

Robust prey detection in a small nervous system

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Vision plays a huge role for us humans, as well as for many other animals. If you have ever tried to walk in a straight line with your eyes closed, you know how important self-generated optic flow is for maintaining a straight trajectory. Besides such widefield optic flow cues, we can also visualize the motion of objects that move independently of the remaining visual surround. Such targets may represent the motion of a ball during a game of cricket, tennis, or baseball (take your pick, depending on your cultural heritage and location in the world). Despite the fact that you are moving, and thereby generating optic flow across your visual field, you can still visualize and identify the independent trajectory of the ball. Motion vision is not only important for human sports stars (1), but also for insects who use these cues for tasks such as maintaining a straight flight trajectory (2), avoiding colliding with approaching tree trunks, and, importantly, identifying targets such as potential prey (3), the subject of a paper published in PNAS (4).

Studying the neurophysiology underlying target detection in human subjects, and other vertebrates, quickly becomes quite complicated. Besides the relative inaccessibility of the vertebrate visual cortex, there is the additional inconvenient complication of the eyes being able to move independently of the head (5). In insects, however, the eyes are fixed to the head's exoskeleton, which means we know what the insect looks at if we know what direction the head is facing. Intriguingly, however, despite vertebrates and insects being separated by huge evolutionary distances (6), and being equipped with completely different eyes (7), motion vision is coded in remarkably similar ways in the vertebrate visual cortex and the insect brain (8). We can therefore, somewhat surprisingly, use the insect visual system to understand the coding of visual cues in our own brain. Dragonflies do not play tennis, but they are extremely efficient predators who intercept tiny prey with astonishing success rates, entirely guided by visual cues (9). This tells us that they must have the neural machinery in place for detecting target motion, even in complex visual surrounds.

So how many neurons do you need to reliably detect the trajectory of a target? In the ingenious study by Gonzalez-Bellido et al. (4), the answer seems to be surprisingly few. Gonzalez-Bellido et al. (4) set

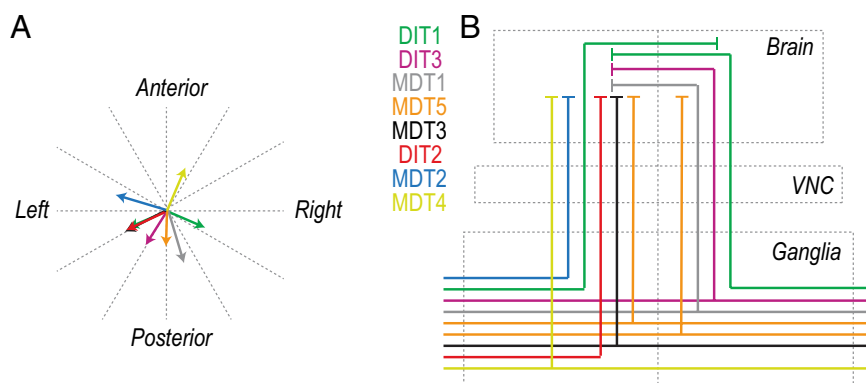


Fig. 1. (A) Diagram of the directional selectivity of those TSDNs responding to target motion in the left visual field. The arrows show the preferred direction of each TSDN (color-coded according to legend), with arrow lengths indicating strength of directional sensitivity. Target direction is displayed in relation to the dragonfly's field of view. (B) A representation of the projections of the TSDNs that respond to target motion in the left visual field. DIT1, DIT3, and MDT1 project to the contralateral ventral nerve cord (VNC; compared with their inputs and the location of the soma in the brain), whereas the others have ipsilateral axons. DIT1, DIT2, and MDT2 target ipsilateral locations in the thoracic ganglia, whereas the others have bilateral outputs.

out to study a group of target-selective descending neurons (TSDNs) in the dragonfly ventral nerve cord. Insects, and many other invertebrates, have a ventral nerve cord, which transmits information from the brain to the body, instead of a dorsal spine, like us vertebrates. The TSDNs consist of 16 neurons, eight on each side of the nerve cord (10). Earlier work has shown that stimulating the TSDNs electrically activates the four wings (11), indicating a more or less direct coupling with behavioral output associated with prey capture. The limited set of neurons, combined with a well-described behavioral output (3), gives us an excellent hardwired system for investigating the neural mechanisms underlying coding of vital visual cues.

Gonzalez-Bellido et al. (4) map the receptive fields and directional sensitivity of the 16 TSDNs. They then use a population vector analysis approach to show that these 16 neurons reliably code for all possible directions of target motion within the visual field. Population vector analysis approaches have been used previously in other biological systems (e.g., ref. 12) However, here it is used to understand how a complete population of visual neurons control a well-described visual behavior. As such, it provides us with a wealth of useful information. Intriguingly, the authors show that six TSDNs would be sufficient to reliably code for target direction to within 10° precision (4). The use of all 16 TSDNs, however,

adds precision and robustness to target detection.

Gonzalez-Bellido et al. (4) morphologically reconstruct the complete dendritic trees of the full set of TSDNs. TSDNs receive their input from small target motion detectors (STMDs) in the brain and travel through the ventral nerve cord (where the recordings in the study are done) down to the thoracic ganglia, where they affect the wings. The authors (4) find that the outputs of some TSDNs are restricted to the ipsilateral ganglia, whereas several TSDNs have bilateral outputs, thus potentially affecting the behavior of the wings on the right and the left sides of the body. All TSDNs were found to target four identifiable locations in the thoracic ganglia, suggesting that the fore and hind wings are controlled independently. Maybe having 16 TSDNs allows for more intricate and sophisticated control of the attack angle of each of the four wings (13) than would be possible with just six.

Consider a target moving in the left visual field (Fig. 1). The luminance change associated with the motion of this target is absorbed by the photoreceptors in the dragonfly's compound eye, and then transmitted for further processing in the peripheral optic ganglia. In the lobula,

Author contributions: K.N. wrote the paper.

The author declares no conflict of interest.

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the third optic ganglion, STMDs generate selective responses to the target's motion (14) and pass this information to the TSDNs. Depending on the direction and the location of the target's motion within the dragonfly's visual field, different TSDNs will fire (4). For example, if the target moves leftward and slightly toward the animal's anterior visual field, MDT2 will fire maximally (Fig. 1A, blue). The MDT2 axon is located in the ipsilateral ventral nerve cord (Fig. 1B). When the axon has reached the thoracic ganglia, MDT2 targets two discrete ipsilateral locations, where it presumably synapses with neurons controlling the left hind and fore wings. If the target instead moves toward the dragonfly's posterior visual field, and slightly leftward (still in the left visual field), DIT3 will fire maximally (Fig. 1A, pink). The DIT3 axon is located in the contralateral ventral nerve cord, i.e., on the right side of the nervous system (Fig. 1B, pink). At the output end, DIT3 targets both sides of the thoracic ganglia, thereby allowing control of the left and right hind and fore wings.

The authors also map the TSDN receptive fields in detail (4). Although this had been done crudely approximately 20 y ago (15), the study by Gonzalez-Bellido et al. (4) provides much more detailed resolution of each receptive field, which is an important addition to the neurons' directional sensitivity and morphology. For example, DIT1, MDT3, and DIT2 have incredibly similar directional preferences (Fig. 1A), but their receptive fields

differ substantially. Whereas the receptive field of MDT3 is quite large, and covers a large part of the ipsilateral visual field, the receptive fields of DIT1 and DIT2 are much smaller. DIT2's receptive field sharply delineates the visual midline, and DIT1's receptive field is confined to

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a small part of the dragonfly's dorsofrontal visual field. This suggests that, whereas MDT3 would signal the target's heading across a broad part of the visual field, DIT1 and DIT2 would provide much more detailed positional information, which would subsequently allow for precise positioning of the dragonfly for successful prey capture (3). The overlapping receptive fields might additionally provide further information about the target's movements through 3D space, rather than the 2D screens used in experimental setups, which could be another reason for having more than six TSDNs.

By providing the detailed receptive field organization, directional sensitivity, and morphological structure of the complete set of neurons responsible for transmitting information about target motion from the brain to the thoracic ganglia, the study by Gonzalez-Bellido et al. (4) provides a wealth of information for further investigations of single neurons or at a neuronal population level. For example, the authors find that the average of all TSDN receptive fields is located in the dorsofrontal visual field (4). Dragonflies have compound eyes, which limit the spatial resolution severely compared with the single lens eyes of vertebrates (7). In a compound eye, the maximum resolution is given by the spacing of the individual lenses. Dragonflies, and many other insects that depend on successful target detection, have therefore evolved areas in the compound eye with increased spatial resolution, called acute zones (16). The dragonfly's acute zone is located in the dorsofrontal visual field, in the same area as Gonzalez-Bellido et al. describe the peak TSDN sensitivity (4). This is also the part of the visual field where STMD receptive fields tend to cluster (17), and where dragonflies position their prey during target pursuit (3, 9). Taken together, this highlights the coevolution of optics, neural machinery, and behavior for optimizing successful target pursuit despite the limited hardware—in the form of poor optics and a small brain—provided.

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