Target detection in insects: optical, neural and behavioral optimizations
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Motion vision provides important cues for many tasks. Flying insects, for example, may pursue small, fast moving targets for mating or feeding purposes, even when these are detected against self-generated optic flow. Since insects are small, with size-constrained eyes and brains, they have evolved to optimize their optical, neural and behavioral target visualization solutions. Indeed, even if evolutionarily distant insects display different pursuit strategies, target neuron physiology is strikingly similar. Furthermore, the coarse spatial resolution of the insect compound eye might actually be beneficial when it comes to detection of moving targets. In conclusion, tiny insects show higher than expected performance in target visualization tasks.

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Introduction
Many animals, including ourselves, use visual information to perform crucial tasks. Besides stationary cues, such as an object’s color and brightness, motion vision also provides vital information. Motion vision can be broadly subdivided into widefield optic flow, which is generated by the observer’s own movements, and the motion of objects that move independently of the background. For example, when playing basketball (Figure 1), running across the court generates widefield optic flow, whereas the ball displays a type of independent object motion.

Large moving objects are often referred to as figures [1] and small ones as targets [2*]. We here propose that the term target be exclusive for objects that move independently of the background and which are actively pursued with mating, defensive or feeding purposes, such as prey chased by predators or a ball pursued by basketball players (Figure 1). The term figure should be used for other objects towards which the observer displays attention, such as the backboard in Figure 1, or for course stabilization or landing in insects. Thus, although targets are usually small and fast and figures are usually large and slow, it is the observer’s perception of the object and the behavior it triggers that is important for the stimulus distinction, not its physical attributes. Subsequently, depending on an animal’s internal state, the same physical object could be perceived as a figure or as a target, as recently shown in zebrafish [3].

Although modern humans use the ability to detect moving objects in sports (Figure 1), in nature it is needed for survival. For example, insects rely on target detection for avoiding predators [4], visualizing prey [5] or identifying conspecifics [6]. Since insects are small and many of them fly, which is energetically expensive [7], they suffer strong evolutionary pressure to keep their mass down, including that of their eyes and brain [8]. Thus, the morphological, neural and behavioral adaptations to specific visual tasks found among insects can teach us about design optimization, and especially how size constraints affect visual processing. In this review we focus on visual target detection as optic flow and visual course control have recently been extensively and excellently reviewed [9–11].

What is a suitable target?
Predatory insects need to determine whether a target is suitable, that is, whether it is small enough to eat and close enough to catch. Many predatory insects are generalist predators, including killer flies [2**], dragonflies [5], tiger beetles [12] and praying mantises [13**]. As generalists, they do not have sharply defined prey size preference [2**,13**], but at least dragonfly prey capture success and efficiency decreases when prey size increases [5]. Furthermore, since the aim is to catch food, pursuit probability is strongly modulated by metabolic state and, for example, killer flies only chase artificial prey (beads) if starved [2**].

Determining the distance to and the size of a target is difficult when equipped with a small head and a compound eye with poor spatial resolution, as this limits the
power of stereo vision, while the motion of the target limits the usability of motion parallax [14]. It is not surprising then that killer flies cannot estimate absolute prey size before take-off, and instead use the ratio between the prey’s angular speed and angular size as a loosely matched filter [2**]. However, miniature robber fly opties have the potential to allow stereo vision up to 30 cm distance [15] and mantises successfully use stereo vision to determine striking distance [13**]. Sun beetle larvae appear to calculate target distance from monocular cues [16], showing that binocularity is not a requisite, potentially using a multi-retina target detection mechanism [177].

Although predatory insects respond optimally to small, rapidly moving targets as these are likely to represent walking or flying prey [2**,5,15,18**], prey insects typically escape from larger object motion, which likely represents an approaching predator [4,19]. Non-predatory insects, such as blowflies and hoverflies, mainly utilize target detection to visualize conspecifics [6,20]. Since the size of a conspecific is known, and its velocity distribution is constrained [21], these parameters can be hardwired into a neural ‘matched filter’ [22], allowing high detection probability [23].

**Pursuit strategies**

Once a suitable target has been identified it needs to be brought into contact range. A simple method is for the pursuer to align its heading with the line of sight [24], also referred to as the range vector [18**], which is the straight line between the pursuer’s eye and the target (Figure 2a). This navigational strategy is referred to as classical, simple, or smooth pursuit (Figure 2d, [20,24]), and relies on the pursuer being able to outrun the prey, as its path will tend to be longer [25]. The alternative is interception, or parallel navigation (Figure 2e,f), where the pursuer aims its heading towards the target’s future location [24,26]. As prey could move erratically [27] the pursuer must display a fast reaction time, either to minimize the error angle for smooth pursuit (ε, Figure 2a,e), or to keep it fixed for interception (β, Figure 2a,e). Such closed-loop feedback mechanisms continuously update the flight trajectory to minimize delays between error and correction, which otherwise lead to tracking instabilities and overcompensation [28]. Delays of 20 ms have been described for male hoverflies following females [29], 28 ms for tiger beetles chasing prey [12], and 25 ms for dragonfly head movements [30].

Corrective head movements are important as the pursuer’s pitch and roll maneuvers could cause extensive retinal target movement, making it hard to perform appropriate compensatory turns. Dragonflies [18**,31] therefore stabilize their gaze towards the target in flight, rotating their head via neck muscles against the body axis. Note, that in dragonflies internal models may be in place, since this delay has been reported to be as brief as 4 ms [18**].

One method of error minimization used in both smooth tracking and interception is proportional control [24] in which corrective turns are in proportion to the magnitude...
of the heading error (Figure 2c). Tiger beetles, houseflies and hoverflies may add an additional derivative element (i.e. target angular speed) into the proportional control pursuit [12,21,25]. If the target displays constant heading and speed, proportional navigation in interception is achieved by holding the error constant (ε, Figure 2e), hence termed the constant error model [18**,32,33]. However, once the prey changes its speed or direction in response to the approaching predator [27], the pursuer must compensate, by for example, fixing the line of sight at a constant angle relative to an exocentric axis (β, Figure 2f). This is termed constant bearing or constant absolute target direction [30,34], results in parallel navigation, and is exhibited by robber flies [15]. From the perspective of the target, the pursuer’s image is seen as a looming stimulus lacking independent lateral translation, thus concealing it via motion camouflage [24,33].

Neural circuits for target motion

Parallel processing channels in the optic lobes separate optic flow and target detection, with physiologically similar lobula plate widefield motion detectors in evolutionarily distant moths [35] and flies [9], and lobula small target motion detectors (STMDs) in hoverflies and dragonflies [36]. Target driven steering is likely mediated by target selective descending neurons (TSDNs), 8 pairs of which code directional retinal target motion in dragonflies [37]. Dragonfly STMDs are only excited by moving dark targets and not by otherwise identical leading or trailing
Neural responses to biologically relevant target motion. (a) Dragonfly STMDs are tuned to the motion of dark targets and give no response to otherwise identical leading or trailing edges, to a dark target followed by an even darker edge, or to a bright target against a dark background [38]. (b) Optic-glomeruli interneurons, OGINs, are excited by target motion (top panel). If the fruit fly performs a saccade that would generate retinal motion of a stationary target, the OGIN is instead inhibited (bottom panel) [40].

Spatial performance and target detection by compound eyes

For a given size, the static spatial resolution of an insect compound (Figure 4a) is far inferior to that of a camera type eye (also called a chambered type eye or single lens eye), therefore often viewed as suffering from a fundamental design flaw (e.g. [41]). However, the compound eyes of adult insects must have been subject to natural selection for millions of years, supported by a recent finding of a diurnal predator with compound eyes from the Jurassic period [42]. Moreover, a departure from the compound eye, although relatively uncommon, is possible. Indeed, while many insect larvae evolved chambered eyes from compound ones, adults of the same species did not [43], and a parasitic insect harbors an intermediate form between a compound and chambered type eye [44].

Modeling shows that systems that copy the compound eye anatomy benefit from the extended visual field without spherical aberration (see [45,46]) and simple motion correlation across sampling ommatidia can help detect objects that are not salient against a cluttered background (Figure 4b). Indeed, the dipteran compound eye displays other properties that could improve target detection, such as retinal micro saccadic movements that can improve spatial resolution 40 fold (Figure 4d, [47,48]). In addition, the photoreceptor signal summation of the fly neural superposition eye displays a slight photoreceptor axis misalignment, which could help localizing objects smaller than the interommatidial angle (Figure 4c, [49]). Furthermore, an intrinsic compound eye property is image blurring by the overlapping fields of view of individual detecting units, each shaped as an Airy disk due to the
Compound eye optics and optimization for target detection. (a) Compound eyes have a lens over each functional sampling unit. When the target (Wikimedia commons license) is close by, many such ‘pixels’ cover it, but when the target is far away and contrasted against the sky, it may be seen as a single, darker pixel (Mosaic Maker, [http://damienclarke.me/code/mosaic-maker](http://damienclarke.me/code/mosaic-maker)). (b) In motion correlation targets moving in clutter are detected by simple background subtraction. (c) The dipteran neural superposition eye sums information from photoreceptors under different lenses, with visual axes that are almost, but not perfectly aligned (redrawn from [52]). This slight misalignment can be used for static hyperacuity [49]. (d) Retina microsaccadic movements move the photoreceptors independently of the lenses (redrawn with permission from Adam Tofilski, [www.honeybee.drawing.org](http://www.honeybee.drawing.org)) and provide the insect with motion hyperacuity [47,48]. (e) The overlapping receptive fields of neighboring ommatidia have an Airy Disk shape, which pre-blurs the image and produces static and motion hyperacuity [50].

small lenses. Despite its counterintuitive notion, pre-blurring may improve target detection of artificial compound eyes (Figure 4e, [50]). Finally, it is likely that acceptance angles that are larger than the preferred target are optimal, since a target that expands several ommatidia produces lateral inhibition in STMDs [36], and higher spatial resolution adds energetic costs [8]. Taking the above into consideration, it is thus not surprising that targets smaller than the interommatidial angles are detected by, for example, killer flies and black flies (behavior [27]), hoverflies (neuronal [51]), and robber flies (behavior [15]).

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References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest


This paper shows that tiny killer flies cannot determine absolute target size before take-off, but instead successfully use the ratio between the...
target’s angular subtense and its angular speed. By keeping this ratio close to 0.27 the killer flies in effect create a loosely matched filter to their common Drosophila prey, while still allowing capture of other prey species. This is confirmed in the field and by using artificial prey (beads) of different sizes.


In this wonderful study the authors use tiny 3D glasses fitted to praying mantises to show that they use stereo vision to determine if a potential target is within striking distance. Indeed, if the target is 2-3 times too far away, the mantis will still strike if the 3D glasses create the illusion of the target being close. Even if stereovision has been suggested for mantises before, this is the first time that it was conclusively shown, in an applaudingly convincing way.


As all predators, diving beetle larvae need to assess the distance to their prey. The authors have previously shown that the larvae strike at artificial prey without the use of motion parallax, knowledge of prey size, or binocular information. Here they elegantly show that the retina is divided into two parts, one optimized for viewing at a distance and one for near vision. Using a bifocal lens the larvae can then shift the image across retinal layers to successfully determine prey distance.


Dragonflies have long been the preferred species for studying insect target pursuit, with a solid foundation coming from Olberg’s pioneering studies. However, whereas dragonflies were previously described as using a closed-loop interception style pursuit, this study shows that the delays are too short (3-4 ms) for an external mechanism to function, and it is instead suggested that dragonflies use internal models based on initial conditions. The study was enabled by the development of amazing technology, allowing sub-millisecond resolution.


Fruit flies are typical prey animals, and have therefore evolved fast evasive sensory reflexes to avoid aerial predators. The authors use an elegant combination of high-speed filming, automated tracking and flapping robots, to show that the fruit flies evade predators using directed banked turns. The evasive maneuvers are extremely fast, far quicker than previous descriptions, suggesting that the fruit fly sensory-motor reorientation circuitry allows direction changes within a few wingbeats.


Insects display a strong optomotor response, similar to the human optokinetic reflex, in which visual stimuli moving in one direction create a motor-turn in the opposite direction. Since this would in effect work against voluntary turns, efference copies that supress the perception of self-generated visual motion have been suggested to be fundamental. In this beautiful study, the authors for the first time show direct electrophysiological evidence that such efference copies exist in the fruit fly visual system, both in classic neurons responding to widefield optic flow, and in newly described target sensitive neurons.


