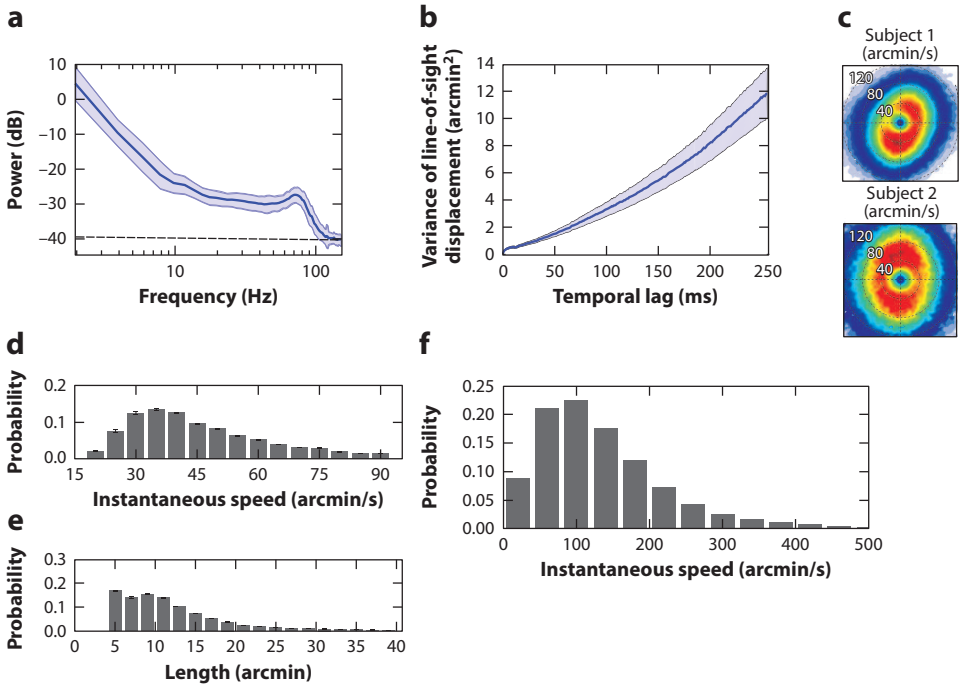

Figure 2

General characteristics of ocular drifts and tremor. (*a*) Power spectrum of the oculomotor activity recorded in the periods between saccades and/or microsaccades. The dashed line represents the background noise level of the eye tracker. (*b*) Variance of the displacement of the line of sight as a function of time. The increment is approximately linear, as is distinctive of Brownian motion. (*c*) Probability distributions of instantaneous drift velocity for two observers during sustained fixation on a marker (Cherici et al. 2012). (*d*,*e*) Average distributions of ocular drift speed (*d*) and path length (*e*) during free viewing of natural scenes (Kuang et al. 2012). (*f*) Drift speed distribution for one observer during normal head-free viewing (Aytekin et al. 2014).

jiggle incessantly shift the projection of the stimulus over many retinal receptors. The slow motion occupies the frequency range from 0 Hz to approximately 40 Hz and is most prominent at low temporal frequencies. The faster component possesses a smaller amplitude and a spectral peak in the range of 40 to 100 Hz. The slow and fast components are often referred to by the terms ocular drift (Cornsweet 1956, Fiorentini & Ercoles 1966) and tremor (Adler & Fliegelman 1934, Eizenman et al. 1985), respectively, but no clear-cut separation exists in terms of their frequency bandwidths (**Figure 2*a***). Also note that the amplitude of tremor (∼1 arcmin) is at the resolution limit of even the most sophisticated eye trackers (dashed line in **Figure 2*c***), and its frequency bandwidth includes the power line frequency. Both factors contribute to the difficulty of distinguishing tremor from recording noise, so little is known about the characteristics and possible functions of this oculomotor behavior.

Most of what we know about fixational eye movements comes from experiments in which the subject's head is immobilized, a standard practice for resolving very small eye movements. Under these conditions, the eyes appear to move in an erratic fashion during fixation, yielding trajectories that resemble the random motion of a particle in a fluid. The variance of gaze displacement increases approximately linearly with time, a behavior characteristic of Brownian motion (Engbert et al. 2011) (**Figure 2*b***). This behavior carries the beneficial consequence that the

standard deviation of the eye position increases at a rate slower than linear, so that the projection of the target remains within a relatively narrow retinal region during the naturally brief periods of intersaccadic fixation. A resemblance to Brownian motion should not be taken to imply lack of oculomotor control, however; control could be exerted in several ways, for example, by changing the diffusion coefficient (the parameter that regulates the speed of the Brownian process). Considerable evidence indicates that drift is indeed controlled (Nachmias 1961, Steinman et al. 1973, Kowler 2011), and the term slow-control is sometimes used in the literature to refer to this motion.

Ocular drift is commonly believed to move the eyes very little and very slowly. Classical studies have typically reported drift displacements ranging from approximately 1.5 to 4 arcmin and a median drift speed of approximately 4 arcmin/s (Ditchburn 1973). However, these numbers severely underestimate the real drift displacement and speed for multiple reasons. They represent measurements from highly experienced observers attempting to maintain strict fixation on a single point, which are not representative of the faster motion occurring during normal intersaccadic fixation. Furthermore, they are average estimates obtained over long intervals (and commonly on a single axis), a procedure that implicitly selects only low temporal frequencies. But ocular drift has a broad spectrum (**Figure 2*a***) and changes direction very frequently (**Figure 2*c***). **Figure 2*d,e*** shows the mean two-dimensional (2D) characteristics of ocular drift (the signal below 30 Hz) as subjects freely examined natural scenes. The resulting speed (mean ~50 arcmin/s) is more than one order of magnitude larger than classical estimates, covering a considerable length in visual space.

Special equipment is necessary to resolve ocular drift during normal, head-free viewing. One device with demonstrated sufficient resolution is the coil-based Revolving Field Monitor developed by Steinman and collaborators (1990). Studies using this system have shown that ocular drift becomes much faster when the head is not immobilized. **Figure 2*f*** shows an example for one observer. Note that the median drift speed is approximately three times higher when measured under head-free conditions than when measured under head-immobilization conditions. Drift also shows clear signs of control during head-free viewing, partially compensating for the instability of the head, so as to preserve the spatiotemporal characteristics of retinal stimulation (Skavenski et al. 1979, Aytekin et al. 2014).

Microsaccades

Microsaccades are miniature replicas of the rapid gaze shifts (saccades) that humans normally use to explore a visual scene. These movements are more easily detected than other fixational eye movements and thus have been the focus of extensive research. For these reasons, microsaccades are commonly the first to come to mind in discussions of fixational instability. Unlike the smooth intersaccadic motion described in the subsection titled "Intersaccadic Movements," however, microsaccades are episodic events that generally occur at rates lower than one or two events per second.

Much of the literature on microsaccades has focused on experiments using sustained fixation, a frequent condition in vision research in which observers maintain a steady gaze on a cue for a prolonged period of time. Under these conditions, microsaccades appear to be involuntary—subjects are usually not aware of their occurrence—and unnecessary movements, and thus their function has remained unclear. Note, however, that sustained fixation rarely, if ever, happens in natural tasks; most fixations in natural tasks last for only a fraction of a second. Thus, it is not surprising that saccades cannot be suppressed for very long (Kowler & Steinman 1980). It has also long been known that sustained fixation affects the pattern of fixational eye movements (Steinman et al. 1973), including microsaccades (Cornsweet 1956).

Under more natural conditions, in which observers are not requested to maintain fixation, the term microsaccade has been traditionally used to refer to the very small saccades that minimally

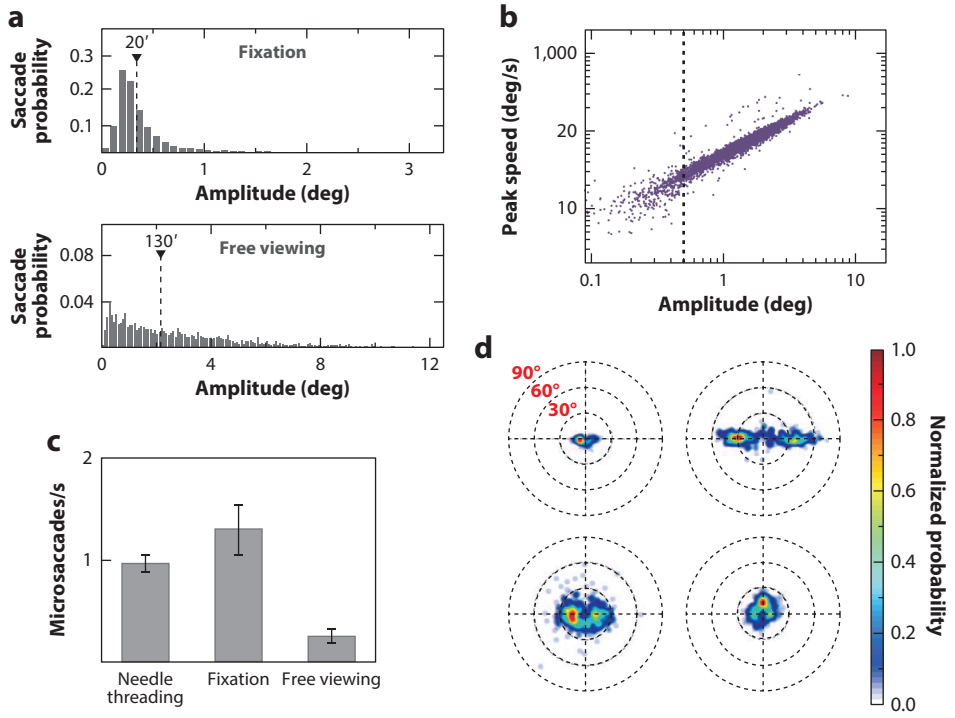

Figure 3

General characteristics of microsaccades. (*a*) Saccade amplitude distribution during sustained fixation and free viewing. Note the different ranges of amplitudes. Data represent average distributions across six observers; triangles mark the medians of the distributions. (*b*) Peak saccade speed as a function of amplitude during free viewing. Points to the left of the dashed line represent saccades smaller than half a degree. (*c*) Microsaccade rates in three different tasks: needle threading, sustained fixation on a single dot, and free viewing of a natural scene (Ko et al. 2010). (*d*) Individual variability in microsaccades during sustained fixation. Each plot shows the (normalized) two-dimensional probability distribution of microsaccade displacements for an individual observer (Cherici et al. 2012).

change the luminance pattern experienced by the foveola (Collewijn & Kowler 2008). The amplitudes of these saccades are smaller than a predefined threshold, but the actual threshold value has varied across studies. As saccade amplitude distributions are normally unimodal and have no separation between small and large movements (**Figure 3*a***), a common practical approach to setting the threshold has been to choose a value that encompasses the range of saccade amplitudes measured under sustained fixation. Following this or similar criteria, classical studies have usually restricted the use of the term microsaccade to tiny saccades: smaller than 30 (e.g., Zuber et al. 1965; Fiorentini & Ercoles 1966) or even 12 arcmin (e.g., Ditchburn & Ginsborg 1953, Boyce 1967, St. Cyr & Fender 1969).

It should be noted that several recent studies have reported broader amplitude distributions during sustained fixation and consequently raised the microsaccade threshold to include much larger movements, up to 1.5 or even 2 deg (Rolfs 2009). Various factors may have contributed to this discrepancy, and the use of different recording methods is likely a key element. However, such a large increment in threshold alters the nature of traditional debates on microsaccades (Collewijn & Kowler 2008): As the average radius of the foveola is approximately 30 arcmin (Curcio et al.

1990), saccades that have amplitudes greater than 1 deg completely change the portion of the visual field within this region.

In this article, we focus on conditions in which fixation is not explicitly enforced and continue the classical tradition of using the term microsaccade to indicate the very small saccades that maintain the stimulus within the foveola. All data reported here refer to saccades with amplitudes smaller than 30 arcmin (20 arcmin in some cases); microsaccades with these amplitudes yield overlap of 50% or more between the presaccadic and postsaccadic images. This threshold also conveniently coincides with the 90th percentile of the average saccade distribution measured during sustained fixation by means of an eye tracker demonstrated to have high resolution (Cherici et al. 2012).

Because microsaccades are essentially a subclass of saccades, they share many characteristics with their larger counterparts. For example, it has long been known that the linear relationship between amplitude and velocity observed for saccades (the main sequence) also extends to the microsaccade range (Bahill et al. 1975) (see **Figure 3*b***). Similar to larger saccades, the amplitudes, directions, and frequencies of microsaccades vary significantly depending on the experimental conditions (e.g., Malinov et al. 2000), the task (e.g., Ko et al. 2010), the stimulus (e.g.,Thaler et al. 2013), and attention (e.g., Hafed & Clark 2002). As **Figure 3*c*** shows, microsaccades tend to be frequent during sustained fixation and in tasks that require high visual acuity, and they are usually rare in tasks that favor larger saccades, such as free viewing of a scene. However, microsaccade rates vary both with the specific conditions (e.g., the type of fixation marker and the characteristics of the scene) and the instructions given to the subject. Interestingly, microsaccade characteristics also vary considerably across observers (**Figure 3*d***), although the reason for such large individual variability remains unclear.

When fixation is not enforced, microsaccades also show clear signs of voluntary control. For example, they can be made in response to small displacements of a target (Timberlake et al. 1972, Wyman & Steinman 1973, Havermann et al. 2014) and to look in specified directions (Haddad & Steinman 1973, Ko et al. 2010). Even under sustained fixation, microsaccades can be made less frequent simply by changing the instruction from "fixate" to "hold the eyes still" (Steinman et al. 1967); it has long been suggested that these movements may correct for fixational displacements (Cornsweet 1956). In the section titled "Visual Functions of Microsaccades," we argue that even microsaccades smaller than 20 arcmin, which yield a 66% overlap between the presaccadic and postsaccadic images, serve the same exploratory function as larger saccades.

VISUAL FUNCTIONS OF INTERSACCADIC FIXATIONAL MOVEMENTS

Considerable evidence indicates that the smooth motion of intersaccadic fixation helps stabilize the image on the retina (Skavenski et al. 1979, Epelboim & Kowler 1993). This stabilization is far from perfect, however, leaving a residual motion with approximately Brownian characteristics (Aytekin et al. 2014) that appears to be generated on purpose (Collewijn et al. 1981). The resulting retinal image motion is commonly thought to refresh neural responses to prevent the image fading experienced under retinal stabilization. But, examination of the luminance signals impinging onto retinal receptors reveals that this description is misleading: Fixational instability implements a much more interesting reformatting of the visual input.

A Space–Time Conversion

During viewing of a static scene, eye movements convert a spatial pattern into a spatiotemporal input signal to the retina. The resulting luminance modulations depend on both the characteristics of the scene and how the eye moves. Rather than just refreshing the retinal image, intersaccadic

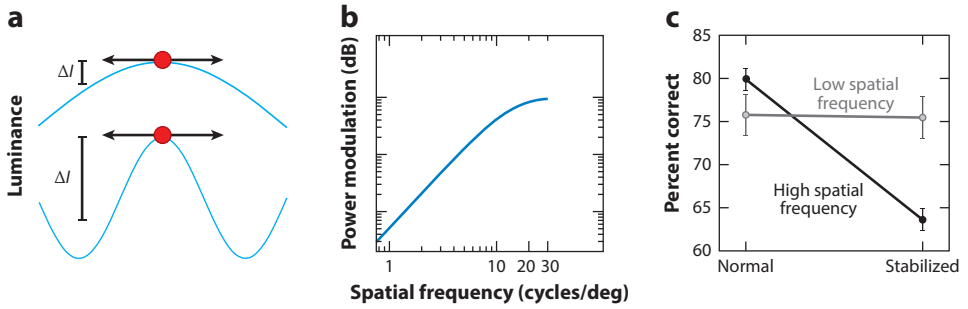

Figure 4

Enhancement of high spatial frequencies resulting from fixational drift. (*a*) Schematic showing exposure of retinal receptors (*circles*) to low (*top*) and high (*bottom*) spatial frequency gratings during fixational instability (*arrows*). Exposure to the higher-frequency grating gives a larger change in luminance (ΔI). (*b*) Mean amplification resulting from ocular drift as a function of spatial frequency. Data represent averages across 5 observers (Mostofi et al. 2015). (*c*) Results of experiments in which subjects judged the orientation of a noisy grating [±45° either at low (*gray*) or high (*black*) spatial frequency] in the presence (normal) and absence (stabilized) of fixational eye movements. In the stabilized condition, the stimulus position was updated continually according to the eye movements of the observer to eliminate retinal image motion. Removal of fixational modulations via retinal stabilization selectively impaired high spatial frequency vision (Rucci et al. 2007).

fixational eye movements restructure spatial information into a spatiotemporal format that emphasizes high spatial frequencies. As **Figure 4** shows, this amplification occurs up to a cutoff frequency close to the spatial resolution of the photoreceptor array.

An intuitive understanding of this phenomenon can be gained by considering the luminance change experienced by a retinal receptor during an infinitesimally brief interval: In this period, ocular drift can be regarded as uniform motion (a constant-speed translation), and the amplitude of the modulation is determined by the spatial gradient of the image. For sinusoidal luminance patterns, such as those shown in **Figure 4*a***, the gradient is proportional to the spatial frequency of the stimulus. Consequently, gratings at higher spatial frequencies yield larger fixational modulations. For longer periods of time, ocular drift can no longer be approximated by uniform motion, and its Brownian character must be taken into account. The main implication is that amplification occurs only at spatial frequencies for which drift covers a small fraction of the period. For sufficiently high spatial frequencies for which the eyes move over a larger fraction of the period, attenuation occurs instead.

Figure 4*b* shows the actual spatial frequency amplification resulting from ocular drift averaged over several observers. For spatial frequencies up to approximately 15 cycles/deg, the amplitude of the modulations (or, equivalently, the amount of spatial power that spreads into the temporal domain) tends to increase proportionally with the square of the spatial frequency. The effect starts to be attenuated, but an enhancement can be observed up to 30 cycles/deg.

Perceptual Consequences

The spatiotemporal conversion shown in **Figure 4*b*** makes a counterintuitive prediction. Fixational instability is usually assumed to be helpful primarily at low spatial frequencies, namely, those for which fading is most pronounced when stimuli are stabilized on the retina for long periods of time (Koenderink 1972, Kelly 1979, Tulunay-Keesey 1982). In contrast, the amplification in **Figure 4*b***

suggests that intersaccadic fixational eye movements enhance high-spatial-frequency vision, a proposal with a very long history (Averill & Weymouth 1925, Marshall & Talbot 1942, Arend 1973, Ahissar & Arieli 2012).

To test this prediction, we developed a new method of retinal stabilization that enabled selective elimination of retinal image motion during natural postsaccadic fixation (Santini et al. 2007). **Figure 4*c*** shows the results of an experiment in which subjects reported whether a noisy grating was tilted clockwise or counterclockwise by 45°. Following the predictions of **Figure 4*b***, we presented two stimuli: one in which the target (a grating) was at a higher spatial frequency than the noise and one in which it was at a lower spatial frequency. These two stimuli yield different predictions: Fixational modulations are expected to enhance visibility of the high-spatial-frequency target, but not the low-spatial-frequency one.

Figure 4*c* compares the average percentages of correct discrimination measured in the presence of the normal fixational modulations to those reported when they were stabilized on the retina by counteracting the effects of eye movements. Results confirm the predictions of **Figure 4*b***: Eliminating retinal image motion drastically impaired discrimination of the high frequency gratings but had little effect on the low frequency gratings.

Temporal Reformatting of Natural Images

Natural scenes provide highly structured visual input signals. Statistical regularities are present at multiple scales, and it has long been argued that sensory systems exploit these regularities when establishing neural representations (Barlow 1961). A well-known feature of natural images is their very specific spectral density, which declines approximately as the square of their spatial frequency (Field 1987; see **Figure 5*a***), and a considerable amount of work has focused on the consequences this spectral distribution has for early visual representations (Simoncelli & Olshausen 2001, Hyvärinen et al. 2009). How does the space–time conversion shown in **Figure 4*b*** interact with the characteristics of natural images?

To address this question, **Figure 5*a*** analyzes the consequences of eye movements during fixation on a natural image. The specific power spectrum of natural images implies that the contrast of each frequency component decreases as its spatial frequency increases; that is, high-spatial-frequency gratings are fainter than low-spatial-frequency gratings. Note that when compared with the oculomotor amplification shown in **Figure 4**, this contrast attenuation has the opposite relation to spatial frequency: The motion of the eye enhances high spatial frequencies, whereas natural images possess the most power at low spatial frequencies.

Remarkably, the two effects counterbalance each other. **Figure 5*a*** compares the power spectra of a set of images to the average temporal power made available in the form of modulations by normal intersaccadic fixational instability. The net effect of the interaction between ocular drift and the spectral distribution of natural images is to yield modulations with approximately equal amplitudes over a wide range of spatial frequencies (Kuang et al. 2012). Very similar results have also been obtained during head-free viewing, a condition in which eye and head movements combine to form a retinal stimulus that has almost identical characteristics to those observed when the head is immobilized (Aytekin et al. 2014).

These data show that ocular drift causes very specific input reformatting during natural fixation. Fixational fluctuations of luminance at different spatial frequencies possess similar power. This equalization—a transformation known as spectral whitening—requires images with the spectral density of natural scenes and normal oculomotor activity. It reveals a form of matching between the characteristics of the natural world and those of normal eye movements.

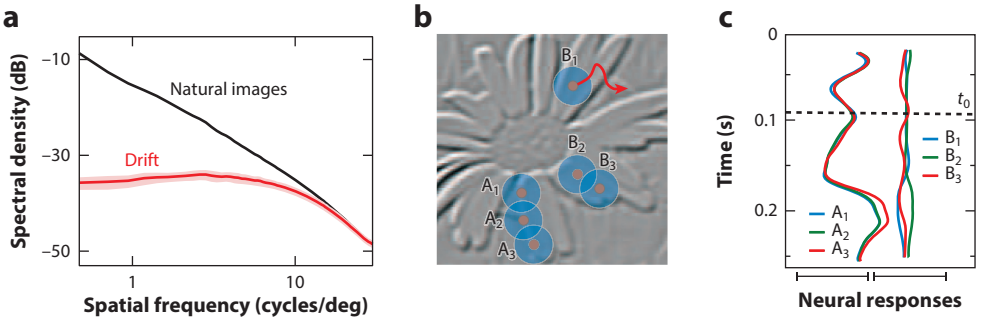

Figure 5

Interaction with natural images and possible neural consequences of ocular drift. (*a*) Comparison between the power of a set of natural images and the temporal power (the sum over all nonzero temporal frequencies) in the modulations caused by ocular drift. Normal drift equalizes power over a broad range of spatial frequencies (Kuang et al. 2012). (*b*) Activity in a simulated array of retinal ganglion cells. Each pixel represents the mean instantaneous firing rate at time t_0 of a simulated neuron. The receptive fields (*circles*) of six neurons are shown: The receptive fields of the units labeled A_1–A_3 are centered on an edge, whereas those of units B_1–B_3 cover more uniform regions. (*c*) Time courses of the responses of the six neurons shown in panel *b*. Note the enhancement of edges conveyed by synchronous modulations.

Neural Consequences

Spatial and temporal reformatting of visual input as described in the previous sections has deep implications for the mechanisms of neural encoding. In the temporal domain, this transformation creates power at temporal frequencies within the range of frequencies to which retinal neurons are most sensitive (Kaplan & Benardete 2001). Thus, fixational luminance fluctuations are likely to strongly influence neural responses (Snodderly et al. 2001). In the spatial domain, the frequency enhancement shown in **Figure 4*b*** implies that neurons respond both less to low spatial frequencies and more to high spatial frequencies than their contrast sensitivity functions measured with immobile retinas suggest.

Further important consequences follow from the interaction between eye movements and natural images shown in **Figure 5*a***. As an equalization of power in frequency is equivalent to the removal of correlations in space, the spectral distribution in **Figure 5*a*** implies that pairs of retinal receptors experience uncorrelated luminance fluctuations during fixation on a natural image (Rucci & Casile 2004, Desbordes & Rucci 2007). A similar decorrelation has long been argued to be an important function of retinal processing because it removes predictable regularities from the input signals and enables the visual system to focus resources on more informative input components (Attneave 1954, Barlow 1961). The center–surround organization of the receptive fields of ganglion cells has been implicated in this process (Srinivasan et al. 1982, van Hateren 1992, Atick & Redlich 1992), but these proposals did not consider the impact of eye movements. Thus, the incessant presence of ocular drift implies a reexamination of well-known theories of retinal encoding.

As decorrelation is already accomplished by eye movements, the amplification of high spatial frequencies operated by the contrast sensitivity of ganglion cells must serve a different function than counterbalancing the spectral distribution of natural scenes. An interesting possibility is that this neural filtering combines with fixational instability to start the process of feature extraction, which is commonly believed to take place at higher stages in the visual system. **Figure 5*b,c*** shows an example of activity in an array of modeled retinal ganglion cells. The interaction among eye movements, natural images, and the spatiotemporal sensitivity of ganglion cells yields synchronous responses, which emphasize luminance discontinuities. This edge enhancement

occurs even if modeled neurons such as those in **Figure 5*c*** are circularly symmetric and do not possess a preference for oriented stimuli. Thus, ocular drift may allow for a neural code that uses synchrony for encoding edges (Greschner et al. 2002, Poletti & Rucci 2008) and that can take advantage of the robustness of temporally synchronous responses in propagating through neural networks (Dan et al. 1998, Bruno & Sakmann 2006).

VISUAL FUNCTIONS OF MICROSACCADES

The possible visual functions of microsaccades have been intensely debated. Much confusion seems to have originated from the use of unnatural viewing conditions (Steinman 2003) as well as from the chronic difficulty in spatially localizing the line of sight. Although eye trackers can resolve very small changes in eye position, absolute determination of the line of sight in the scene is usually only approximate (Holmqvist et al. 2011).

A widespread proposal—originally derived from false assumptions about the characteristics of ocular drift (Ditchburn & Ginsborg 1953)—is that microsaccade may serve a special function in preventing perceptual fading (Ditchburn et al. 1959, Martinez-Conde et al. 2006). However, multiple observations argue against this idea (Collewijn & Kowler 2008, Poletti & Rucci 2010, Kagan 2012), including the recent report that no fading occurs under total paralysis (Whitham et al. 2011). Under sustained fixation, another prominent idea has been that microsaccades help centering gaze, a notion supported by a considerable body of evidence (Cornsweet 1956, Engbert & Kliegl 2004, Cherici et al. 2012). Here we focus on the function of microsaccades under more natural conditions, when fixation is not explicitly enforced and observers are free to move their eyes normally.

Exploration of Fine Spatial Details

Cunitz & Steinman (1969) were the first to propose that by precisely redirecting a tiny preferred locus of fixation, microsaccades could be helpful in the examination of fine spatial detail. This idea was later abandoned following the observation that microsaccades appear to be suppressed in high-acuity tasks (Winterson & Collewijn 1976, Bridgeman & Palca 1980). Specifically, it was noted that microsaccade rates tend to progressively decrease during the execution of finely guided visuomotor tasks, such as threading a sewing needle or aiming a rifle, even when the task is successfully accomplished. Microsaccades also tend to be less frequent in these tasks than during sustained fixation on a small cue.

These findings were taken to imply that microsaccades are detrimental for high visual acuity. However, several considerations caution that this conclusion might have been premature. First, a reduction in the rate of microsaccades toward the end of an experimental trial does not imply that microsaccades did not provide helpful information at earlier times. Second, as pointed out in the subsection titled "Microsaccades," sustained fixation is an unnatural condition that elicits a particularly high number of microsaccades and therefore may not constitute an optimal reference baseline. Moreover, analysis of the rate of microsaccades alone might not be the best way to determine whether microsaccades serve a useful function. The specific patterns of gaze shifts resulting from microsaccades are more informative, but examination of how exactly microsaccades position the stimulus on the retina requires absolute localization of the line of sight to a level beyond the accuracy of most eye trackers.

To circumvent this problem, we have recently developed a gaze-contingent calibration procedure coupled with a high-resolution dual-Purkinje-image (DPI) eye tracker; this combination effectively improves gaze localization by almost one order of magnitude compared with standard methods (Poletti et al. 2013; see their supplemental information). This approach has enabled

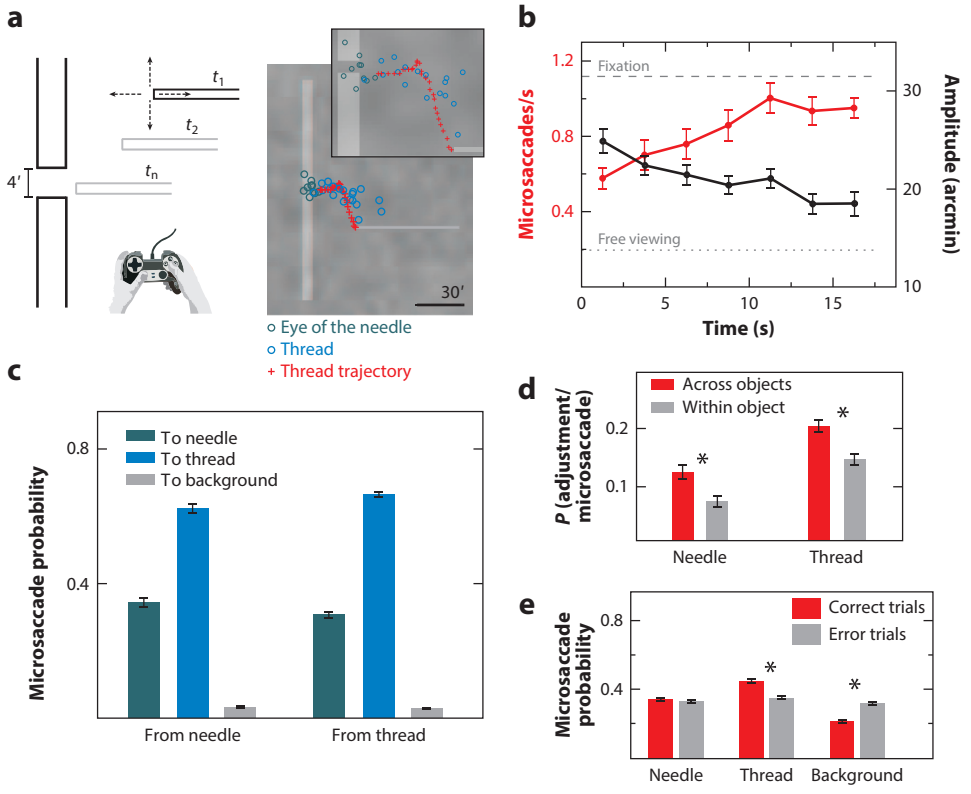

Figure 6

Microsaccades in a high-acuity task. (*a*) Threading a needle in a virtual environment. Subjects moved a horizontal bar (the thread) toward the small gap in a vertical bar (the needle). The right panel and inset show the spatial distribution of fixations in a trial. Fixations were primarily allocated to the thread (*blue circles*) and the eye of the needle (*green circles*). The red crosses mark the thread trajectory. (*b*) Mean instantaneous frequencies (*red*) and amplitudes (*black*) of microsaccades. The two horizontal lines represent mean values of microsaccade rates during sustained fixation (*dashed line*) and free viewing (*dotted line*). (*c*) Probabilities of various types of microsaccades, classified according to their starting and landing points. Microsaccades almost always brought the line of sight onto the thread and needle; they rarely landed on the background. (*d*) Conditional probabilities of realigning the thread following different types of microsaccades. Adjustments were more likely to occur immediately after microsaccades across different objects. (*e*) Microsaccade landing probabilities for successful and unsuccessful trials. Microsaccades were more precise in the trials in which the thread was correctly aligned with the needle. Asterisks indicate a significant difference between conditions. All data refer to saccades shorter than 20 minutes. Figure adapted with permission from Ko et al. (2010).

us to reexamine how microsaccades move the center of gaze during execution of a high-acuity visuomotor task similar to that used in the previous studies, namely, the threading of a needle. To better control experimental variables, we created a virtual environment (**Figure 6*a***): Rather than threading a real needle, subjects controlled the motion of a thin horizontal bar (the thread) by means of a joystick and were asked to insert the thread into a small aperture at the center of a stationary vertical bar (the needle). Similar to the threading of a real needle, the stimulus covered a very small visual angle (<1 deg^2), allowing it to fit entirely within the foveola.

Our experiments confirmed previous findings (Winterson & Collewijn 1976, Bridgeman & Palca 1980). On average, the microsaccade rate measured in our experiment was lower than that

measured during sustained fixation (**Figure 3*c***), and it decreased toward the end of the trial, when the specific conditions of previous experiments were also replicated. However, microsaccades were frequent at earlier times in the trial, when subjects adjusted the alignment between the thread and the needle. Overall, the average rate of microsaccades was five times higher than that measured during free viewing of natural images (**Figure 3*c***).

To examine the functions of these microsaccades, we (*a*) terminated each trial when the thread was close to the needle but still had not reached it and (*b*) restricted control of the thread to the vertical axis, moving it at constant speed toward the needle on the horizontal axis. This approach ensured that adjustments in the position of the thread reflected a perceived misalignment and excluded possible changes in attention toward the end of the trial.

Figure 6 summarizes the main results of our experiment. Microsaccades clearly were influenced by the characteristics of the stimulus and the ongoing demands of the task: They became progressively smaller and more frequent as the thread approached the needle (**Figure 6*b***). Furthermore, careful localization of the line of sight revealed that microsaccades shifted gaze in a very precise manner. Fixations were clustered at salient locations of the scene. Most fixations were either on the thread or around the eye of the needle, and very few fell far from one of these two regions. That is, microsaccades precisely shifted the gaze between the thread and the eye of the needle, and they rarely landed on other, task-irrelevant regions of the scene (**Figure 6*c***).

These results suggest that observers used microsaccades to acquire useful information from the scene. To confirm this hypothesis, we examined whether a link existed between microsaccades and adjustments in the position of the thread. We estimated the probabilities of (*a*) correcting the alignment between the thread and the needle immediately after a microsaccade and (*b*) performing a microsaccade immediately after changing the position of the thread. We found that subjects were more likely to realign the thread after executing a microsaccade that shifted the center of gaze from one object (the thread or the needle) to the other than when they maintained gaze on the same object or region (see **Figure 6*d***). In contrast, microsaccades were likely to move the line of sight toward the thread after the subject adjusted its position. Furthermore, microsaccades were less precise in the trials in which subjects failed to thread the needle (**Figure 6*e***). These data corroborate the idea that subjects performed microsaccades to judge the alignment between the thread and the needle.

Implications for Foveal Vision

The oculomotor strategy followed by our subjects in **Figure 6** may appear paradoxical. In principle, given the small size of the stimulus, a fixation at the center of the display would have enabled the entire stimulus to fall within the high-acuity foveola without any need for eye movements. The observers did not take this approach, however; instead, they preferred to execute precisely directed microsaccades. What was the benefit of this strategy?

Anatomical examinations of the retina have revealed the presence of considerable nonhomogeneity within the foveola. Although substantial individual variability exists, cone density has been observed to fall with increasing eccentricity not only outside the central fovea, but also within the foveola itself. The region of maximum cone concentration is on average restricted to an area smaller than 0.032 deg^2 (Curcio et al. 1990). Thus, microsaccades may contribute to fine spatial vision by properly centering this region or a similar preferred fixation locus—not necessarily coincident with the region of highest cone density (Putnam et al. 2005)—that facilitates fine spatial judgments.

Previous studies that attempted to systematically map visual acuity within the central fovea have given conflicting results. Some reported a decline in performance with eccentricity, whereas

others found minimal changes (Weymouth et al. 1928, Adler & Meyer 1935, Millodot 1966). However, it is critical to realize that testing visual acuity at very small eccentricities is extremely challenging. This operation requires both (*a*) very high accuracy in localizing the line of sight (such accuracy is necessary to determine the eccentricity of retinal stimulation reliably) and (*b*) real-time compensation for fixational eye movements during stimulus exposure (without compensation, these eye movements would move the stimulus on the retina). Together the uncertainty in gaze localization and the fixational motion of the retinal image effectively prevent isolation of closely spaced regions on the retina and are likely to homogenize measurements at adjacent locations. These factors may have contributed to previous reports of approximately uniform acuity across the foveola.

The gray line in **Figure 7*b*** shows the consequence of not properly controlling for the presence of fixational eye movements. In this experiment, subjects were confronted with a forced-choice paradigm designed to confine stimulation at fixed eccentricities. They reported whether two noisy gratings displayed within narrow rectangular bars were parallel or orthogonal (**Figure 7*a***). The two bars were located symmetrically around the point of fixation at one of three very small distances (5, 10, or 15 arcmin). Gratings were presented sequentially: first in the left bar, then in the right one. The data summarized by the gray line were collected following the same procedure used in most previous experiments. Subjects were simply asked to maintain strict fixation at the center of the display while their performance was measured using stimuli presented at different eccentricities. Under these conditions, performance varied little as the distance of the two bars increased from 5 to 15 arcmin, a result which could be interpreted mistakenly as supporting the notion of uniform vision within the foveola.

In reality, however, eye movements occurred continually during the course of the trial as observers attempted to maintain fixation. Similar to the study depicted in **Figure 6**, careful examination of oculomotor activity reveals that microsaccades were frequent and not random. As **Figure 7*c*** shows, microsaccades closely followed the sequence of experimental events: They first shifted the center of gaze to the left of the fixation point when the grating appeared in the left bar, and they then relocated the line of sight to the right of the fixation point when the grating was displayed in the right bar. Therefore, because of microsaccades, stimuli systematically moved toward the preferred fixation locus instead of remaining at a fixed eccentricity on the retina (see the examples in **Figure 7*d***).

The black line in **Figure 7*b*** shows results obtained in the same experiment when proper precautions were taken to control for the effects of eye movements. The eccentricity axis in **Figure 7*b*** represents the distance of the stimulus from the center of the preferred locus on the retina rather than the distance of the bar from the fixation cue on the display. The position of this locus (or equivalently, the line of sight) was measured during a preliminary, gaze-contingent calibration procedure similar to that used in the experiments depicted in **Figure 6**. Furthermore, stimuli were maintained at fixed retinal eccentricities throughout the course of the trial by continually updating their positions on the display according to the eye movements of the subjects. Perceptual fading was not an issue in this experiment, as gratings were flashed for brief periods of time.

Note the difference in results between the two conditions. Performance decreased sharply with eccentricity after eliminating the consequences of eye movements, an effect which was visible even at eccentricities of just 10 arcmin. This impairment was not the consequence of retinal stabilization; a similar drop in performance was also observed during normal viewing (no retinal stabilization) in the rare trials in which microsaccades did not occur or were not precise and thus failed to bring the projection of the stimulus onto the preferred retinal locus (**Figure 7*b***). These results support the existence of a narrow retinal locus, smaller than the foveola, that observers use in tasks involving high visual acuity.

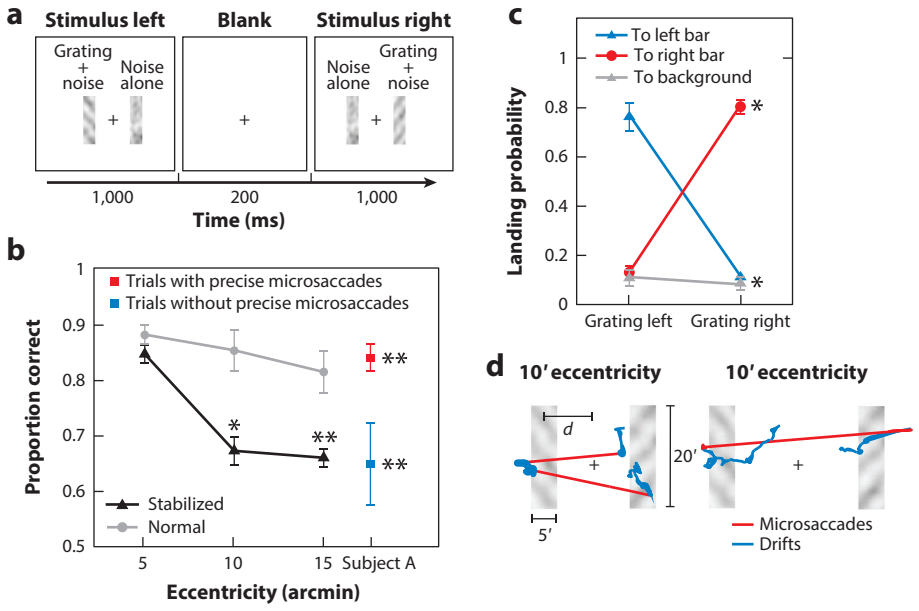

Figure 7

Consequences of microsaccades for foveal vision. (*a*) Subjects reported whether the orientations of two sequentially presented noisy gratings were parallel or orthogonal. Gratings with spatial frequencies of 11 cycles/deg were tilted by ±45° and appeared within two rectangular bars centered at the desired eccentricity, *d*. In the first interval (*left*), the grating always appeared in the left bar, and the right bar contained a noise pattern. In the second interval, the grating appeared in the right bar, and the left bar contained a noise pattern. (*b*) Stimuli were displayed either at fixed positions on the screen and moved with normal motion on the retina arising from fixational eye movements (Normal; *gray circles*) or at fixed locations on the retina and moved on the display under computer control to compensate for the eye movements of the subject (Stabilized; *black triangles*). Performance decreased sharply with eccentricity in the Stabilized condition. Discrimination was also impaired on trials in which microsaccades did occur but were less precise (a *single asterisk* indicates significance at $p < 0.05$, and a *double asterisk* indicates significance at $p < 0.005$ in a two-tailed paired *t*-test). (*c*) Proportions of microsaccades landing on different regions of the display for stimuli at an eccentricity of 15 arcmin. Most microsaccades moved the line of sight on the bar containing the stimulus (*asterisks* indicate significance at $p < 0.01$ in a two-tailed paired *t*-test). (*d*) Eye movements in two example trials. Red and blue segments represent microsaccades and drifts, respectively. Subjects were asked to maintain fixation at the center of the display (*cross* in panel *a*). Figure adapted with permission from Poletti et al. (2013).

A Finely Controlled Oculomotor Strategy

In sum, accurate gaze localization during high-acuity visual and visuomotor tasks has revealed a surprisingly fine level of control in microsaccades and a clear dependence on the ongoing task. Microsaccades precisely move the eye to center the retinal projection of the stimulus onto a preferred fixation locus, a behavioral strategy that gives the false impression of a broader high-acuity region if oculomotor activity is not monitored at high resolution.

Together with recent findings highlighting the similarity between saccades and microsaccades in terms of production mechanisms and extraretinal influences (Hafed et al. 2009, Hafed 2013, Havermann et al. 2014, Snodderly 2015), the results presented in **Figures 6** and **7** provide strong support to Cunitz & Steinman's (1969) proposal that microsaccades are exploratory movements similar to larger saccades. They indicate that outside of the laboratory, when fixation

is not enforced, a subdivision between saccades and microsaccades is not warranted. All saccades, independent of their amplitudes, enable inspection of regions of interest by properly positioning the stimulus on the retina.

More broadly, the results described in this section and in the section titled "Visual Functions of Intersaccadic Fixational Movements" suggest that fixational eye movements are essential components of the strategy by which the visual system achieves high acuity. Both precise positioning of the center of gaze and reformatting of fine-scale spatial information into the temporal structure of the responses of neuronal ensembles appear to be critical. New questions now emerge: What are the perceptual consequences of the spatiotemporal transformation that results from fixational eye movements during natural postsaccadic fixation? How is spatial information decoded from the time-varying input to the retina? Is the reformatting of this input flexible, allowing it to be tuned to the task? Future research will need to address these questions, among others.

SUMMARY POINTS

1. Small eye movements, including incessant jitter (ocular drift and tremor) and occasional small saccades (microsaccades), are always present during natural visual fixation.
2. Fixational eye movements do not merely prevent the image from fading; they reformat the stimulus on the retina into a spatiotemporal signal suited for neural processing.
3. The luminance modulations that result from intersaccadic fixational eye movements enhance high spatial frequencies in the retinal input and in contrast sensitivity.
4. Luminance modulations are matched to the characteristics of the natural world. They eliminate broad correlations in natural images prior to neural processing and initiate the process of edge extraction.
5. Vision is not uniform across the fovea. Fine spatial vision is optimal within a small foveal subregion.
6. During natural execution of high-acuity tasks, microsaccades precisely move a high-acuity retinal locus within the foveola, serving similar functions to larger saccades.

FUTURE ISSUES

1. Recent studies have revealed precise control of fixational eye movements. What neural structures and mechanisms are responsible for this fine degree of control?
2. How does the visual system decode the spatial information contained in the modulations resulting from fixational eye movements? How is this information integrated within spatial representations?
3. Neural copies of the motor commands for larger eye movements are normally used in interpreting the visual input. Do similar extraretinal signals also accompany fixational eye movements?
4. What are the visual consequences of abnormal fixational eye movements? Might some impairments in visual acuity have unrecognized oculomotor contributions?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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