

The retina's fancy tricks

Richard H. Masland

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 issue¹, 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.

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



Figure 1 Catching the action. In vision, certain objects pop out of the general scene with a perceptual vividness that overshadows others, even though the competing objects may have the same colours and brightness. One of the neural mechanisms involved has been revealed by Ölveczky *et al.*¹. Movement of an object relative to its background creates correlated firing in a group of retinal neurons. This neural activity serves to signal the unity of the moving object to the brain, with a final result artificially illustrated in the version of the image on the right.

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 microcircuitry². 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, overleaf), 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 'blinking' signal that aborts the firing of the retinal ganglion cell when the visual input moves coherently across the retina.

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 object⁷. There are now hints that not just movement but also the spatial pattern of the moving target affect the retina's responses⁸. The great turn-of-the-century anatomists recognized the retina as one of evolution's masterpieces. Our

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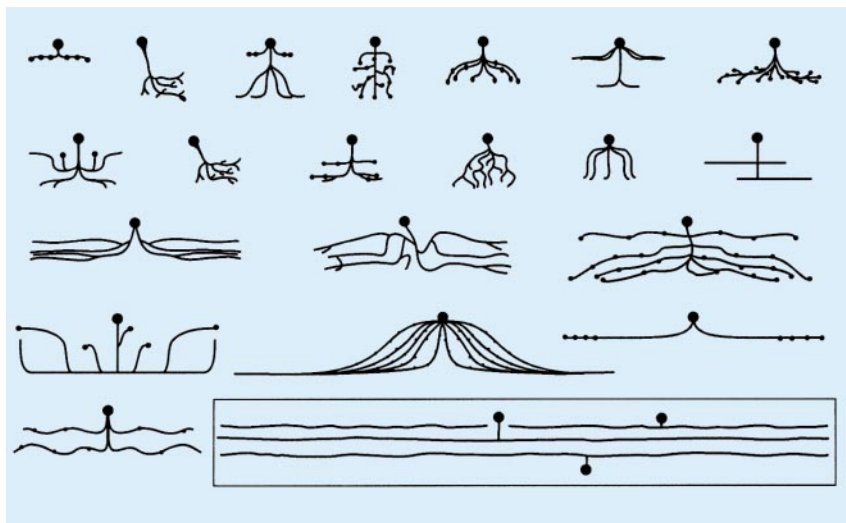


Figure 2 Information-processing machinery in the retina. As well as the input (rods and cones) and output (ganglion) cells, the retina contains a hugely diverse population of neurons. Each cell type is thought to have a specific role in vision⁹. The most extreme diversity is exhibited by amacrine cells, 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 Öveczky *et al.*¹ suggest provide the mechanistic basis of local motion detection. (Data for the rabbit, adapted from ref. 2.)

understanding of its signalling repertoire is finally beginning to catch up.

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Astronomy

New direction for γ -rays

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The origin of energetic γ -ray bursts is still unknown. But the detection of polarization of the γ -rays provides fresh insight into the mechanism driving these powerful explosions.

Gamma-ray bursts (GRBs) are short flashes of γ -rays, typically tens of seconds long¹. First detected in the 1960s, GRBs are observed at a rate of roughly one per day. Although their sources are known to reside in distant galaxies, several billion light years away, what these sources are remains a mystery. But a new clue is provided by Wayne Coburn and Steven Boggs², who, on page 415 of this issue, report the detection of polarization — a particular orientation of the electric-field vector — in γ -rays from a burst. This discovery may shed light on the identity of the sources of GRBs, as well as on the mechanism by which the γ -rays are produced.

The huge energy release associated with a GRB is thought to be created by the gravita-

tional collapse of a star to form a black hole or neutron star³. The contraction causes gravitational energy to be released. The typical energy output of a GRB corresponds to the conversion of about 1% of the Sun's mass into energy: in comparison, the energy output of an atom bomb is equivalent to the conversion to energy of about 1 gram of matter.

The energy released in the collapse seems to be carried away from the source in the form of a highly relativistic jet (Fig. 1), in which particles move at nearly the speed of light. As the jet reaches a radius of about 100 million kilometres from its source, part of this energy is converted to γ -rays, which become the GRB. At a later stage still, as the jet expands to a scale of 10 billion kilometres, an 'afterglow'

of lower-energy radiation, at X-ray, optical and radio wavelengths, is produced.

The detection over the past few years of GRB afterglows⁴ provides strong support for this picture. But as afterglow radiation is produced at a large distance from the collapsing object, key questions remain unanswered⁵: what, for instance, is the nature of the collapsing object? The most popular candidate is a massive star, about ten times the mass of the Sun, whose life ends with the collapse of its core. How the gravitational energy released becomes a relativistic jet and how jet energy is converted to γ -rays are also not well understood.

From earlier observations of the γ -ray spectrum of GRBs¹, it was concluded that the most likely mechanism for γ -ray production is 'synchrotron emission' — the emission of radiation by highly energetic electrons gyrating in a strong magnetic field. But other mechanisms, such as thermal emission or energy loss by relativistic electrons in intense radiation fields, are also possibilities³. The radiation released through synchrotron emission is highly polarized, but the other suggested mechanisms do not naturally produce large polarization. That Coburn and Boggs detect a clear polarization in the γ -rays from a burst provides direct evidence in support of synchrotron emission as the mechanism of γ -ray production.

Their observations also reveal more about the nature of the magnetic field in which synchrotron emission occurs. In a GRB, the γ -rays are produced in different regions inside the jet (Fig. 2). These regions are unresolved by detectors close to the Earth, so the source appears to be point-like. The detected polarization signal is, then, an average over the polarization of radiation produced at different points within the source. If the direction of polarization varies randomly from place to place in the jet, then the observed polarization signal is likely to average out to zero. But this 'washing out' of the polarization signal will not happen if the polarization direction is the same everywhere. For polarization produced by the synchrotron mechanism, this means that the γ -ray-producing region is suffused by an ordered magnetic field, oriented in the same direction everywhere (Fig. 2a).

The direction of polarization reported by Coburn and Boggs² remained constant throughout the duration of the GRB, but the γ -ray flux varied significantly. So it seems unlikely that such a strong, constant, ordered field could be generated in the region where the γ -rays are produced. Rather, this suggests that the strong field originates near the collapsing object, and is then carried by (or perhaps even drives) the jet outwards from the source: the mechanism by which gravitational energy is extracted and powers the jet is, possibly, electromagnetic.

But there could be another explanation.