

13. Guo, Y., Lang, S., and Ellis, R.E. (2009). Independent recruitment of F box genes to regulate hermaphrodite development during nematode evolution. *Curr. Biol.* *19*, 1853–1860.
14. Ellis, R.E., and Lin, S.Y. (2014). The evolutionary origins and consequences of self-fertility in nematodes. *F1000Prime Rep.* *6*, 62.
15. Baker, H.G. (1955). Self-compatibility and establishment after “long-distance” dispersal. *Evolution* *9*, 347–348.
16. Tandonnet, S., and Pires-daSilva, A. (2016). Phenotypic plasticity and developmental innovations in nematodes. *Curr. Opin. Genet. Dev.* *39*, 8–13.
17. McCaig, C.M., Lin, X., Farrell, M., Rehain-Bell, K., and Shakes, D.C. (2017). Germ cell cysts and simultaneous sperm and oocyte production in a hermaphroditic nematode. *Dev. Biol.* *430*, 362–373.

## Collision Avoidance: Broadening the Toolkit for Directionally Selective Motion Computations

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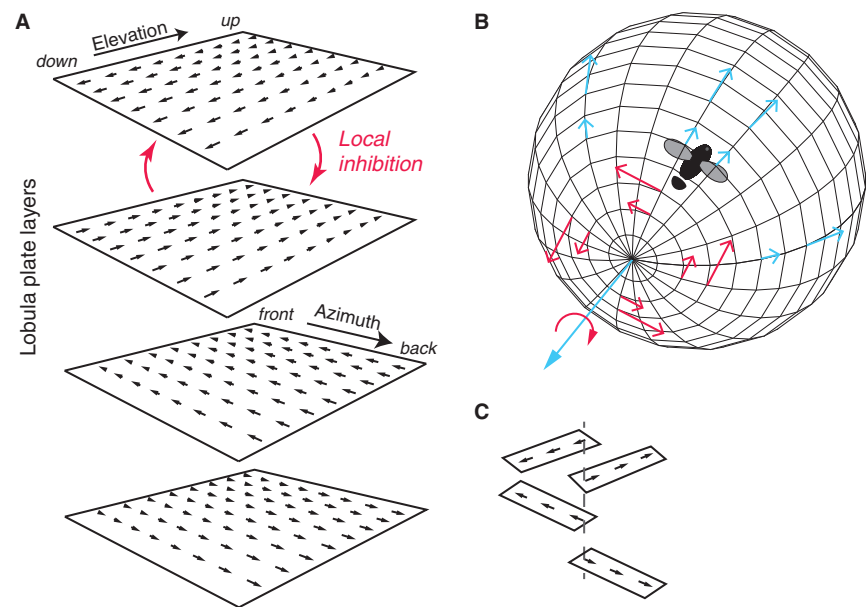
Visually-guided escape behaviors are critical for survival. New research reveals how neurons selectively coding for local motion directions can be assembled into collision detecting ones using a simple recipe.

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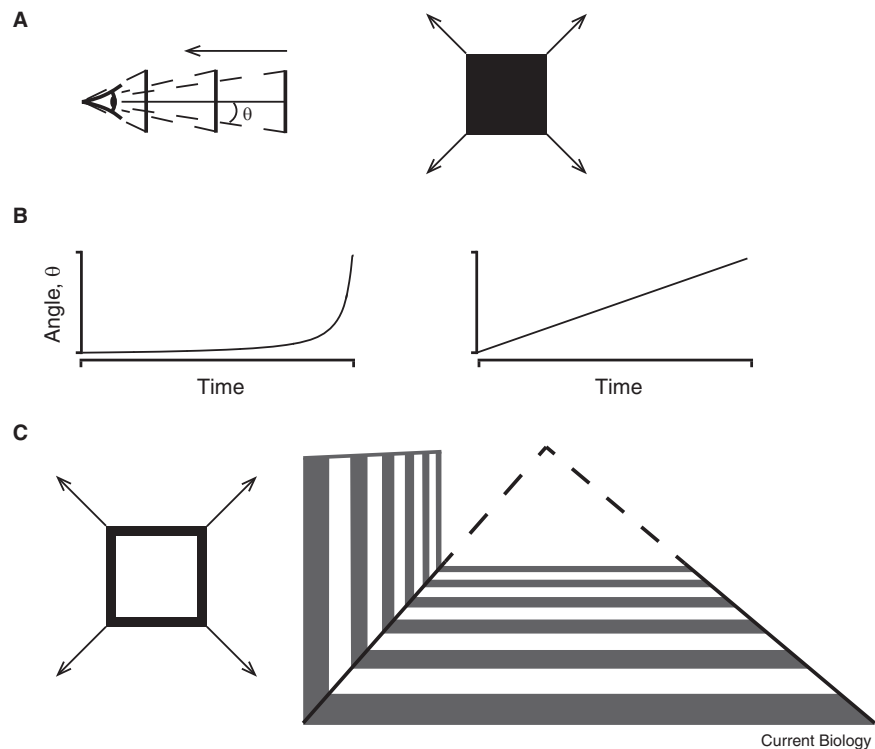
**Figure 1. Wiring locally direction selective neurons for navigation and collision avoidance.**

(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].

#### REFERENCES

- Maisak, M.S., Haag, J., Ammer, G., Serbe, E., Meier, M., Leonhardt, A., Schilling, T., Bahl, A., Rubin, G.M., Nern, A., *et al.* (2013). A directional tuning map of *Drosophila* elementary motion detectors. *Nature* **500**, 212–216.
- Krapp, H.G., and Hengstenberg, R. (1996). Estimation of self-motion by optic flow processing in single visual interneurons. *Nature* **384**, 463–466.
- Longden, K.D., Wicklein, M., Hardcastle, B.J., Huston, S.J., and Krapp, H.G. (2017). Spike burst coding of translatory optic flow and depth from motion in the fly visual system. *Curr. Biol.* **27**, 3225–3236.
- Klapoetke, N.C., Nern, A., Peek, M.Y., Rogers, E.M., Breads, P., Rubin, G.M., Reiser, M.B., and Card, G.M. (2017). Ultra-selective looming detection from radial motion opponency. *Nature* **551**, 237–241.
- Sun, H., and Frost, B.J. (1998). Computation of different optical variables of looming objects in pigeon nucleus rotundus neurons. *Nat. Neurosci.* **1**, 296–303.
- Oliva, D., and Tomsic, D. (2014). Computation of object approach by a system of visual motion sensitive neurons in the crab *Neohelice*. *J. Neurophysiol.* **112**, 1477–1490.
- de Vries, S.E.J., and Clandinin, T.R. (2012). Loom-sensitive neurons link computation to action in the *Drosophila* visual system. *Curr. Biol.* **22**, 353–362.
- Temizer, I., Donovan, J.C., Baier, H., and Semmelhack, J.L. (2015). A visual pathway for looming-evoked escape in larval zebrafish. *Curr. Biol.* **25**, 1823–1834.
- Dunn, T.W., Gebhardt, C., Naumann, E.A., Riegler, C., Ahrens, M.B., Engert, F., and Del Bene, F. (2016). Neural circuits underlying visually evoked escapes in larval zebrafish. *Neuron* **89**, 613–628.
- Zhao, X., Liu, M., and Cang, J. (2014). Visual cortex modulates the magnitude but not the selectivity of looming-evoked responses in the superior colliculus of awake mice. *Neuron* **80**, 202–213.
- Gabbiani, F., Krapp, H.G., and Laurent, G. (1999). Computation of object approach by a wide-field, motion-sensitive neuron. *J. Neurosci.* **19**, 1122–1141.
- Rind, F.C., and Simmons, P.J. (1992). Orthopteran DCMD neuron: a reevaluation of responses to moving objects. I. Selective responses to approaching objects. *J. Neurophysiol.* **68**, 1654–1666.
- Zhu, Y., Dewell, R.B., Wang, H., and Gabbiani, F. (2017). Muscarinic lateral excitation contributes visual object segmentation during collision avoidance. *bioRxiv*, <https://doi.org/10.1101/216945>.
- Dewell, R.B., and Gabbiani, F. (2017). Biophysics of object segmentation in a collision-detecting neuron. *bioRxiv*, <https://doi.org/10.1101/216333>.
- Gabbiani, F., Krapp, H.G., Koch, C., and Laurent, G. (2002). Multiplicative computation in a visual neuron sensitive to looming. *Nature* **420**, 320–324.
- Wu, M., Nern, A., Williamson, W.R., Morimoto, M.M., Reiser, M.B., Card, G.M., and Rubin, G.M. (2016). Visual projection neurons in the *Drosophila* lobula link feature detection to distinct behavioral programs. *eLife* **5**, e21022.
- von Reyn, C.R., Breads, P., Peek, M.Y., Zheng, G.Z., Williamson, W.R., Yee, A.L., Leonardo, A., and Card, G.M. (2014). A spike-timing mechanism for action selection. *Nat. Neurosci.* **17**, 962–970.
- von Reyn, C.R., Nern, A., Williamson, W.R., Breads, P., Wu, M., Namiki, S., and Card, G.M. (2017). Feature integration drives probabilistic behavior in the *Drosophila* escape response. *Neuron* **94**, 1190–1204.
- Shang, C., Liu, Z., Chen, Z., Shi, Y., Wang, Q., Liu, S., Li, D., and Cao, P. (2015). Brain circuits: a parvalbumin-positive excitatory visual pathway to trigger fear responses in mice. *Science* **348**, 1472–1477.
- Cléry, J., Guipponi, O., Odouard, S., Pinède, S., Wardak, C., and Ben Hamed, S. (2017). The prediction of impact of a looming stimulus onto the body is subserved by multisensory integration mechanisms. *J. Neurosci.* **37**, 10656–10670.