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Escape behaviors in insects

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Escape behaviors are, by necessity, fast and robust, making them excellent systems with which to study the neural basis of behavior. This is especially true in insects, which have comparatively tractable nervous systems and members who are amenable to manipulation with genetic tools. Recent technical developments in high-speed video reveal that, despite their short duration, insect escape behaviors are more complex than previously appreciated. For example, before initiating an escape jump, a fly performs sophisticated posture and stimulus-dependent preparatory leg movements that enable it to jump away from a looming threat. This newfound flexibility raises the question of how the nervous system generates a behavior that is both rapid and flexible. Recordings from the cricket nervous system suggest that synchrony between the activity of specific interneuron pairs may provide a rapid cue for the cricket to detect the direction of an approaching predator and thus which direction it should run. Technical advances make possible wireless recording from neurons while locusts escape from a looming threat, enabling, for the first time, a direct correlation between the activity of multiple neurons and the time-course of an insect escape behavior.

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Introduction

Survival is an evolutionary arms race between predator and prey. To eat, a frog must fling its tongue faster than a fly can jump away, but to live, the fly must detect and evade the frog first. Over millennia, this selective pressure has driven animal nervous systems to develop escape reflexes that are accurate, robust, and fast. These features necessitate underlying neural circuits that can reliably detect and transform sensory information about a predator into an appropriate escape, using only a relatively small number of synapses to limit processing time. Researchers

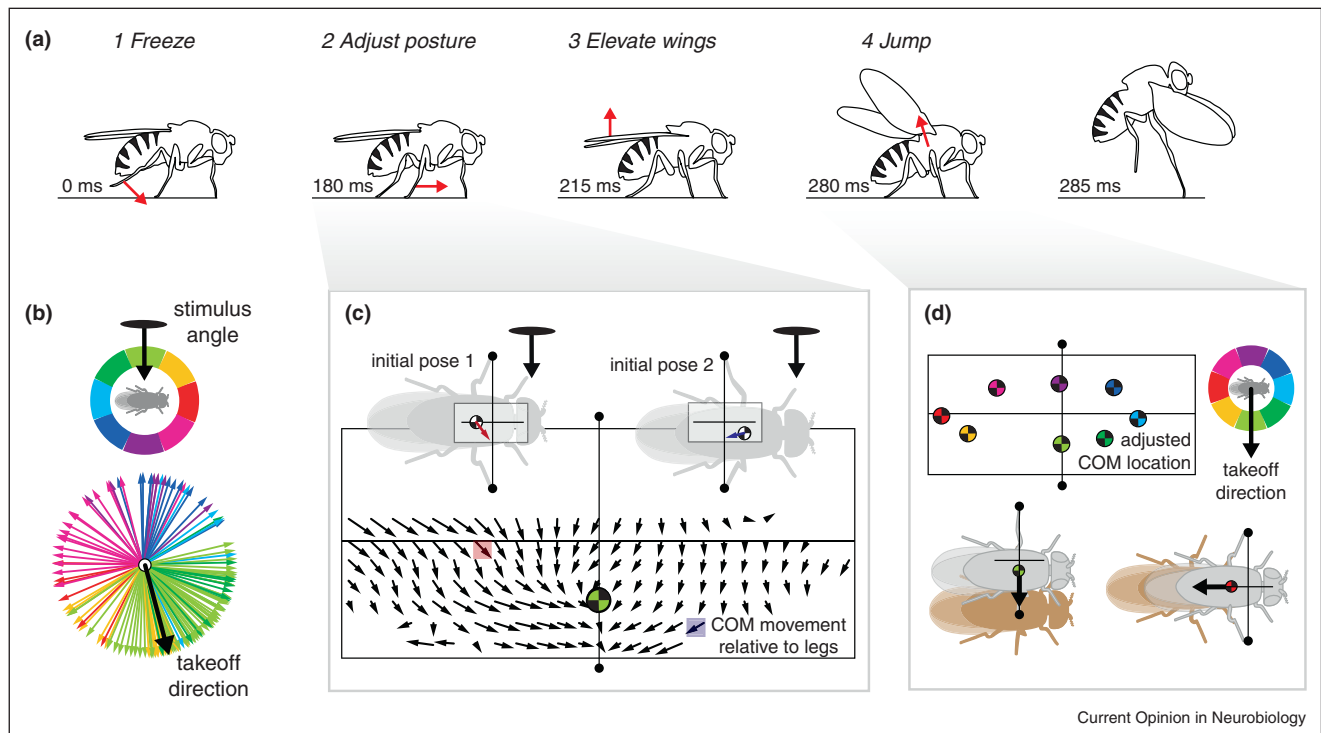
may take advantage of these compact escape circuits to investigate the architecture and neural coding strategies of sensorimotor circuits in the nervous system. Insects are especially appealing experimental subjects for physiology because their nervous systems contain accessible, identifiable cells, allowing the same neuron to be monitored repeatedly in different individuals. Recently, new technologies, such as high-speed videography and the miniaturization of electronics for implanted neural recording, have enabled the field to examine insect escape systems under more natural conditions. This provides crucial context for interpreting the neural data in relation to the function of escape circuits. In this review I focus on new behavioral and physiological studies of classic insect escape systems in their natural context.

Escape sequences

There is an often-assumed tradeoff between behaviors that are fast and those that are flexible. Escape behaviors are generally regarded as occupying the fast side of this tradeoff, as the penalty for a slow escape is severe. Recent work indicates, however, that some insects have modular escape responses, which allow them to be both fast and flexible.

Taking advantage of new high-speed video technology, experimenters examined in detail a fly's response to a naturalistic threatening stimulus, a looming object [1–3,4**]. This response turns out to be more elaborate than the simple takeoff jump performed by mutant white-eyed flies in response to a light-off stimulus [5]. Instead, a fly's escape response comprises a sequence of at least four maneuvers that occur while the object is approaching [4**]: (#1) freeze, (#2) a body lean or leg postural adjustment, (#3) wing-elevation, (#4) jump (Figure 1a). The sequential behaviors are independent enough that the fly can abort the progression midway if it so chooses [2,4**], indicating that the response is not a fixed action pattern. The data also suggest that each sub-behavior in the sequence makes an independent contribution to the overall performance of the escape: the postural adjustment (#2) determines takeoff direction, the extent of preparatory wing elevation (#3) correlates with initial flight steadiness, and the speed of mesothoracic leg extension during the final jump (#4) determines escape velocity [3,4**]. This strategy is not limited to flies. A locust's escape response to a looming object also consists of a sequence of behaviors that begins with leg and body postural adjustments to orient escape direction [6] followed by the three hind leg actions (flexion, co-contraction, and triggering) that first store energy before quickly releasing it during the jump [7].

Figure 1



Drosophila escape behavior consists of a sequence of tunable modules. (a) An example sequence of the maneuvers performed by a fly when confronted by a looming object: (1) first the fly places all its legs in contact with the substrate and ‘freezes,’ (2) the fly then moves its legs to adjust its center of mass (COM) in anticipation of its eventual escape direction, (3) it next elevates its wings, and, finally, (4) jumps off the ground by rapidly extending its middle legs and commences flapping flight. In the example depicted, the looming object approached the fly from the front over approximately 0–300 ms. The red arrows indicate which part of the body is moving during the specified behavior. (b) The fly can orient its escape direction away from the stimulus. Each colored arrow indicates the escape direction of an individual trial. The arrows are color coded by the direction of the stimulus relative to the fly’s body axis as shown in the color-wheel schematic above. The color distribution of takeoff directions is rotated approximately 180° from the stimulus, indicating flies generally escape away from the stimulus. (c) Postural adjustments made by the fly during the escape sequence (1A, #2) move the fly’s COM (white and black circle) towards a specific target location (green and black circle) relative to the fly’s two jumping (mesothoracic) legs. The target location is determined by the stimulus direction, but the direction in which the fly moves its COM incorporates feedback about its initial posture, as shown in the vector field. The vertical axis of the vector field is defined by the tarsal ground contact points of the two jumping legs. The base of each black arrow indicates a COM starting position, and the arrow orientation and length represent the direction and magnitude of the COM movement from that starting position (some data points interpolated for display purposes, see [4**]). The same example starting COM positions (white and black circles) and movement are shown both relative to the fly body (red and blue arrows) and on the vector field (red and blue shaded vectors). (d) The COM location achieved after postural adjustment (behavior #2) determines the direction the fly will move during the escape jump (behavior #4). Each colored COM circle represents the average adjusted COM location before a fly escapes in one of eight different direction bins (indicated by the color wheel). The fly diagrams illustrate the direction the fly jumps for two different example COM locations. By separating the preparation for directional escape and the execution of the escape, the fly is able to respond rapidly when a threat is imminent, while retaining flexibility in choosing the direction of the response. Adapted from [4**].

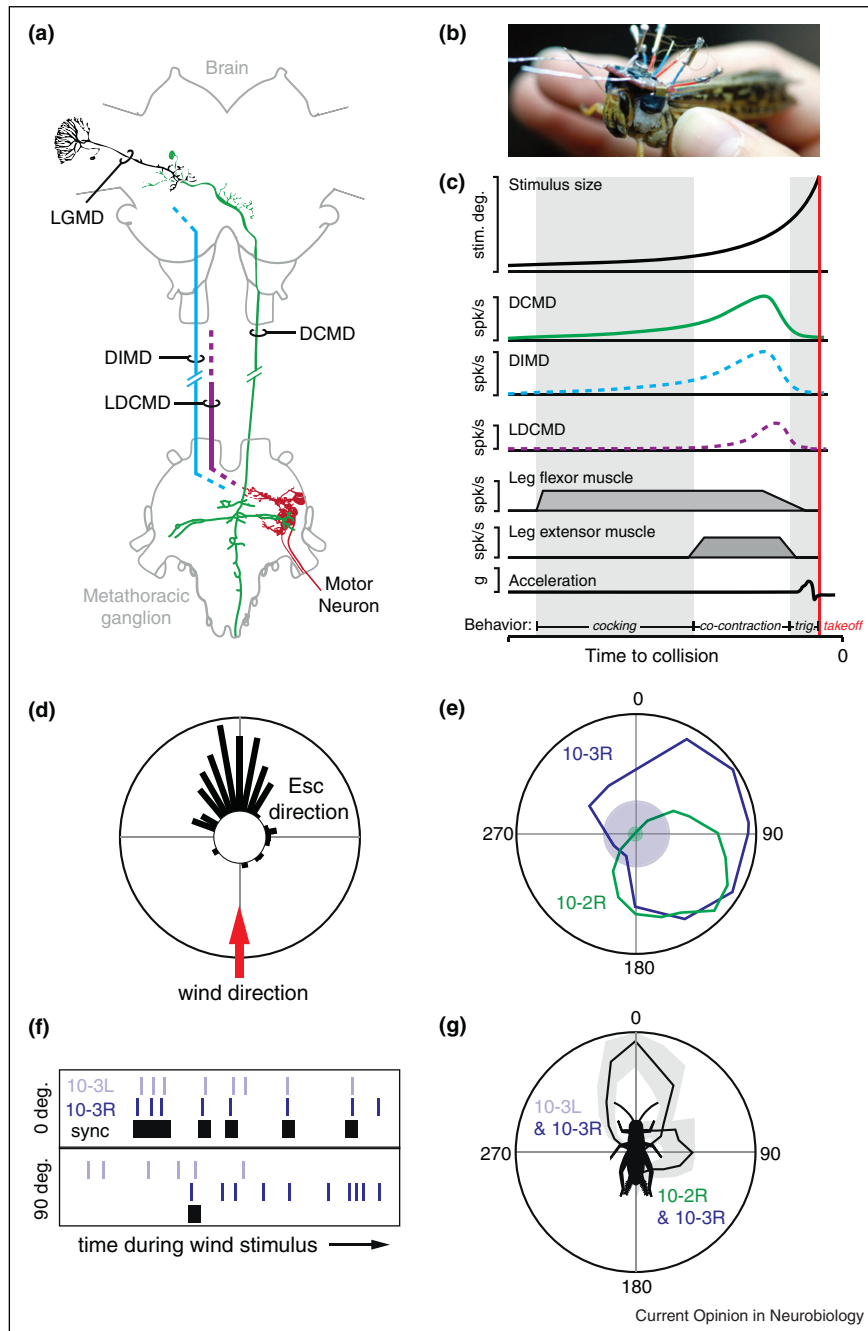
A sequential escape program, as described above, allows a fly the flexibility to orient its escape direction (Figure 1b) without compromising reaction time. The fly prepares its escape direction when the looming threat is still relatively distant by positioning its center of mass at a specific target location relative to its jumping legs (behavior #2, [4**]). This adjustment is flexible and incorporates proprioceptive feedback about the fly’s initial posture (Figure 1c). The fly can then delay the final takeoff decision until later, when it is more certain of the threat. When the threat is imminent, the fly completes the escape with a rapid, 3-ms, leg extension (behavior #4, [3]). Because of

the earlier positioning of its center of mass, the simple leg extension will move the fly away from the threat (Figure 1d).

Optimal escape strategy?

If insects can control the direction of their escape trajectories, what strategy should they adopt to optimally evade a predator? If an insect always escapes directly away from a threat, a predator can anticipate its escape trajectory, giving the predator the advantage. But if instead the insect maximizes unpredictability by choosing a trajectory at random, some escapes will be directed towards the

Figure 2



Neural mechanisms for directing escape behaviors. **(a)** Descending pathways for escape coordination in the locust. A well-known pathway involved in locust escape includes LGMD (black), an interneuron in the locust optic lobe (adapted from [30]), which is responsive to looming stimuli and synapses onto DCMD (green; profile in brain adapted from [30]), a wide-axon descending neuron that contacts thoracic motor areas (descending profile adapted from [25]), including direct contact with a motor neuron of the jumping leg extensor muscle (red; adapted from [50], shown with overlapping dendrites of a flexor motor neuron). Two additional descending pathways have recently been identified as looming-responsive: DIMD (blue) and LDCMD (purple), though their full anatomy has yet to be determined. **(b)** A new miniature telemetry system makes it possible to record from locust DCMD neurons, leg flexor and extensor muscles in a freely moving locust. The telemetry components are pictured on a locust (reprinted with permission from [35]). **(c)** Diagrammatic representation of locust neural and behavioral responses to looming stimuli based on recordings from both restrained preparations and free animals using telemetry. Extracellular DCMD responses, muscle activity, and acceleration were measured simultaneously in a free locust using the telemetry equipment pictured in **(b)** [36**]. Early leg flexor, DIMD [37], and LDCMD [38] responses are based upon data from restrained locusts. DCMD and DIMD peak response times are identical, whereas LDCMD peaks later. In the free animals recorded, DCMD firing rate peaks after the onset of co-contraction (though see also [32]). DCMD activity is required for the timing of the jump events, but other pathways, possibly DIMD or LDCMD, are sufficient to produce a takeoff without DCMD. **(d)** Cricket escape runs are narrowly directed away from an air puff stimulus. The polar frequency plot

predator, again increasing the odds the insect is captured [8]. In a meta-analysis of their own and historic cockroach escape data, Domenici *et al.* [9] suggest that cockroaches employ an advantageous middle-ground strategy of selecting their escape bearing from a set of possible trajectories at fixed angles away from the threat. This allows the cockroach to remain unpredictable while still moving rapidly away from a predator. A survey of escape strategies across taxa suggests this may be a general, though not universal, strategy [10].

Of course, in the field, most animals must be equipped to evade multiple types of predator and hence a variety of attack strategies. A single escape strategy could leave an animal vulnerable to predators with the capability to exploit this response. For example, the redstart is an uncommon predator of drosophilid flies, and so is able to take advantage of the fly's escape response by flicking its tail to mimic looming stimuli, triggering the fly jump response. By this method, the redstart flushes flies from their perches and then catches them in the air [11,12].

Escape circuits

Flexible escape programs require neural circuitry sophisticated enough to generate that flexibility. In *Drosophila*, visually triggered escape is associated with a pair of large descending interneurons, the giant fibers (GFs), which synapse directly on the largest motoneuron of the fly's 'jump' muscle (mesothoracic leg extensor) and activate the wing depressors via an interneuron [13,14]. Direct activation of this pathway has been shown to be sufficient to cause a fly to take off [15], thus the expectation has been that the *Drosophila* GFs are command neurons for a visually triggered escape response that consists of a rapid 'tuck and jump' takeoff [5].

From the behavioral observations discussed above, however, it is clear that the *Drosophila* GF motor pathways cannot alone account for the observed posture (#1 and #2) and wing (#3) behaviors in the escape sequence, thus other descending pathways must be involved. Fotowat *et al.* [16^{*}] demonstrated, in fact, that the GF are not at all active in response to certain looming stimuli that trigger a jump. Recording extracellularly from the neck connective of restrained mutant white-eyed flies, they see no GF

action potential in response to a loom [16^{*}], even though a light-off stimulus reliably produces an action potential [16^{*},17,18]. Furthermore, in wild type flies, a looming stimulus fails to produce the stereotypical timing of muscle activation known to result from a GF action potential [13,18,19]. Instead, Fotowat *et al.* [16^{*}] found, by recording from the fly nerve cord, another unit that responded consistently to looming stimuli, with spiking activity reminiscent of a known locust loom-sensitive interneuron (see below). Though their method did not allow them to identify this neuron anatomically, their results suggest that the *Drosophila* GFs are not involved in visual looming escape behaviors but instead an alternate pathway (or pathways) mediates the response. This is consistent with data from other fly species, which also found no GF response to a looming stimulus [20]. While it is possible that the GFs may be unnaturally quiescent in restrained physiology preparations, the surprising result could also be explained if real predators provide a multimodal cue, such as simultaneous visual and wind disturbances, to which the GF pathway is better tuned. Either way, it is clear that *Drosophila* escape responses involve more neural control elements than a single command neuron.

The locust descending contralateral movement detector (DCMD) pathway: a new look

Locusts have a well-described neural pathway that is responsive to looming stimuli [21–23] and involved in jumping [24–28]. It has been a challenge to interpret the pathway's causal role in locust escape behavior, however, without an experimental preparation in which neural and muscle activity can be observed concurrently during natural behavior. The thoracic motor areas that coordinate locust jumping receive input from a pair of large interneurons, the descending contralateral movement detectors (DCMDs) [24,25] that are directly postsynaptic to a pair of looming-responsive optic lobe interneurons, the lobula giant movement detectors (LGMDs) [29,30] (Figure 2a).

The ability to monitor neural activity in freely behaving animals has been crucial to interpreting neural data in other systems [31]. Unfortunately the small size of insects does not leave much area on which to support apparatus for physiological recording. In a proxy for free behavior,

shows the distribution of cricket (*G. bimaculatus*) escape trajectories in response to an air puff stimulus from the direction of the red arrow (adapted from [10], data re-plotted from [41]). (e) Polar tuning curves for two different cricket giant interneurons of the cricket (*A. domesticus*) (blue: 10-3, adapted from [43], and green: 10-2, adapted from [39]). For each point (θ, r) on the curve, θ represents the stimulus angle relative to the cricket's body axis, with 0° directly in front of the cricket, and distance from the center of the circle, r , represents the normalized spike rate of the cell in response to a stimulus. Shaded areas are the resting rate of the cell and tuning curve values inside this area indicate that the cell was inhibited by stimuli from the corresponding direction. (f) Pairs of GIs in the cricket (*G. bimaculatus*) respond with synchronous spikes to particular directions of wind stimuli (0°), but not others (90°). Light and dark purple responses are spikes recorded extracellularly from the left (L) and right (R) 10-3 giant cercal interneurons. Black trace shows the synchronous response when 10-3L and 10-3R spikes occurred with less than 10 ms latency (width of individual black rasters is 10 ms). (g) Directional tuning curves based on synchronous firing rate for chosen pairs of cercal interneurons (10-3R and 10-3L, 10-2R and 10-2L). The synchronous firing is more narrowly tuned to specific wind stimulus directions than the responses from the individual GIs alone (compare (g) to (e)) and are thus more comparable to the narrowly tuned behavior (compare (g) to (d); (f) and (g) adapted from [46^{*}]).

Santer *et al.* [32] studied tethered locusts walking on a ball. In this situation, locusts shown movies of looming objects perform pre-takeoff leg adjustments, but do not complete the final hind leg extension for the takeoff jump. Nevertheless, using simultaneous high-speed videography and extracellular recording, Santer *et al.* [32] were able to correlate DCMD responses with the timing of hind leg flexion. Ablating DCMD altered the flexion timing but did not eliminate it, suggesting that pathways beyond DCMD must be involved.

Recently, Harrison and colleagues [33–35,36**] have taken an impressive step towards neural recording in unrestrained insects. They developed a miniature telemetry system that uses custom-designed integrated circuits to transmit four neural or EMG signals and accelerometer output wirelessly to a remote receiver (Figure 2b). They employed this device to record DCMD, flexor, and extensor muscle signals, simultaneous with locust behavioral responses to looming stimuli [36**]. These are the first recordings of concurrent DCMD activity and unrestrained locust escape behavior. Fotowat *et al.* [36**,37] found that the different stages of the behavior correlate with different aspects of DCMD's response, and they suggest that DCMD could be multiplexing information down to the motor centers. However, their results also indicate that other descending pathways must be involved, since ablation of DCMD did not eliminate jump responses. A candidate second pathway is the descending ipsilateral motion detector (DIMD), the counterpart of DCMD found in the ipsilateral nerve cord, which has near identical looming responses to those of DCMD [36**]. Gray *et al.* [38] have also found a novel descending interneuron, LDCMD, which responds robustly to looming stimuli. Similar to DCMD and DIMD, LDCMD firing rate increases to a peak as a looming object expands on the animal's retina. However, LDCMD peak firing occurred later than the peak for DCMD and DIMD (7 ms later in the case of a 1 m/s object approach) and LDCMD conduction velocity was slower than DCMD's, suggesting that LDCMD is a smaller diameter axon. It is thus likely that the visual information triggering the locust escape jump is distributed across at least three different descending pathways, including DCMD, DIMD, and LDCMD (Figure 2a,c), though their precise roles in the escape behavior remain to be elucidated.

Coding in the cricket cercal system

Distributing sensory information across multiple pathways is well established in other insect escape circuits, such as the Orthopeteran cercal system. In this case, wind-sensitive hairs on two posterior abdominal appendages, the cerci, activate primary sensory neurons that make monosynaptic connections with a handful of giant interneurons (GIs) in the animal's abdominal ganglion (see [39] for a recent review). These sensory organs allow

the animal to detect air movement resulting from an approaching predator and make a directed escape turn and run [40–42]. However, it has long been a matter of some speculation how these GIs encode a directional motor command. The escape behavior is tightly oriented directly away from a wind source (Figure 2d) [10,41], whereas the GIs are each broadly tuned and respond to a wide range of wind directions (Figure 2e) [39,43]. This tuning mismatch makes infeasible a simple command line architecture, in which maximal firing of a single GI causes an appropriately directed turn. Instead, GI activity likely provides a population code for wind direction [44,45], which then must be read out by the motor system to implement an appropriate turn. Recent work by Yono and Shimozawa [46*] suggests what that code might be. Simultaneous recordings reveal that certain GI pairs fire synchronously only in response to a specific direction of wind stimulation (Figure 2f) [46*]. The directional tuning of the synchronous responses is much narrower than that of individual GIs (compare Figure 2e and Figure 2g). Furthermore, they speculate that the clusters of wind directions, relative to the cricket's body axis, that produce synchronous activity may correspond to the clusters of escape directions that crickets use most commonly.

A paired synchrony code could be even faster for the motor system to read out than a command line system. If direction is signaled by increased firing rate in a particular neuron, that neuron's output must be sampled over some time window to determine if the rate has increased. With paired synchrony, however, synchronous spikes in two particular GIs instantly convey the direction of the threat. A paired synchrony code also enables GIs to multiplex information about both wind direction and intensity; neural synchrony can specify wind direction, while firing rate of individual GIs represents stimulus intensity [46*].

Conclusions and outlook

Examining insect escape behaviors in a natural context has exposed more behavioral and neural complexity than previously appreciated in insect escape circuits. Similar observations have been made in other phyla, such as the crayfish [47].

On the behavioral side, escape from looming predator-like objects consists of a sequence of escape sub-behaviors that confer flexibility on the escape program, including the ability to control escape direction without compromising reaction time. On the neural side, experiments with naturalistic stimuli and telemetry technology suggest new ideas for how the observed behavioral flexibility could be implemented by these insect nervous systems, including novel descending pathways, and information encoding strategies such as multiplexing or paired synchrony.

The visual-looming and wind-sensitive escape circuits discussed here have in common the involvement of large-axon giant interneurons (GIs, with the possible exception of *Drosophila* in the stimulus regime evaluated), which provide a direct conduit between sensory and motor areas. The systems may differ, however, in the function of the GIs with respect to oriented escape behavior: GIs involved in looming responses, such as in locust, encode information about the size and speed of the approaching object and whether the object is on a collision versus passing course with the animal [48]. However, DCMD responses differ only subtly to looming from different azimuthal directions [49]. Conversely, the GIs of the cercal system robustly encode the direction of a wind stimulus. This suggests that the circuit elements encoding directional information about looming stimuli may have yet to be discovered.

Insect escape responses represent one of the few systems that connect quantified natural behavior with identified neural circuitry. Recent technological advances take the system a tantalizing step further—enabling electrophysiological recordings from individual neurons during free behavior. Insect escape responses are thus a powerful system for exploring the neural basis of sensory motor transformation and neural circuitry mediating behavior.

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