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Editorial

Fixational eye movements and perception

Visual perception is a fundamentally active process. In humans and other foveated species, many functions, including acuity, are not uniform across the visual field, but deteriorate with increasing distance from the foveola, the tiny rod-free region of the retina where cones are most densely packed. This strategy offers clear evolutionary advantages, since it enables monitoring of a large extent of visual space while keeping computational resources limited. However, it also implies the establishment of a very tight coupling between perception and action: eye movements are required to sequentially inspect regions of interest with the high-acuity foveola. Once an object is imaged on the foveola another class of ocular movements, termed fixational eye movements, are used to assist in analyzing the visual image in important and interesting ways.

The goal of this Special Issue is to highlight the significance and value of fixational eye movements to visual analysis. In this editorial, we start by briefly introducing the topic of fixational eye movements, and then provide an overview of the articles that make up this issue.

1. A brief introduction to fixational eye movements

During viewing of a stationary scene, rapid gaze shifts, known as saccades, occur every few hundreds of milliseconds. Saccades separate fixations, the periods of apparent eye immobility in which visual information is acquired and processed. Close inspection of oculomotor activity in these periods reveals, however, that the very word “fixation” is misleading: small eye movements incessantly occur in the inter-saccadic intervals, suggesting an even deeper coupling between visual functions and oculomotor activity. These gaze shifts come in different varieties and are collectively known as fixational eye movements. Although humans are normally not aware of making them, they displace the retinal image at speeds that would be clearly visible had the motion originated from the visual scene rather than the observer.

Fixational eye movements are at the same time small and large. They are small—to the point that they are often labeled as microscopic—relative to the resolution of standard eye-tracking methods, making their experimental study challenging. They are, in contrast, large relative to the size of cell receptive fields on the retina, where they shift the image by considerable distances across the photoreceptor array. For historical reasons, fixational eye movements are traditionally subdivided into three categories: microsaccades, ocular drift, and tremor (Kowler, 2011). However, it is important to keep in mind that the boundaries between the different types are not as clearly defined as one may intuitively assume: categorization is particularly

challenging for the movements with the smallest amplitudes (Rucci & Poletti, 2015).

Microsaccades are miniature replicas of the saccadic gaze shifts normally used to look at different objects in the scene. Unlike their larger counterparts, these movements maintain the stimulus within the foveola, raising the question of why observers make them. Note that the same term is also often used to indicate any saccades, independent of their amplitude, that occur when attempting to maintain steady gaze on a target – a common situation in vision research experiments. This ambiguity in the use of the term has generated considerable discussion in the literature (e.g., Collewijn & Kowler, 2008) and some authors refer to the saccades present during enforced fixation as “fixational saccades” to distinguish them from the microsaccades occurring under more natural conditions (Snodderly, 2016; see Poletti & Rucci in this issue for an in-depth discussion). Among all types of fixational eye movements, microsaccades are the ones that can be measured most readily and reliably. It is, therefore, not surprising that they have been the preferred focus of most studies in the field (Rolf, 2009).

In the intervals between saccades, microsaccades, and other types of eye movements, the eyes move incessantly following seemingly erratic trajectories. The terms ocular drift and tremor refer to two components of this smooth but jittery motion. Ocular drift is commonly used to indicate the slower, meandering component with frequency below 40 Hz (Cornsweet, 1956), but the term is also sometimes used to refer to the inter-saccadic motion of the eye as a whole, without attempting further subdivisions. Ocular drift resembles the Brownian motion of a particle in a fluid (Engbert & Kliegl, 2004; Kuang, Poletti, Victor, & Rucci, 2012). Since it changes direction frequently, its average cruise speed over the inter-saccadic interval – the speed value frequently reported in the literature (Ditchburn, 1973) – is very low. But the eyes actually drift quite rapidly, with a mean instantaneous speed that can reach 1 deg/s when the head is immobilized (Cherici, Kuang, Poletti, & Rucci, 2012), and even larger values during normal head-free fixation (Aytekin, Victor, & Rucci, 2014; Poletti, Aytekin, & Rucci, 2016; Skavenski, Hansen, Steinman, & Winterson, 1979).

Tremor is the higher-frequency (>40 Hz) component of inter-saccadic eye motion (Adler & Fliegelman, 1934; Steinman, Haddad, Skavenski, & Wyman, 1973). It has minute amplitude, just slightly larger than the width of a photoreceptor in the foveola, which is at the very limit of the resolution of the most sophisticated eye-trackers, making experimental analysis difficult. Little is therefore known about the characteristics and possible visual functions of tremor. It should be observed, however, that the distinction between ocular drift and tremor is somewhat artificial.

In the spectral domain, the tremor component in the 40–100 Hz bandwidth appears to fully overlap a broader-band process with scale-invariant power spectrum (Eizenman, Hallett, & Frecker, 1985).

Since many observations indirectly provide evidence that the eyes are always in motion, the existence of fixational eye movements was known long before the availability of eye-trackers. For example, it was noted by Robert Darwin (Charles's father) in 1786 that the jiggling of color after-effects was presumably the consequence of small eye movements (Darwin, 1786). The first recordings of fixational eye movements go back to the middle of last century, when eye-tracking methods with sufficient resolution were finally developed (Barlow, 1952; Ditchburn, 1973; Ratliff & Riggs, 1950). This is also the time when it first became possible to immobilize a stimulus on the retina, a procedure known as retinal stabilization. These experiments led to the surprising finding that visual percepts tend to fade and may even disappear completely in the absence of retinal image motion (Ditchburn, 1973; Yarbus, 1967). Given that visual functions seem normal during steady fixation, when eye movements are the only source of retinal image motion, it appears that fixational eye movements are sufficient for enabling vision of a stationary stimulus. How they do so remains an open question, but a plethora of mounting evidence suggests that these movements play important perceptual roles and that their study will reveal fundamental properties of the visual system.

After a period of quiescence at the end of last millennium, the study of fixational eye movements has now gained wide popularity among vision scientists. Important steps forward have been made in recent years toward elucidating the functions of both microsaccades and drift. For example, it is now known that microsaccades modulate neural responses in various cortical areas (e.g., Herrington et al., 2009; Kagan, Gur, & Snodderly, 2008; Martinez-Conde, Macknik, & Hubel, 2000), and the neural mechanisms responsible for their production are starting to emerge (Hafed, Goffart, & Krauzlis, 2009). The link between microsaccades and attention is also becoming increasingly clear (Engbert & Kliegl, 2003; Hafed & Clark, 2002), and new techniques for finely estimating the line of sight have shown that microsaccades precisely shift gaze during execution of high-acuity tasks (Ko, Poletti, & Rucci, 2010), an adaptive strategy (Havermann, Chericci, Rucci, & Lappe, 2014) which appears to take advantage of the retinal locus with highest acuity (Poletti, Listorti, & Rucci, 2013). Furthermore, a substantial body of emerging evidence has highlighted the similarity between microsaccades and larger saccades in terms of both control and function (e.g., Goffart, Hafed, & Krauzlis, 2012; Hafed, 2013).

Although less intensely investigated, ocular drift too has been the subject of an increasing number of studies. Various aspects of the characteristics of this motion have been clarified (reviewed in Rucci & Poletti, 2015), and drift is now frequently incorporated in general models of eye movements and in the input to models of visual functions (e.g., Burak, Rokni, Meister, & Sompolinsky, 2010; Engbert, Mergenthaler, Sinn, & Pikovskiy, 2011). Furthermore, many recent findings (see Rucci & Victor, 2015; for a review) have provided support to the long-standing proposal that this motion is part of a strategy for encoding space in time (Ahissar & Arieli, 2001; Marshall & Talbot, 1942).

2. Overview of the articles in this Special Issue

Given the recent body of results and the growing wave of interest in the subject, this Special Issue represents a very timely contribution to the field. It provides a panoramic snapshot of ongoing work from laboratories across the world on the many interesting questions that remain unanswered.

The relationship between fixational eye movements and visual perception still contains many unresolved issues. In principle, microsaccades may enhance vision in at least two separate ways: in space, by precisely positioning the preferred retinal locus on the stimulus (Poletti et al., 2013); and in time, by generating useful temporal transients in the retinal input (Ditchburn, 1973). Psychophysical experiments with parametrically-controlled uniform stimuli, such as gratings, may help disentangle the role of spatial and temporal mechanisms. For example, Spotorno, Masson, and Montagnini (2016) examined whether the characteristics of fixational saccades vary with the frequency of a grating. Spatial and temporal mechanisms lead to different predictions under these conditions; whereas the characteristics of microsaccade transients vary with stimulus frequency, microsaccade re-centering should always be toward the region of maximum contrast—the center of the display where subjects are asked to fixate. Spotorno et al. found that, although fixational saccades were affected by general factors such as the type of perceptual task, they bore no obvious relationship to the spatial frequency of the stimulus or to task performance, suggesting that microsaccade transients do not have a strong perceptual impact. Mostofi, Boi, and Rucci (2016) further investigated this question, by analyzing the possible influence of microsaccades on contrast sensitivity. They report strong suppression of microsaccades and similar contrast thresholds measured in their presence and absence; both of these effects indicate a marginal influence of microsaccade transients in determining visual sensitivity. Thus, these experimental results suggest that temporal modulations resulting from microsaccades do not play a major role in vision.

On the other hand, fixational eye movements have large effects on the representation of stimuli in the visual cortex. The article by Snodderly (2016) provides an insightful survey of how fixational eye movements alter the spiking activity of neurons in primary visual cortex. The effects are multifaceted: changes in neuronal activity caused by ocular drift may enhance the encoding of fine spatial detail, but the synchronized bursts caused by small saccades could contribute to the saccadic suppression that transiently interrupts visual processing. These observations highlight the importance of collecting neuronal data simultaneously during the performance of perceptual tasks, in order to document how fixational eye movements affect the encoding steps underlying visual perception.

Computational models are another fruitful approach for exploring both the complications caused by fixational eye movements and their possible benefits to vision. Greene, Gollisch, and Wachtler (2016) put forward a model of visual processing that suppresses the motion signals caused by fixational eye movements, using a nonlinear mechanism in the retina that does not require information about the eye movements but that can nonetheless distinguish between self-induced visual motion caused by fixational eye movements versus real-world motion caused by physical movement in the environment. Ahissar, Arieli, Fried, and Bonnef (2016) explore the possible functional roles of microsaccades and ocular drift, drawing a contrast between the analysis of visual features and the targeting of new items, and consider potential control strategies for regulating fixational eye movements.

Another open question is how fixational eye movements are generated? The final motor pathways for fixational eye movements are shared with all other eye movements, but the upstream mechanisms are not fully understood. Sinn and Engbert (2016) present experimental and modeling results that draw a distinction between microsaccades and small voluntary saccades. Using data recorded with a video-based eye-tracker, they argue that microsaccades are correlated with preceding ocular drift whereas small voluntary saccades are not. Thus although microsaccades and

small goal-directed saccades may be part of an “oculomotor continuum” because they share the same output motor pathways, they may also be driven by signals that originate from different sources.

Other articles provide new insight into how fixational eye movements are controlled by the population activity in visual-motor maps, such as the one contained in the superior colliculus (Hafed et al., 2009). Wang, Yuval-Greenberg, and Heeger (2016) investigated the spatial organization of the mechanisms that give rise to microsaccades by probing fixation with visual stimuli at different eccentricities and contrasts. They find that visual probes alter the probability and direction of microsaccades, but the effects strongly depend on eccentricity, allowing them to model the suppressive interactions that may take place in the visual-motor maps that control microsaccades. Godlove and Schall (2016) used a “countermanding” task, in which a planned voluntary saccade is suddenly canceled, to investigate the possible interactions between signals that generate microsaccades and those that control fixation. Their results suggest that the process for canceling movements is separate from the process for preparing saccades, including microsaccades. These results provide important constraints for understanding how visual-motor maps in the superior colliculus and elsewhere contribute to the generation of fixational saccades.

This Special Issue also touches on an emerging area of research: the study of fixational eye movements in different populations of subjects. Port, Trimberger, Hitzeman, Redick, and Beckerman (2016) documented fixational saccades in a large cohort of subjects during a visual search task, and found that the frequency of both microsaccades and larger saccades increases slightly with age. These types of studies could provide valuable normative data sets when considering fixational eye movements as possible biomarkers for disease or other altered states. Hafed, Stingl, Bartz-Schmidt, Gekeler, and Zrenner (2016) measured the oculomotor behavior of blind patients who have received sub-retinal electronic implants to partially restore their vision. Remarkably, once patients were able to look at visual stimuli, they exhibited the normal components of fixational eye movements including microsaccades and ocular drift. These studies open up exciting new possibilities for understanding the functional role of fixational eye movements and how they might be exploited to improve vision, both over time during normal development and aging, as well as in subjects with impaired visual function.

Finally, there is the long-standing challenge of properly measuring very small eye movements. Poletti and Rucci (2016) provide an introductory guide to the study of microsaccades, reviewing the challenges inherent to the study of small eye movements and describing methods for assessing and improving the quality of the recordings. They also examine the sometimes hidden consequences of common experimental errors and discuss evidence relating to the main proposed functions of microsaccades. Choe, Blake, and Lee (2016) address a major problem with using video eye trackers – changes in pupil size introduces significant artifacts into measurements of fixational eye movements. Helpfully, they also describe how a regression method can be used to minimize the errors introduced by this artifact. Nyström, Hansen, Andersson, and Hooge (2016) point out that, because the eye is not rigid, there can be relative motion between its parts, and these deformations are especially relevant during high-speed movements like saccades. They describe how the differential motion of the pupil leads to a systematic overestimate of the amplitudes of microsaccades, another issue that should be taken into account when using video eye trackers. One way to avoid many of these problems is to measure retinal displacement directly. Stevenson, Sheehy, and Roorda (2016) describe an innovative method using a scanner laser ophthalmoscope to track the retina in both eyes simultaneously. The impressively low noise levels achieved with

this method (less than 1/2 arc minute) could make it possible to not only study microsaccades free of pupil-based distortions, but also further investigate ocular drift, which are at least as important to vision but have received much less attention to date.

3. Conclusions

The articles published in this Special Issue, together with a recent surge of new data, add important new knowledge to this growing field. These findings also set the foundations for future investigations. Many questions remain unanswered and new ones emerge. Pressing questions include: How is spatial information extracted and represented in the presence of continually moving eyes? What are the neural mechanisms underlying the generation of different types of fixational eye movements? What are the consequences of abnormal fixational eye movements?

New technical challenges also lie ahead, including the need to reliably record very small eye movements during normal head-free viewing. With so much to learn and so much work to be done, there is no doubt that exciting years lie ahead for this field and the vision science community.

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