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Neuroscience: Tiny Eye Movements Link Vision and Attention

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Eye movements are essential to human vision. A new study shows that the tiny eye movements we make while holding our gaze on a point of interest are associated with brief, attention-like changes in the sensitivity of visual neurons.

Textbooks sometimes use the analogy of a camera to teach students about human vision. Although the analogy has value, it encourages the false notion that our brain constructs our visual experience from still images of the outside world. The brain's cameras — the eyes — are never truly stationary, even when we feel that our gaze is locked on a point in the visual scene. As a result, the input to the brain is a jerky, drifting, and disjointed image stream. How does the brain make sense of this input? A study by Chen *et al.* [1] published recently in *Current Biology* suggests that a class of tiny eye movements known as 'microsaccades' are closely linked with mechanisms that prioritize how visual information is processed over space and time. Recording from single neurons in alert macaque monkeys, the authors show that neurons in the frontal eye fields and superior colliculus become especially sensitive to visual input just before the onset of these tiny eye movements (Figures 1A,B). Moreover, this enhancement is spatially specific — albeit coarsely — such that the region of the visual field that is prioritized depends on the direction of the eye movement (Figures 1C,D). These changes in visual sensitivity resemble those seen in experiments that manipulate visual attention [2]. This suggests that, even at very fine temporal and spatial scales, sensory and oculomotor systems act in concert to coordinate visual processing.

The Act of Seeing: Vision as a Sensorimotor Behavior

Vision would be of little use if we didn't move our eyes. Unlike a camera (again!), the primate retina has high spatial resolution only within a small central region — the 'fovea'. A scene is therefore not captured in detail instantaneously but rather through a sequence of eye (and head) movements. These fast eye movements, known as 'saccades', occur several times per second during everyday vision and are interspersed with short periods of relative stability known as 'fixations'. It is during these fixations that the most useful visual information is acquired.

In addition to giving the illusion of ubiquitous detail, large saccades give rise to a sense of visual space that is greater than the part of the world that can be seen at any single point in time. Indeed, by taking into account eye position [3,4], the brain can translate an object's ever-changing position in the retinal image into a stable internal representation of its position in the world or relative to the body — a key requirement for goal-directed behaviour, such as reaching or navigation.

In this light, exploratory vision arguably owes as much to the motor neurons that command the eyes to move as it does to the sensory neurons that respond to visual input. Consistent with this view, the visual and oculomotor systems are in close, bidirectional communication; visual signals drive movements of the eyes toward objects, and copies of movement commands known as 'corollary discharge' are sent back to the visual system [5]. Corollary discharge is thought to allow the visual system to compensate for self-induced retinal stimulation, and thereby maintain stable vision. How these signals influence individual visual neurons, however, remains poorly understood.

One putative correlate of corollary discharge that has been observed consistently across studies is a change in the sensitivity of visual neurons around the time of saccades, even before the eyes begin to move [3,6–8]. Some neurons, for example, show *enhanced* responses when stimuli are positioned near the endpoint of an impending saccade, as if spatial attention is

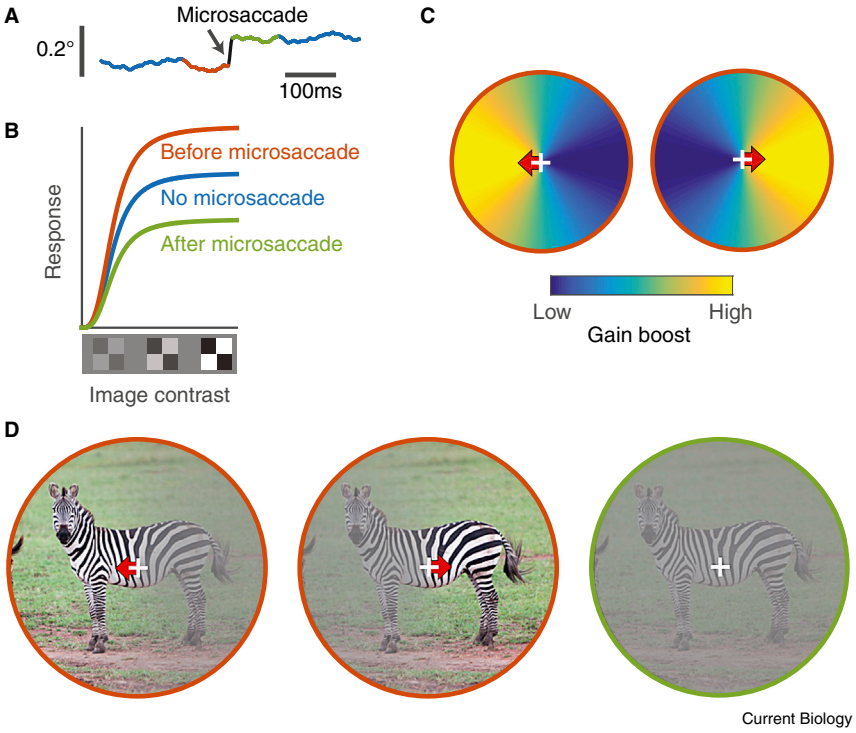

Figure 1. The sensitivity of neurons in the cerebral cortex and midbrain is altered around the time of microsaccades.
(A) Microsaccades are tiny (<1° amplitude) saccades that occur during fixation. The eye position trace shows one example. (B) The plot shows the responses of an idealized neuron in the superior colliculus to images of different contrast, as reported by Chen *et al.* [1]. Sensitivity to contrast (technically, 'response gain') was enhanced just prior to microsaccades (red epoch in (A)), and attenuated just after (green epoch in (A)). Similar effects were found in the frontal eye fields. (C) The enhancement varied in strength across the visual field and depended on the direction of an impending microsaccade. Specifically, locations beyond the eye's landing position were associated with a higher boost in gain than those in the opposite hemifield. Examples are shown for leftward and rightward microsaccades (indicated by red arrows; the white cross indicates the point of fixation (the fovea)). The attenuation effect did not depend on microsaccade direction. (D) Cartoon depiction of the Chen *et al.* [1] result for natural images. Left and middle panels: the gain-enhancement functions in (C) were used to modulate local contrast. Right panel: spatially uniform suppression after a microsaccade. Note that these simulations treat neural responses as a proxy for contrast and should be considered to be figurative only. Photo (modified): Matt Biddulph (https://creativecommons.org/licenses/by-sa/2.0/).

transiently recruited to the target location [8,9]. This interpretation is supported by a corresponding improvement in perceptual performance [10]. Other neurons show a strong *attenuation* of sensitivity around the time of saccades [6,8], consistent with the well-known perceptual phenomenon of 'saccadic suppression' [11]. At both the neural and perceptual level, therefore, changes in sensitivity around the time of saccades have much in common with those associated with shifts of attention in the absence of eye movements.

The results of Chen *et al.* [1], illustrated in Figure 1, fit well into this picture. They suggest that close links between sensory, attentional, and oculomotor systems are not limited to large, exploratory eye movements, but rather form a fundamental feature of visual analysis even during fixation.

How Do Fixational Eye Movements Affect Visual Processing?

The brain and body are noisy biological systems, so some degree of eye movement is inevitable even when we intend to hold our gaze. There are, however, several distinct types of eye movements that occur during fixation. These include tremor (tiny, high frequency movements); drift (slow, smooth motion); and microsaccades — the type studied by Chen *et al.* [1] (Figure 1A). Fixational eye movements appear not to be manifestations of an imperfect control system, but rather an important part of the evolutionary strategy for vision in primates [12]. Drift, for example, alters the image in a way that enhances edge detection by retinal ganglion cells and is likely to be under central control [13]. Similarly, microsaccades serve a corrective function by returning a point of interest to the highest acuity region of the fovea, similar in spirit to their larger counterparts [14]. The two saccade types also share common neural machinery for their generation [15], suggesting again that they differ primarily in scale of movement rather than function [16].

These considerations suggest that changes in visual sensitivity should be expected around the time of microsaccades, as noted above for larger saccades. Chen *et al.* [1] confirm this prediction for neurons in the superior colliculus and the frontal eye fields, and add to a growing body of evidence that suggests this effect is widespread in the brain [16]. Moreover, they report a novel spatial link between microsaccades and momentary, broad enhancements of visual sensitivity across the visual field in these areas. This result aligns well with behavioral studies that show a correlation between the direction of microsaccades and the locus of spatial attention [16,17].

There are, however, some incompatibilities between these neural observations and previous behavioral studies of attention. Yuval-Greenberg *et al.* [17], for example, reported a pattern of perceptual enhancement linked to microsaccades that at first glance resembles that observed in single neurons by Chen *et al.* [1]. They showed that stimuli at locations beyond the end-point of a microsaccade are perceived more accurately than those located in the opposite hemifield — that is, a pattern analogous to the gain effects shown in Figure 1. The behavioral effect, however, was observed for stimuli that were presented just *after* microsaccades; that is, during the time when the authors observed a seemingly uniform attenuation of neural sensitivity. Therefore, it remains unclear how these neural modulations relate to behavioral measurements of attention. Interestingly, however, the pattern of gain modulation observed by Chen *et al.* [1] does seem to account for a different perceptual effect in which

objects are briefly mislocalized before microsaccades [18].

Several other questions remain unanswered. Key among them is which causal mechanism gives rise to the observed link between altered visual responses and microsaccades. One interpretation, perhaps preferred by Chen *et al.* [1], is that the link reflects an influence of corollary discharge from oculomotor neurons on the sensitivity of visually responsive neurons. According to this view, the changes in visual sensitivity would occur only around the time of microsaccades. An alternative possibility, however, is that sensitivity across the visual field fluctuates continuously during fixation even in the absence of microsaccades. In this view, attention-like fluctuations of visual activity bias the likelihood and direction of spontaneous microsaccades [19]. A final, related possibility — also flagged by Chen *et al.* [1] — is that microsaccades and visual sensitivity are potentiated simultaneously through common and far-reaching network influences (such as those that manifest as neuronal oscillations [20]).

Regardless of the specific mechanism, the results of Chen *et al.* [1] suggest a strategy for visual analysis during fixation that is characterized by frequent and coordinated shifts of visual sensitivity and eye position. Their results are an intriguing demonstration of the interplay between sensory, attentional, and motor systems and highlights the active nature of vision in primates.

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Aneuploidy: Tolerating Tolerance

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Individuals, and cells, vary in their ability to tolerate aneuploidy, an unbalanced chromosome complement. Tolerance mechanisms can be karyotype-specific or general. General tolerance mechanisms may allow cells to benefit from the phenotypic plasticity conferred by access to multiple aneuploid states.

At first glance, it would appear that aneuploidy, an imbalanced chromosome complement, should be a universally negative state for cells. Aneuploidy perturbs the relative copy number of large numbers of genes simultaneously. Thus, it has the potential to disrupt biological processes carried out by any or all of the hundreds of genes that reside on the aneuploid chromosome(s). Aneuploidy, which results from mistakes in chromosome segregation when cells divide in mitosis or meiosis, is the leading cause of miscarriage, a major source of birth defects, and rampant in cancer. The most common and well-known aneuploidy in humans is an extra copy of chromosome 21 (trisomy 21), which