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...
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.

REFERENCES
1. Chen, C.Y., Ignashchenkova, A., Thier, P., and Hafed, Z.M. (2015). Neuronal response gain enhancement prior to microsaccades. Curr. Biol. 25, 2065–2074.
2. Williford, T., and Maunsell, J.H. (2006). Effects of spatial attention on contrast response functions in macaque area V4. J. Neurophysiol. 1, 40–54.
3. Morris, A.P., Kubischik, M., Hoffmann, K.P., Krekelberg, B., and Bremmer, F. (2012). Dynamics of eye-position signals in the dorsal visual system. Curr. Biol. 3, 173–179.
4. Morris, A.P., Bremmer, F., and Krekelberg, B. (2013). Eye-position signals in the dorsal visual system are accurate and precise on short timescales. J. Neurosci. 30, 12395–12406.
5. Sommer, M.A., and Wurtz, R.H. (2008). Brain circuits for the internal monitoring of movements. Annu. Rev. Neurosci. 31, 317–338.
6. Bremmer, F., Kubischik, M., Hoffmann, K.P., and Krekelberg, B. (2009). Neural dynamics of saccadic suppression. J. Neurosci. 40, 12374–12383.
7. Tolias, A.S., Moore, T., Smirnakis, S.M., Tehovnik, E.J., Siapas, A.G., and Schiller, P.H. (2001). Eye movements modulate visual receptive fields of V4 neurons. Neuron 3, 757–767.
8. Han, X., Xian, S.X., and Moore, T. (2009). Dynamic sensitivity of area V4 neurons during saccade preparation. Prog. Natl. Acad. Sci. USA 31, 13046–13051.
9. Moore, T., and Chang, M.H. (2009). Presaccadic discrimination of receptive field stimuli by area V4 neurons. Vision Res. 10, 1227–1232.
10. Deubel, H., and Schneider, W.X. (1996). Saccade target selection and object recognition: evidence for a common attentional mechanism. Vision Res. 12, 1827–1837.
11. Iboton, M., and Krekelberg, B. (2011). Visual perception and saccadic eye movements. Curr. Opin. Neurobiol. 4, 553–558.
12. Rucci, M., and Victor, J.D. (2015). The unsteady eye: an information-processing stage, not a bug. Trends Neurosci. 4, 195–206.
13. Aytekin, M., Victor, J.D., and Rucci, M. (2014). The visual input to the retina during natural head-free fixation. J. Neurosci. 38, 12701–12715.
14. Ko, H.K., Poletti, M., and Rucci, M. (2010). Microsaccades precisely relocate gaze in a high visual acuity task. Nat. Neurosci. 12, 1549–1553.
15. Hafed, Z.M., Goffart, L., and Krauzlis, R.J. (2009). A neural mechanism for microsaccade generation in the primate superior colliculus. Science 5916, 940–943.
16. Martinez-Conde, S., Otero-Millan, J., and Macknik, S.L. (2013). The impact of microsaccades on vision: towards a unified theory of saccadic function. Nat. Rev. Neurosci. 2, 83–96.
17. Yuval-Greenberg, S., Merriam, E.P., and Heeger, D.J. (2014). Spontaneous microsaccades reflect shifts in covert attention. J. Neurosci. 41, 13693–13700.
18. Hafed, Z.M. (2013). Alteration of visual perception prior to microsaccades. Neuron 4, 775–786.
19. Hafed, Z.M., Lovejoy, L.P., and Krauzlis, R.J. (2013). Superior colliculus inactivation alters the relationship between covert visual attention and microsaccades. Eur. J. Neurosci. 7, 1169–1181.
20. Varela, F., Lachaux, J.P., Rodriguez, E., and Martinerie, J. (2001). The brainweb: phase synchronization and large-scale integration. Nat. Rev. Neurosci. 4, 229–239.

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

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