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Collision Avoidance: Broadening the Toolkit for Directionally Selective Motion Computations

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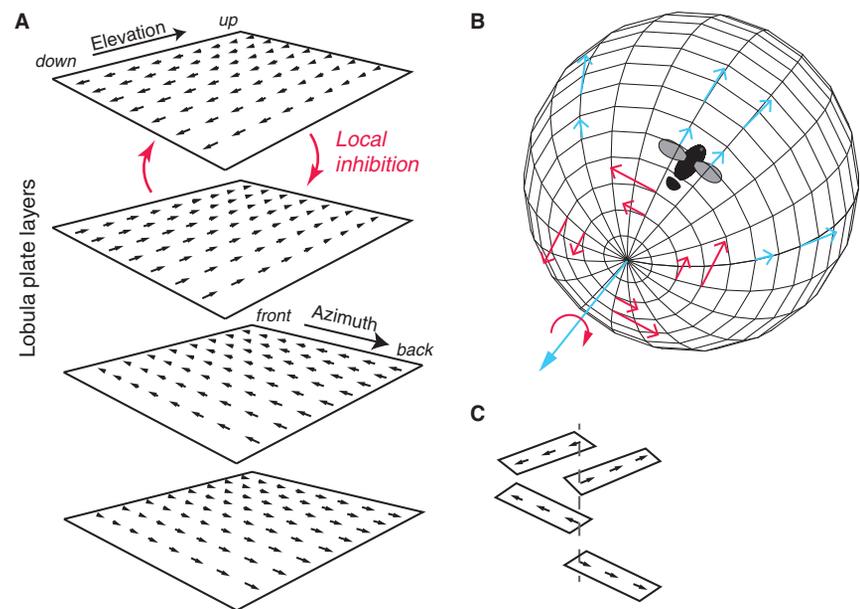
Visually-guided escape behaviors are critical for survival. New research reveals how neurons selectively coding for local motion directions can be assembled into collision detecting ones using a simple recipe.

Flies navigate expertly across complex visual environments avoiding obstacles and swatters alike with seemingly little effort. These abilities are in no small part thought to rely on a set of neurons that extract locally from the visual scene an estimate of the strength and direction of apparent motion of the visual world as the animal moves. The cells executing these computations are subdivided into two subtypes, called T4 and T5, specialized in local motion detection for features brighter or darker, respectively, than their surround. At the level of a brain area called the lobula plate, T4 and T5 neurons jointly form a two-dimensional map of visual space that codes locally for motion directions along four cardinal directions (Figure 1) [1]. Up to now, attention has focused mainly on neurons that collate these inputs over a wide portion of the visual field allowing the animal to extract information from visual input to control its rotational or translational movements [2,3]. Recently reported research [4] has assigned a new role to T4 and T5 as inputs to a class of neurons specialized in detecting the visual signature of an impending collision.

What is the visual signature of an impending collision with an object or predator? An object (dark, for simplicity) that approaches an animal at constant

velocity creates a shadow with edges that expand non-linearly in time on the animal’s retina. It has been known for

some time that these so-called ‘looming stimuli’ are sufficient to elicit escape behaviors across taxa from insects to



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Figure 1. Wiring locally direction selective neurons for navigation and collision avoidance.

(A) The lobula plate contains four layers of retinotopically organized, locally direction selective T4 and T5 cells. Inhibitory neurons suppress locally responses to anti-preferred directions of motion across maps (red arrows). (B) By sampling with the right magnitude and directions from these four maps, wide-field neurons become maximally responsive to specific patterns of motion of the animal in its environment. Illustrated here are the local sampling (at eight positions, for simplicity) required for roll rotations (red arrows) or translations in the direction of motion (blue arrows). (C) By sampling along the four cardinal directions starting from a single point in register across lobula plate layers one obtains a neuronal receptive field sensitive to expansion from the center point (dashed grey line).

humans. One important feature of looming stimuli is that their angular size expands non-linearly with time (Figure 2). In contrast, decelerating approaches result in linear angular expansion, a type of motion signal important for landing behavior, for instance. A selective looming detector should respond preferentially to a solid object approaching at a constant speed (or accelerating), less so to a decelerating object, but not to the object's contour. It should ignore an optic flow pattern that resembles looming stimuli but is generated by self-motion in a textured environment, as well as other whole-field motion patterns, such as translation for example. Another test used to identify looming-sensitive neurons is their vigorous response to footballs, with equal black and white areas, approaching on a grey background guaranteeing that responses are not caused solely by overall luminance changes [5].

Such collision-detecting neurons have by now been described in many species, including crabs, fruit flies, praying mantids, fish, pigeons, frogs, mice and cats (for example [5–10]). The prototypical one is the lobula giant movement detector (LGMD) in locusts, which encodes in its peak firing rate the time when an approaching object reaches a threshold angular size on the animal's retina [11]. Many, though not all, of the collision-sensitive neurons in other species are classified as eta-neurons, because they respond similarly to the LGMD [5]. In most of these species, the biophysical mechanisms that shape looming sensitivity and selectivity remain to be worked out. The LGMD, on the other hand, has been studied for over 60 years [12] and the biophysics of collision avoidance is reasonably well understood, from networks to ion channels [13–15].

Enter *Drosophila* with its arsenal of genetic tools. In their recent work, Klapoetke *et al.* [4] studied a class of neurons, first characterized anatomically and optogenetically in [16], called lobula plate lobula columnar cells, type 2 (LPLC2). These neurons are columnar, meaning that their dendrites sample as an orderly array retinotopic inputs at the level of the lobula plate and lobula, both areas lying three synapses away from photoreceptors. The focus is exclusively on lobula plate dendrites, which possess a striking feature: they roughly form a

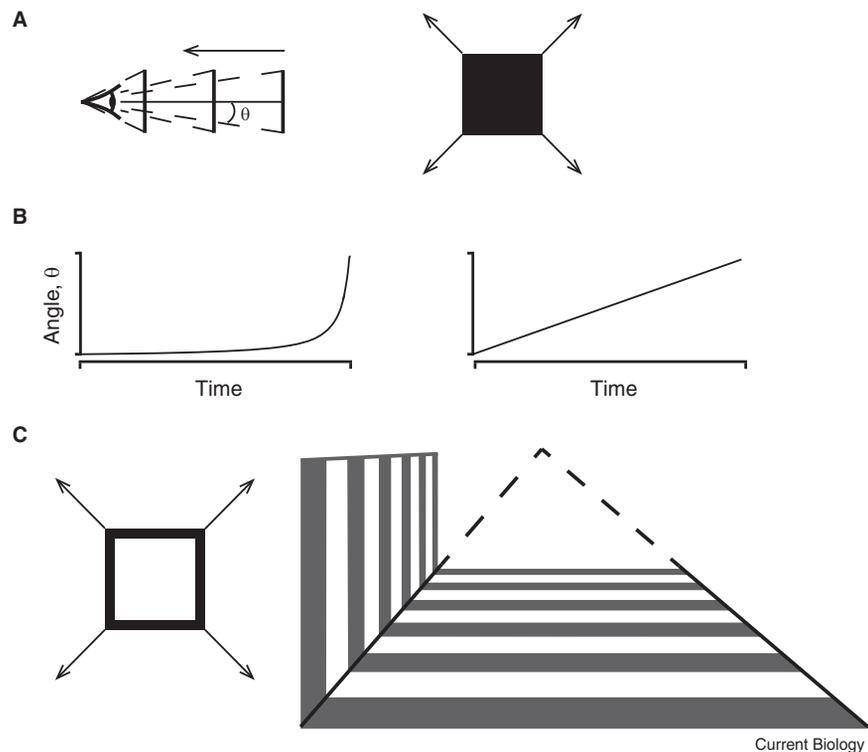


Figure 2. Features defining collision-detecting neurons.

(A) Looming stimuli are the two-dimensional expanding shadows created by an object approaching at constant velocity towards the eye (left, side view; right, frontal view). (B) They are characterized by a nearly exponential increase in the angle subtended by the object on the retina (left). In contrast, approaches with decreasing velocity lead to linear angular expansion (right). (C) Flight through a rectangular hoop (left) or a textured tunnel (right) are not expected to activate looming detectors nearly as well as looming stimuli.

cross radiating out from a central position, each arm being aligned with a cardinal motion direction encoded by the retinotopic array of T4 and T5 cells. This suggests that LPLC2 neurons should respond well to a disc expanding radially out from the receptive field center, as they indeed do. Additionally, the neurons possess several selectivity characteristics of looming detectors outlined in Figure 2; for example, they prefer coherently expanding stimuli over deconstructed ones and do not respond to whole-field motion [4, 16]. The cross-like structure of LPLC2 dendrites in the lobula plate does not immediately explain this last feature. The authors go on to show that local lobula plate inhibitory interneurons connecting across oppositely tuned layers contribute to the responses of LPLC2 neurons and to their looming selectivity: they decrease responses to stimuli whose pattern of motion is inverted with respect to LPLC2 preferred stimuli.

How do LPLC2 neurons affect behavior? Earlier experiments had already shown that their stimulation triggers jump escape [16]. In agreement with this, Klapoetke *et al.* [4] find a synaptic connection with the giant fiber, a wide-field neuron partly responsible for visually guided escape to looming stimuli [17]. In the future, it will be interesting to find out whether LPLC2 neurons connect to other jump escape-triggering neurons and to clarify their role in backward walking, a behavior triggered about as frequently as jumping when they are stimulated optogenetically [16]. Indeed, given their high density — one for every 10 facets on the compound eye — and relatively broad receptive fields (60°), it would seem unwise from an energetic standpoint for flies to use them exclusively for one purpose. From the perspective of neural coding, one would also like to know their contribution to giant fiber excitation, which is also provided by LC4 cells that code for the angular

velocity of a looming stimulus [18]. These new results [4] offer a new perspective on the role played by local directionally selective motion detectors and nicely complement a flurry of recent work that has shed light on various aspects of collision avoidance, including their role in fear responses [19] and body impact prediction [20].

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