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Insect Vision: Novel Mechanism for Contrast Constancy in Dim Light

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A general problem of sensory systems is how to simultaneously encode prevailing input as well as deviations from this baseline. A new study shows how the fly visual system has solved this by using parallel processing.

Whether it be a human or an insect, the role of early visual processing is to capture light from the environment and to transform this into neural signals that the brain can interpret. Visual signals are, in their most basic form, light that has reflected off surrounding surfaces and entered the eye. The intensity of this light is called the luminance, and the (temporal or spatial) derivative of luminance is called contrast. We know from years of experimentation that visually guided behaviours often scale in strength as contrast is increased. This is not unique to vision, but is a general principle of sensory systems. The primary benefit of using contrast signals to control behaviour is that they allow sensory systems to encode the large range of stimulus intensities that occur in the real world, within the limited dynamic range of neural signaling [1]. A new study by Ketkar *et al*. [2], reported in this issue of *Current Biology*, elaborates on this view by showing that early visual processing retains luminance information from the environment alongside contrast information.

Contrast constancy ensures that the contrast of a feature remains constant amidst varying levels of illumination. For example, if you read this text printed on a white piece of paper, the contrast of the text appears to be similar whether you read it outside on a bright, sunny day, or inside a comparatively dim room, even if the light intensity reaching your eyes varies enormously between these two scenarios. Contrast constancy is achieved by comparing the current contrast with the mean intensity of the recent past [3]. Because of this comparison with the past, however, contrast constancy begins to fail when the visual system is presented with rapid changes in light intensity. We can experience this ourselves if we try to keep reading this text immediately on entering a dimly lit room after spending time outside in bright sunshine. Over time, however, our visual system adapts to the new lower luminance levels, allowing us to read the text, but until that occurs our contrast sensitivity is impaired [4]. The new work of Ketkar *et al*. [2] suggests that flies may not experience similar problems.

A less extreme example of rapid luminance changes occurs when a fly moves through a natural environment. During its flight, shadows caused, for example, by clouds and trees (Figure 1A) cause the luminance reaching the eyes to fluctuate (Figure 1B). These luminance changes can be described by a temporal contrast profile (Figure 1C). For example, when the fly moves from a brighter to a darker space, it will experience a negative temporal contrast signal (arrow, Figure 1C). Contrast is important, because features that are important to the fly, including potential predators or food, are often identified by their contrast against the background [5]. There are many ways to quantify contrast, but a commonly used one is the Weber contrast, which subtracts the luminance of the background from the luminance of the object, and divides this difference by the average luminance of the background (Figure 1F). As the denominator reflects the mean intensity of the recent past, a problem arises when the viewer experiences rapid decreases in luminance levels. In this case the denominator is a much larger number than the background against which the object is compared, which if left unaddressed

results in contrast underestimation (bottom left, Figure 1G), and therefore a failure to detect prominent visual features.

Flies have a pair compound eyes, each formed by hundreds of repeating, hexagonal optical units called ommatidia. Light that enters an ommatidium is directed onto photoreceptor cells, which generate a strong contrast sensitive transient followed by a sustained response to the absolute luminance level [6]. In the next processing stage, visual signals remain repeated in individual, hexagonal cartridges. Each cartridge contains five lamina monopolar cells, referred to as L1–L5 [7]. In the lamina, the photoreceptor signals are separated into intensity increments and decrements, called ON and OFF channels [8]. Similar ON and OFF channel separation is seen in the mammalian retina [9]. In *Drosophila*, L2 and L3 both provide input to the OFF pathway [10]. Ketkar *et al*. [2] studied the function of L2 and L3 in detail, elegantly combining the use of genetic tools, calcium imaging and behavioural experiments to demonstrate that these two OFF pathway neurons signal different properties. Indeed, the parallel visual OFF pathways allow luminance information from the environment to be retained alongside contrast information.

Ketkar *et al*. [2] found that when a fly is presented with temporal luminance steps, such as a screen switching between different grey levels, the L2 and L3 neurons behave differently (Figure 1D, E). The authors measured intracellular calcium signals in either L2 and L3 neurons using two-photon microscopy to detect the fluorescence of the genetically inserted calcium indicator *GCaMP6f*. They found that when exposed to OFF contrast changes (for example, arrow in Figure 1C), L2 neurons produce a strong initial response, which quickly returns to baseline (Figure 1E). This is consistent with earlier work [11], which suggested that the role of the lamina is to highlight contrast changes. Before the genetic tools of *Drosophila* allowed us to investigate responses from individual neuron types, the responses of the five different lamina neurons were inevitably pooled in recordings, suggesting that L2 neuron responses (Figure 1E)

dominated. When using the new genetic tools, however, it was found that luminance steps (Figure 1B) generate quite different responses in the five lamina neurons [12], and that L3 responses to OFF stimuli remain sustained (Figure 1D).

To investigate this in more detail, Ketkar *et al*. [2] developed a clever stimulus that incorporated two sequential OFF steps, the first representing a drop in luminance which varied across trials, and the second representing a constant 25% drop in contrast, based on the luminance of the first step. By varying the magnitude of the first OFF step, this allowed the separation of contrast and luminance signals. The authors found that L2 responses were constant for steps of equal contrast but varying luminance, suggesting that stimulus contrast is the driving factor. Conversely, L3 responses varied considerably for steps of equal contrast, and instead scaled with luminance.

What is the purpose of having two separate channels in the OFF pathway with different response kinetics? Earlier recordings showed that the pooled responses of the lamina neurons become substantially reduced when luminance is decreased [13]. However, Ketkar *et al*. [2] show that there is no similar reduction in behavioral contrast sensitivity. The authors were able to solve this discrepancy using a combination of genetic manipulation and measurement of behavioural turning responses to moving dark edges of varying contrast under different luminance levels. They found that wild-type flies followed the dark edge, with a turning amplitude that scaled with the edge contrast, across background luminance levels that varied 10,000-fold.

Ketkar *et al*. [2] next selectively silenced L3 neurons by expressing the temperature-sensitive, dominant-negative dynamin allele *shibire*^{ts}. They found that flies with silenced L3 neurons were unable to follow the dark edge effectively, especially at low light intensities. Instead, the behavior of L3-silenced flies more closely resembled the prediction based on earlier pooled lamina recordings (based for example on [13]), where contrast sensitive L1 and

L2 responses likely dominated. Thus, to maintain high behavioural performance under dim light conditions, flies require the luminance-sensitive L3 neurons to monitor background luminance changes (Figure 1D) and to scale responses accordingly.

Rapid shifts in luminance levels are not only encountered by flying insects, they also pose a considerable challenge to human vision. Unlike flies, our eyes can turn rapidly and independently of our head, during involuntary movements known as saccades. These movements cause our eyes to view different parts of a scene in a short period of time, each potentially containing very different luminance levels [14]. Humans have mechanisms for independently adjusting sensitivity for contrast and luminance [15]. But when instantaneous luminance drops are simulated in lab conditions, human subjects underestimate the contrast of features in a scene [4], highlighting the extreme difficulty of this visual processing challenge. Given the powerful genetic and electrophysiological tools available in the fly visual system, future studies could use the fly as a model for understanding how the brain uses luminance and contrast signals synergistically to improve the robustness of visual behaviours in naturalistic scenarios.

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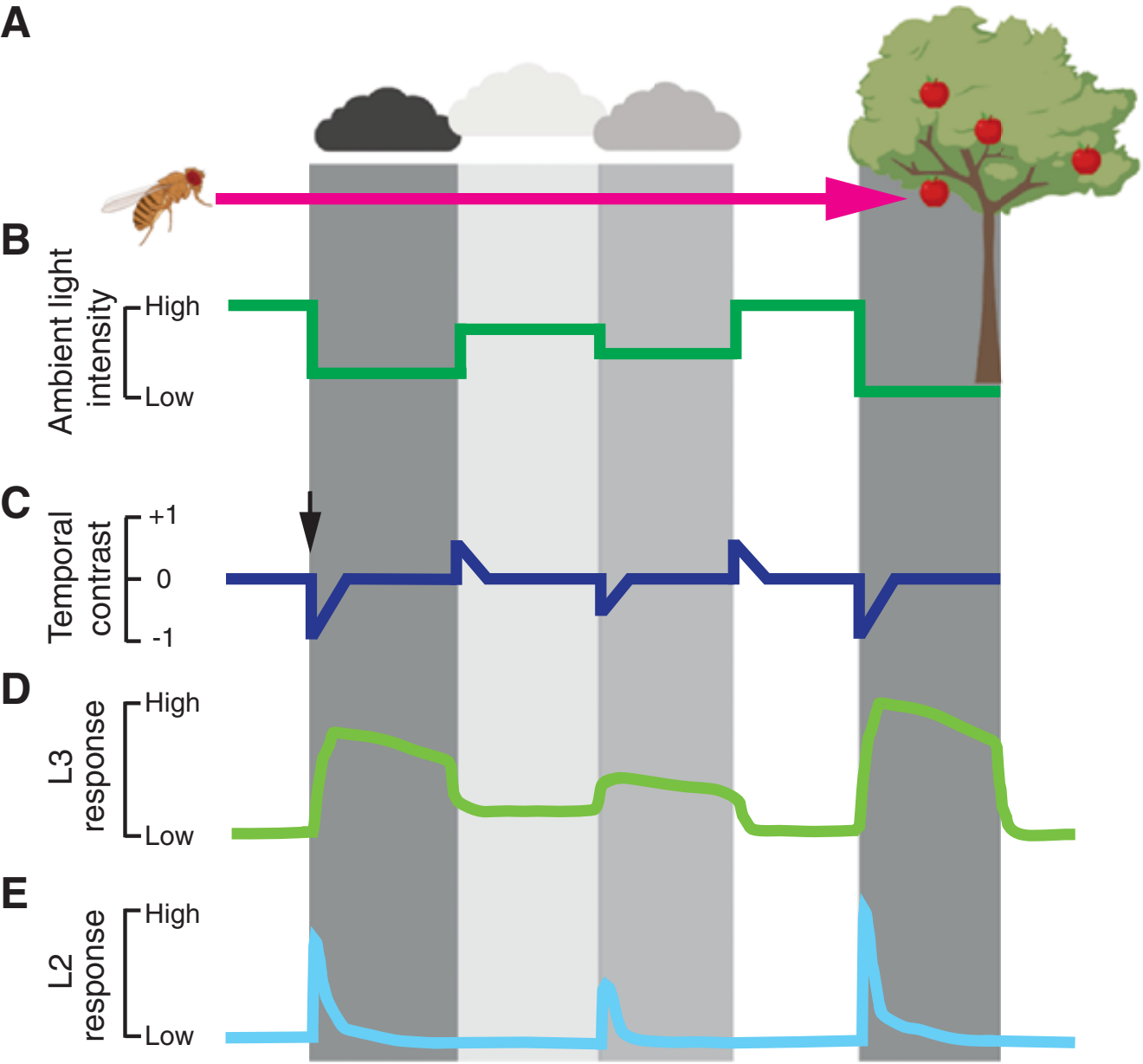
Figure 1. Luminance and contrast sensitive neurons in early visual processing.

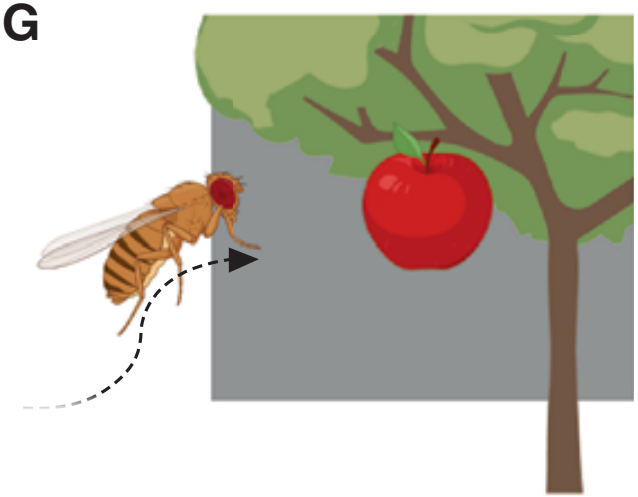
(A) As a fly moves through a natural environment to approach an apple under a tree it experiences fluctuating illumination levels caused for example by clouds and trees. (B) The green line shows the ambient light intensity changes associated with the flight trajectory in panel A. (C) The dark blue line shows the temporal contrast profile associated with the flight trajectory in panel A. (D) In this situation the L3 neuron would give sustained responses to the decreases in luminance described in the panels above (data simulated from [2]). (E) The L2 neuron would give transient responses to the OFF contrast changes described in panel C (data simulated from [2]). (F) The spatial contrast of an object (apple) is determined by the luminance of the object and the background. (G) Immediately after the fly passes from brightness to shade, a sudden background luminance reduction occurs. Since the eye requires time to adapt to the new lower luminance levels, and the denominator reflects the recent stimulus history, the contrast of the apple could be temporarily underestimated.



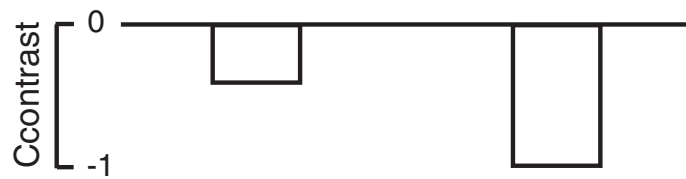
F

$$\text{Weber contrast} = \frac{I_{Object} - I_{Background}}{I_{Background}}$$

G



$$\frac{I_{Apple} - I_{Dim\ bg}}{I_{Bright\ bg}} \qquad \frac{I_{Apple} - I_{Dim\ bg}}{I_{Dim\ bg}}$$



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