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The unsteady eye: an information-processing stage, not a bug

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How is space represented in the visual system? At first glance, the answer to this fundamental question appears straightforward: spatial information is directly encoded in the locations of neurons within maps. This concept has long dominated visual neuroscience, leading to mainstream theories of how neurons encode information. However, an accumulation of evidence indicates that this purely spatial view is incomplete and that, even for static images, the representation is fundamentally spatiotemporal. The evidence for this new understanding centers on recent experimental findings concerning the functional role of fixational eye movements, the tiny movements humans and other species continually perform, even when attending to a single point. We review some of these findings and discuss their functional implications.

The unsteady eye

Sensory perception and motor behavior are closely coupled. Most species are not passively exposed to the incoming flow of sensory data, but actively seek useful information by coordinating sensory processing with motor activity. A clear example of this interaction is given by the role of eye movements in visual perception. In humans, as in many other species, acuity is not uniform throughout the visual field, but rapidly declines with increasing distance from the foveola (see Glossary), the small rod-free region of the retina covering a visual area the size of the full moon in the sky. As a consequence, humans acquire visual information during brief periods of 'fixation' separated by saccades, rapid gaze-shifts that enable inspection of the objects of interest with the high-acuity region (Figure 1A).

This coupling between visual sensation and eye movements goes beyond the fixational sequence enabled by saccades. Close examination of gaze position in the intervals in between saccades reveals that the term 'fixation' is misleading as the eyes are never at rest. Tiny eye movements – known as fixational eye movements – incessantly occur during the periods between saccades (Figure 1B). These movements are often labeled as microscopic, but they shift the projection of the stimulus over many receptors on the retina. It is remarkable that we are normally not aware of them because they yield motion signals with speeds that would be immediately visible had they originated from objects in the scene rather than from our own eyes [1].

Fixational eye movements have been observed in a wide variety of species [2] including the owl [3], a predator commonly believed not to move its eyes. However, they are often ignored by theoreticians and are regarded as a nuisance by experimentalists. When they are taken into account, they are frequently regarded as a problem that the visual system has to overcome to establish fine spatial representations [4] and to avoid perceptual blurring of the image [5].

Glossary

Brownian motion: a random-walk process that mimics the jiggling motion of a particle in a fluid. Brownian motion provides a good approximation for the inter-saccadic motion of the retinal image.
Diffusion coefficient: a parameter describing the speed of Brownian motion. The diffusion constant gives the ratio between the expected value of the square of the distance moved and the time elapsed since the onset of the motion.
Fixation: the period in between saccades, in which visual information is acquired and the image on the retina moves relatively little.
Fixational eye movements: small eye movements that incessantly occur during fixation. They include occasional microsaccades, ocular drift, and tremor.
Fovea centralis (fovea, in brief): a depression in the surface of the retina with diameter ~1.5 mm used for high-acuity vision.
Foveola: the central region of the fovea (~0.2 mm in diameter, approximately 1° in visual angle) without rod photoreceptors and where cones are most densely packed.
Image (or perceptual, or Troxler) fading: the progressive disappearance of the visual percept experienced under retinal stabilization.
Microsaccade: a very small saccade, traditionally with amplitude smaller than 30′ or less, which keeps the attended stimulus within the foveola.
Minute of arc (or arcmin, or minarc): a measurement unit of angle, corresponding to 1/60th of 1 degree. It is usually indicated by the prime symbol (′).
Ocular drift: the relatively slow incessant motion of the eye during the inter-saccadic interval. Here we use this term to also include tremor, a superimposed very small high-frequency motion.
Power spectrum: a representation of how the power of a random signal is distributed across the various frequencies composing the signal.
Retinal ganglion cells: the neurons in the output stage of the retina, which relay information to the thalamus, midbrain, and other central areas.
Retinal stabilization: a laboratory procedure that completely eliminates the physiological motion of the retinal image.
Saccade: a very rapid eye movement normally used to bring the retinal projection of the object of interest onto the high-acuity fovea. Saccades typically occur 2–3 times per second.
Whitening: a signal-processing operation that equalizes the power across all frequencies. After whitening a signal, its power spectrum is flat. This process removes pairwise correlations in the signal.

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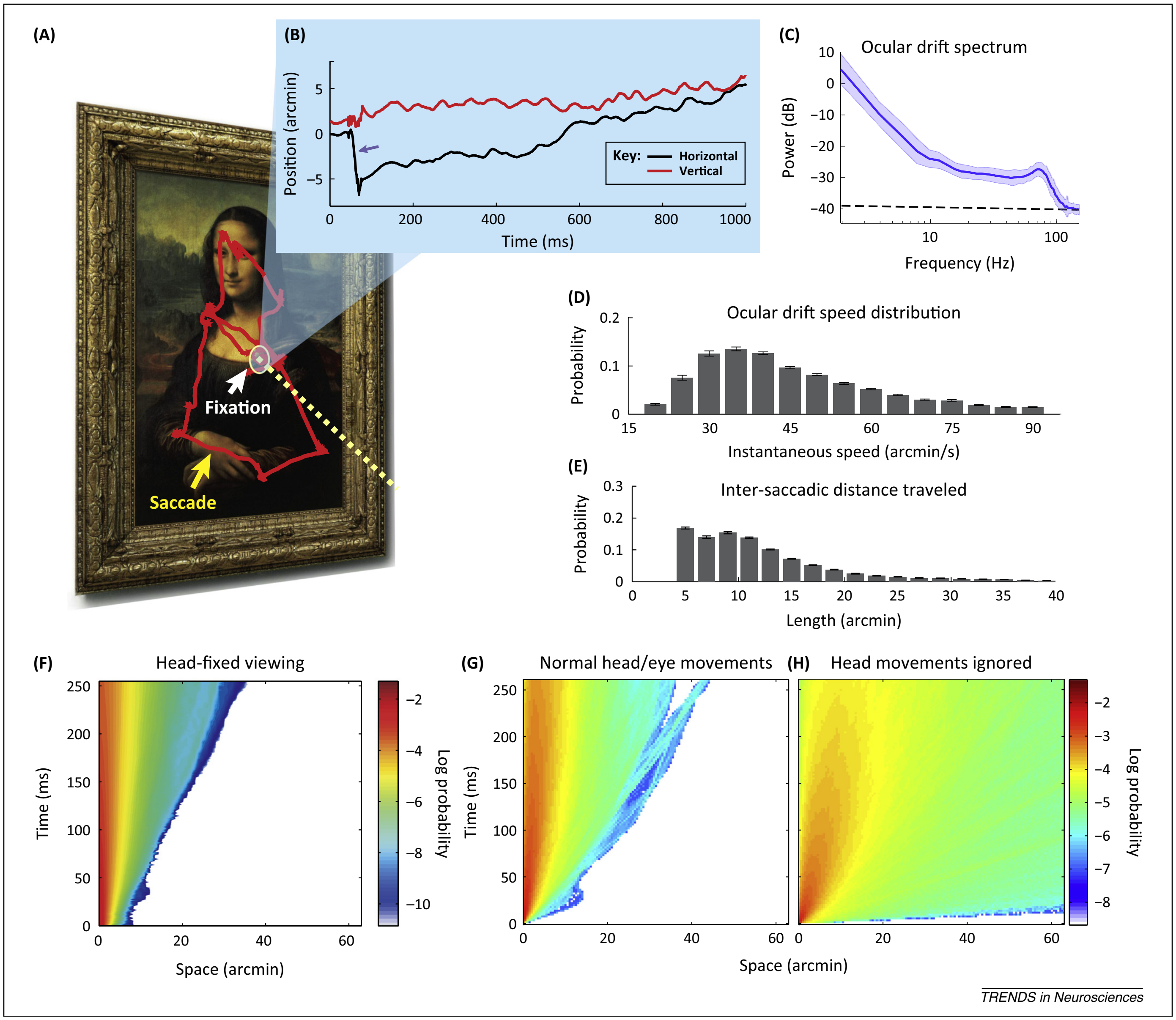

Figure 1. Vision and eye movements. **(A)** As an observer looks at a static scene, rapid eye movements (saccades) separate the periods of 'fixation' in which visual information is acquired. **(B)** High-resolution recording of oculomotor activity reveals that the eye moves also during these periods. The line of sight continually wanders with a seemingly random trajectory (ocular drift) occasionally interrupted by saccades with small amplitudes (microsaccades; arrow). (C–F) Characteristics of ocular drift when the head is immobilized, a standard practice to measure small eye movements. Subjects freely observed natural scenes [27]. **(C)** Power spectrum. The dashed line represents the eye-tracker noise level. **(D)** Distribution of mean instantaneous speed. **(E)** Length of the inter-saccadic trajectory. **(F)** Probability (in natural logarithmic scale) that the retinal image shifted by a given distance (horizontal scale) after a given time (vertical scale). **(G)** As in (F), but during normal head-free viewing [28]. **(H)** The same data as in (G), but with head movements artificially eliminated in the reconstruction process. More accurate reconstructions of retinal image motion that also consider the optics of the eye are given in [28].

All eye movements transform a static scene into a spatiotemporal input signal to the retina. This article builds upon the proposal that this transformation constitutes a fundamental step for visual perception: the visual system takes advantage of the resulting temporal modulations to encode spatial information in the joint space–time domain. Within this context, we focus here on the role of fixational eye movements, but similar principles and considerations extend to other types of eye movements, saccades in particular. Furthermore, we restrict our focus to the consequences of fixational eye movements for visual encoding and only marginally touch upon decoding mechanisms. For larger movements, a vast body of evidence indicates that oculomotor signals are taken into account in the interpretation of the retinal input [6,7], and similar strategies may also hold at the scale of fixational eye movements.

What is the function of fixational eye movements?

As with most scientific questions, several types of answers are available for why the eyes move incessantly, some more informative than others. Consider, for example, an unrelated fundamental question: 'what is the function of breathing?'. A possible answer could be that breathing prevents death by suffocation, but few scientists would find this superficial level of explanation satisfactory. Indeed, if we had stopped at this level, we would have never learned that breathing oxygenates the blood and about the associated chains of events. However, as explained