Active Vision: Microsaccades Direct the Eye to Where It Matters Most

Even in the most sensitive part of human retina, the fovea, perception is not uniform. To compensate for such non-uniformity, tiny fixational microsaccades direct the optimal foveal locus to relevant parts of the fixated scene, similarly to larger exploratory saccades but on a miniature scale.

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It is well established that the main function of saccadic eye movements in primates is to direct the part of the retina with the highest spatial resolution, the fovea, to an area of interest in a visual scene. But even between saccades, during attempted fixation periods, small abrupt eye motions — fixational saccades, or microsaccades — as well as slower fixational drifts continue shifting the eyes. Recent studies [1–3] have emphasized the important role of drift in shaping the spatiotemporal characteristics of visual inputs, but the function of small microsaccades has remained controversial despite intense research [4–6]. Indeed, if the fovea has already landed on the feature of interest following a saccade, then why is there a need to make additional eye movements? A new study by Poletti, Listorti and Rucci [7], reported in this issue of *Current Biology*, provides compelling experimental evidence for a similar role of microsaccades in visual exploration as large saccades, albeit on a decidedly miniature scale — *within* the fovea.

The idea that microsaccades are part of a saccade continuum and not a distinct phenomenon dates back to work of Steinman and colleagues in 1960s (reviewed in [5]). In the last decade, this view has received strong support from experimental results showing that microsaccades and saccades share a common generation mechanism in the superior colliculus [8,9], elicit similar visual and extraretinal neuronal responses [10], cause similar perceptual effects [11], and exhibit similar interactions with the cueing of attention [12,13]. Further evidence for a similarity between microsaccade and saccade function was provided by an earlier study of

Rucci and colleagues [14], which showed that, during a demanding high-acuity (i.e. requiring perception of fine spatial detail) 'needle-threading' task, microsaccades shifted the fixation locus between the two most relevant parts of the visual scene, the thread and the needle, with very high precision. It remained unclear however, why subjects made those microsaccades in the first place, especially given that *both* the needle and the thread were well within the fovea. In other words, wasn't the foveal location of the stimuli sufficient to allow accurate evaluation of their relative position without additional oculomotor adjustments [15]?

In the new study, Poletti *et al.* [7] solve this matter with two principal findings. First, they show that, contrary to widespread assumptions, foveal vision is not uniform — instead, maximal perceptual sensitivity is limited to a tiny retinal region coinciding with a preferred fixation locus (Figure 1A). The authors were able to confine a small visual stimulus to a specific part of the fovea and test performance on a visual discrimination task between two sequentially presented noisy stimuli, at 5, 10, and 15 minarc (1 minarc being 1/60 of visual degree) away from the preferred fixation locus. Such precision of stimulus placement is normally not possible given the ever-present uncertainty of actual retinal position caused by fixational eye movements.

Poletti *et al.* [7] were able to overcome this challenge, however, by employing a very accurate eyetracking combined with a technique of retinal image stabilization, which compensates for eye movements in real-time by adjusting the stimulus position on a visual display, so that the retinal position of the stimulus is rendered much more controlled than

without stabilization. Under conditions of retinal image stabilization, the proportion of correct judgments was significantly lower for 10 and 15 minarc eccentricities as compared to 5 minarc eccentricity (Figure 1B), but this dependence disappeared under 'normal' conditions in which the stimuli were fixed on the display and not on the retina. In other words, with careful control of retinal stimulus locations, the authors found that perception deteriorates significantly even for displacements away from the preferred retinal locus that were as small as a fraction of a degree of visual angle.

Poletti *et al.* [7] then turned to the question of why their subjects were equally good in the perceptual task at all foveal eccentricities without retinal image stabilization (i.e. under normal viewing conditions). They reasoned, and this is the second principal finding of the study, that miniature gaze shifts during this task were not random — subjects consistently 'looked' on the relevant parts of stimuli (for example, to the left when the informative stimulus was presented on the left). While this might not seem too surprising when considering large saccades, recall that the stimuli in their experiments were separated by only 5–15 minarc and were all well within the fovea! Thus, small microsaccades of 5–15 minarc amplitude compensated for the suboptimal perceptual sensitivity of the foveal areas outside of the preferred fixation locus, bringing the latter to the relevant stimulus (Figure 1C).

Combined with their earlier work [14], the new findings of Poletti *et al.* [7] offer, in our opinion, a compelling and convincing demonstration for a perceptual *benefit* attributable to microsaccades. Importantly, this benefit did not simply arise from microsaccade occurrence *per se*, for example as a result of a visual transient or a 'refresh' of the image, as has been sometimes suggested [16]. Instead, the benefit came about through the active state of oculomotor

activity during fixation. The distinction between these two mechanisms is important to point out here, especially because the controversial idea that the primary function of microsaccades is to prevent perceptual fading and restore visibility has been repeatedly criticized (largely because in most situations vision does not fade; head and body movements and ocular drift provide enough retinal motion; and because no causal link between reduced visibility and microsaccades was found) [4,17–19]. In the Poletti et al. [7] study, however, the effects of microsaccades were highly specific — in trials where microsaccades did not bring the fixation locus to the stimuli, performance was as low as in trials without microsaccades, and significantly lower than in trials in which subjects fixated each of the two stimuli. The dependence of perceptual effects on particular interactions between visual stimuli and retinal trajectories are in line with specific neuronal responses to different microsaccade patterns found in visual cortex [10,20].

The physiological and perceptual effects of microsaccades have been intensely investigated and debated for decades, but the progress in elucidating these phenomena has been hampered by disagreements about the definitions and incidence during natural viewing, as well as methodological issues [4–6]. One reason for the controversy was the tendency to treat microsaccades in isolation from larger saccades, a trend that is being reversed by recent studies. While some researchers originally contended that smaller microsaccades might be a 'noise' in the system, useless or even detrimental for some visual functions, most reached the consensus that one plausible role for microsaccades would be the same explorative or repositioning function as for larger saccades [4,15]. The direct demonstration of this role by Poletti et al. [7] will consolidate this view further.

The importance of microsaccades for a subset of visual tasks requiring a high-acuity resolution should not obscure the fact that while microsaccades (when they do occur) and saccades serve to position the preferred retinal locus in an optimal way, most visual processing takes
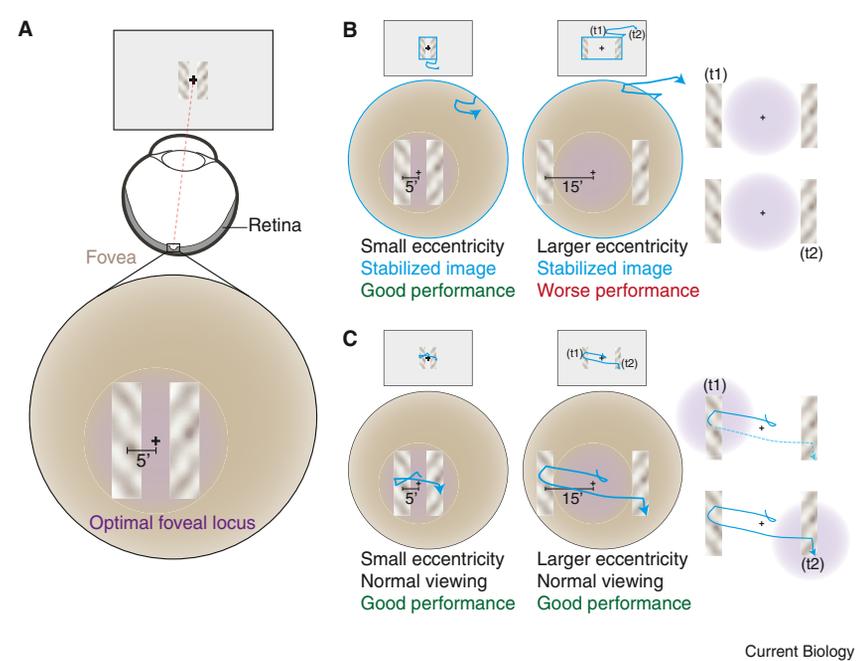

Figure 1. Main experimental conditions used by Poletti et al. [7].
(A) Visual stimuli, retina, fovea and optimal foveal locus. (B) Image stabilization condition (stimuli are fixed on the retina). Performance is good for a small eccentricity (5′) but is worse for a larger eccentricity (15′) because in the latter case, the stimuli stay outside the optimal locus (illustrated for 15′ eccentricity; t1 and t2, time frames corresponding to fixations 1 and 2). (C) Normal viewing condition (no image stabilization, stimuli are fixed on the display). Microsaccades sequentially bring the optimal foveal locus to each stimulus in turn, enabling good performance (illustrated for 15′ eccentricity).

place in inter-saccadic intervals during ensuing ocular drifts. Ocular drift is enhanced both after saccades and microsaccades, which can contribute to post-saccadic enhancement, highlighting the notion that the effects of (micro)saccades and drifts should be considered jointly [19]. It has been demonstrated that during natural viewing, drifts restructure the visual inputs in a specific way, enabling efficient spatiotemporal encoding of natural scenes [2]. From the recent work of Putnam and colleagues (reviewed in [4]) it seems that the preferred retinal locus is not always coinciding with the highest receptor density, further implying that not only spatial but also temporal characteristics of neural circuitry are responsible for optimal extraction of spatial information.

The apparent ability of the visuomotor system to precisely control even the smallest gaze shifts raises some intriguing questions. For example, while we execute exploratory large saccades mostly subconsciously during natural viewing, we are able to switch to the conscious, voluntary

mode, and choose to make or suppress specific saccades. Therefore, saccades are often considered voluntary movements. Can we also become aware of microsaccadic trajectories or even voluntarily control them? In contrast to saccades, microsaccades have been traditionally considered "involuntary" movements, but the recent findings discussed here suggest that the voluntary/involuntary distinction needs to be revisited. Steinman and colleagues have shown that microsaccades can be suppressed by instruction (see [4,5]). Future experiments assessing subjects' ability to implement specific eye movement instructions or asking them to report their eye movement behavior should determine the extent of voluntary control and awareness on the microscopic scale.

Equally intriguing is the implication of the Poletti et al. [7] study on our understanding of vision in the broad sense. The finding that foveal processing is not entirely uniform reveals an unprecedented level of specificity of retinal organization that surely constrains the principles of computation in the visual system. This

study will undoubtedly motivate careful scrutiny of foveal and parafoveal visual processing, and the associated oculomotor activity, in a wide range of behavioral and neurophysiological investigations.

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Carnivorous Plants: Trapping, Digesting and Absorbing All in One

The Venus flytrap digests and absorbs its prey, but how does it coordinate digestion and absorption to maximise the efficiency of this highly evolved mechanism? A new study that combines direct recordings from cells within the trap along with molecular characterization of nutrient transport reveals a complex and coordinated suite of mechanisms that underlie this elegant process.

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The ability to catch and digest insects allows insectivorous plants to acquire nitrogen and other nutrients in very low nutrient habitats. Since the landmark studies of Charles Darwin [1], the Venus flytrap (*Dionaea muscipula*) has provided a source of fascination and is now one of the most commonly cultivated house plants. It also provides a unique model for the study of mechanosensing and the physiological and structural processes underlying rapid plant movements. The Venus flytrap is a remarkable example of adaptive evolution. Its leaves are modified to form trap organs that have the unique ability to snap shut and trap a fly or other small creature that may accidentally touch one of the trigger hair cells located on the inner surface of the trap. The inner surface of the trap is also lined with secretory gland cells that are stimulated to produce lytic enzymes following closure of the trap [2]. The immediate and rapid snapping shut of the trap is a perfect demonstration of a sensory-motor system that involves neither nerves nor muscles. It has been known for some time that the mechanism underlying the closure of the trap involves the generation of very fast electrical depolarizations in the form of action potentials by the cells of the trigger hairs which lead to the rapid closure of the trap [3]. Rapid closure is brought about by a combination of elastic properties and biochemical/biophysical changes in the motor cells [4]. However, unlike animal neuronal action potentials in which Na^+/Ca^{2+} ions carry the depolarizing phase of the action potential, the rapid depolarization component of the Venus flytrap action potential is most likely brought about by the opening of rapid (R-type) anion channels [5] since plants lack the voltage-sensitive cation channels that characterise animal excitability [6].

How these initial signalling events link with the later events that occur following closure of the trap has been less clear. The paper by Scherzer *et al.* in this issue of *Current Biology* [7] provides new information that allows us to understand how digestion of prey and absorption of nutrients following trap closure are facilitated and regulated. In an earlier study by the same group, Escalante-Perez and co-workers [5] demonstrated that sealing of the trap and formation of the 'external stomach' was under the regulation of two plant hormones, abscisic acid (ABA) and 12-oxo-phytodienoic acid (OPDA). OPDA is a precursor of jasmonic acid and was shown to trigger secretion by gland cells as well as making traps more sensitive to mechanical stimulation and promoting long-term trap closure (a requirement for digestion). The jasmonic acid mimic coronatine (COR) was also able to induce secretion. ABA was shown to counter the stimulatory effects of OPDA by making traps less