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Vision: The retina's fancy tricks

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The vertebrate eye is far more than a passive receptor for visual information. The microcircuitry in the retina can, for instance, carry out the job of distinguishing object motion from background motion.

When the first light-sensitive amoeba drifted down a stream, it encountered one of the fundamental problems of vision, which is that the world doesn't sit still. Trees move in the breeze, grass rustles, the sun and stars drift across the sky. The most basic use of an organism's light-sensitivity is to orient itself to (or from) a light source. But how, with so much moving clutter, could the amoeba have charted its position?

Fast-forward in evolutionary time to vertebrates, and things become worse yet. The image of even a peaceful world dances in great whoops and swirls when the eye moves. And it moves whether we command it to or not: the eyes make incessant, unconscious drifts, even when we stare fixedly at a single point. Given this visual dance, how can we see anything except a blur? As described on page 401 of this issue[1], an experiment carried out by Ölveczky *et al.* reveals one of the ways that the visual system does it. The process involves a clever piece of image processing (Fig. 1) — remarkably, that processing occurs in the neural microcircuits of the retina.

Figure 1 Catching the action. Full legend

High resolution image and legend (74k)

The computational task is to distinguish actual motion of an object in the world from motion across the retina caused by the fixational eye movements. The experiment was to record, during one of two conditions, from one of the output neurons of the retina, a retinal ganglion cell (whose collectively bundled axons make up the optic nerve). In the first condition, the stimulus matched the retinal input generated by an eye movement: all of the visual input — for the purposes of this experiment a black-and-white striped grating — moved across the retina with a single trajectory. The second condition simulated an object actually moving in the world: there was motion contrast, such that a test object moved in one direction and the larger, surrounding visual input moved independently.

When Ölveczky *et al.* compared the two conditions, the result was very simple. If an object moved independently of its background, the neuron sent a signal down the optic nerve to the brain. If everything moved together, there was no response. In effect, the circuits of the retina figure out that uniform, undifferentiated movement is only the result of eye movement, and the retina aborts its report to the brain. This behaviour was observed for only a subset of the known types of ganglion cell. So a more complete survey is needed, as is a rationale for why it would be good for particular types of retinal ganglion cell and not others to have the local motion-detecting behaviour. But the fundamental principle is now established.

How is this trick accomplished? One of the surprises of the past few years has been the unsuspected complexity of the retina's microcircuitry[2]. Various kinds of neurons, such as bipolar and amacrine cells, intervene between the photosensitive cells (the rods and cones) and the ganglion cells, and they shape and compress the raw information detected by the photoreceptors for efficient transmission to the brain. The bipolar cells come in roughly a dozen types; these are the retina's through-pathways, an array of parallel channels conducting different types of information from photoreceptors to ganglion cells. Along the way, information is shaped by the even more diverse array of amacrine cells, inhibitory neurons that come in at least 29 varieties (Fig. 2), each with a limited set of synaptic partners. Ölveczky *et al.* went on to record from one type of amacrine cell, termed 'polyaxonal' because it has many axon-like processes that spread widely across the retina[3, 4]. The cells responded with a timing that would well suit them to provide the 'blanking' signal that aborts the firing of the retinal ganglion cell when the visual input moves coherently across the retina.

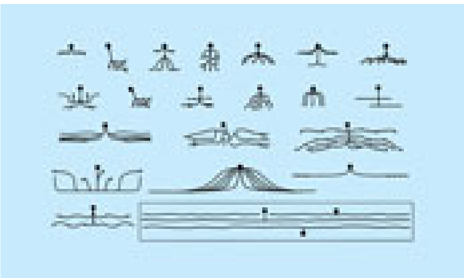

Figure 2 Information-processing machinery in the retina.
Full legend

High resolution image and legend (30k)

Where does this take us? Among other things, it encourages a search for even more sophistication in the retina's computations. Other amacrine cells provide feedback signals for retinal gain control — a crucial function that adjusts the retina's sensitivity to match the ambient illumination and contrast. A single amacrine cell, the starburst cell, appears to compute the fundamental asymmetry that enables some ganglion cells to report the direction of a moving stimulus[5, 6]. Another mechanism compensates for the ballistic eye movements that hurl the eyes from object to object[7]. There are now hints that not just movement but also the spatial pattern of the moving target affect the retina's responses[8]. The great turn-of-the-century anatomists recognized the retina as one of evolution's masterpieces. Our understanding of its signalling repertoire is finally beginning to catch up.

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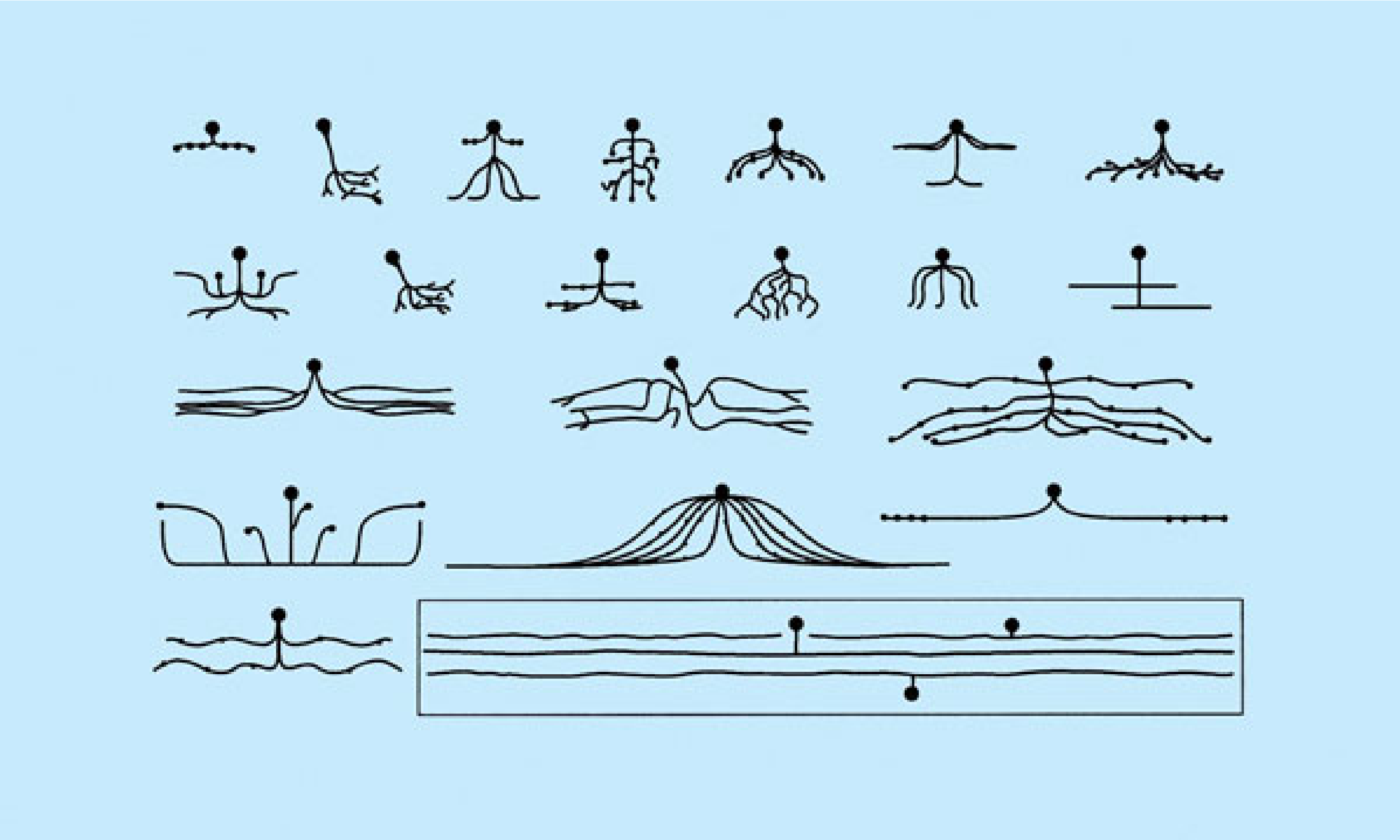

Figure 2 Information-processing machinery in the retina. As well as the input (rods and cones) and output (ganglion) cells, the retina contains a hugely diverse population of neurons. Each cell type is thought to have a specific role in vision[9]. The most extreme diversity is exhibited by amacrine cells, a collection of which is depicted here: their differing shapes and sizes are reflections of their wide variety of synaptic patterns. The widely spreading 'polyaxonal' amacrine cells, which come in several subtypes and are highlighted at lower right, are the type that Ölveczky *et al.*[1] suggest provide the mechanistic basis of local motion detection. (Data for the rabbit, adapted from ref. 2.)

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