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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

Figure 1

Current Opinion in Neurobiology

What is a target? The figure (https://it.wikipedia.org/wiki/Monta_Ellis) illustrates the terminology where we separate optic flow (black), generated by the observer's own motion, from independent object motion. A target is an object that moves independently, and which the observer actively pursues (such as a ball, yellow). Figures are objects towards which the observer displays attention, such as other moving players (blue) or the stationary backboard (red).

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 optics 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 [17•].

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

Figure 2
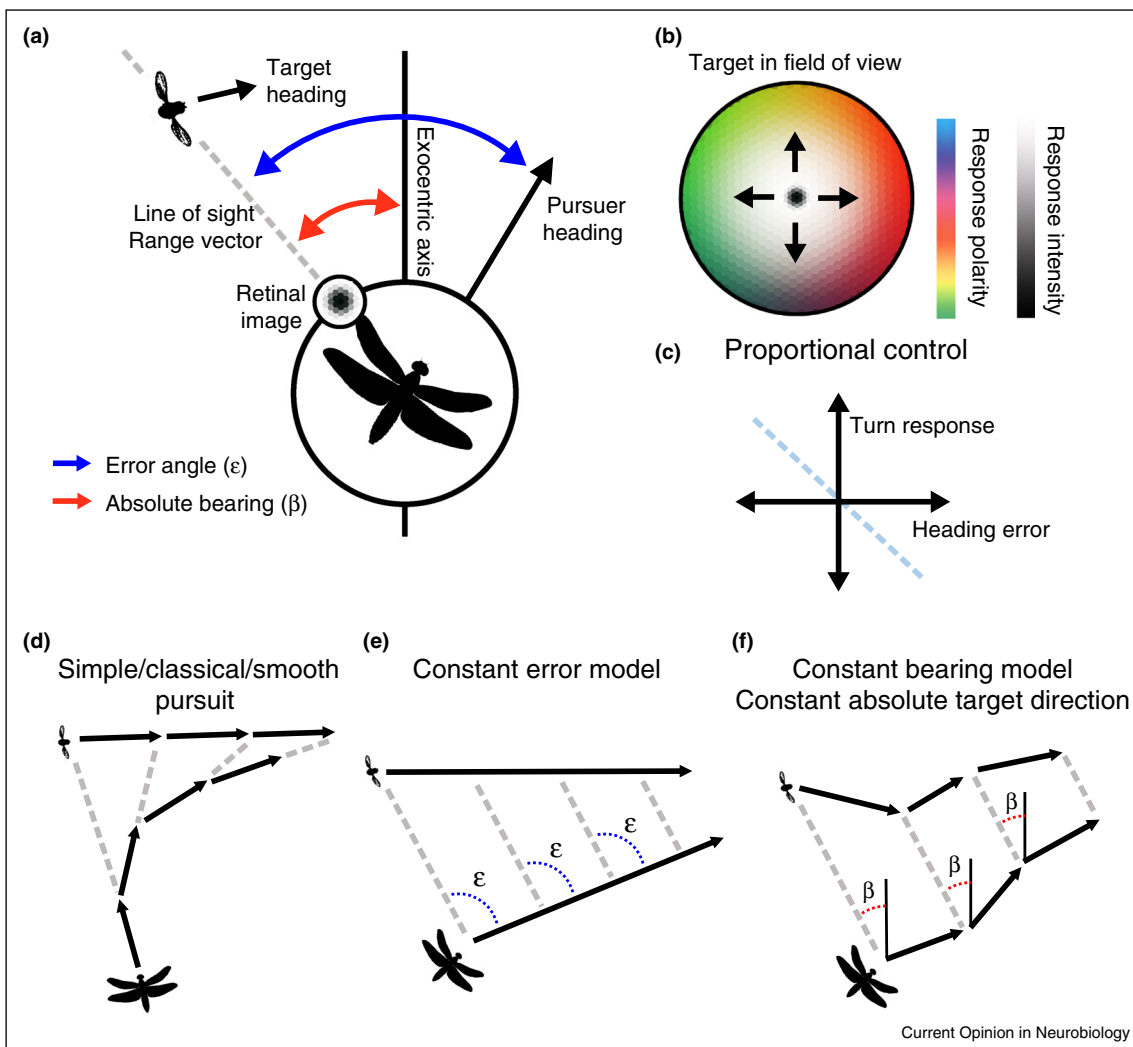
Target pursuit modes. **(a)** Summary of the terminology. **(b)** The target's position in the pursuer's field of view affects its response, such as turning direction and response intensity. **(c)** Proportional navigation is where changes in either the pursuer's forward or angular velocities are proportional to the size of the heading error. **(d)** In simple pursuit the pursuer aligns its axis directly towards the target's current position. (e and f) During interception, or parallel navigation, the pursuer heads towards the target's future position. **(e)** One way is to keep the error angle (ε) constant. **(f)** Alternatively, the absolute bearing angle (β) is held constant against an external reference point.

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

Figure 3
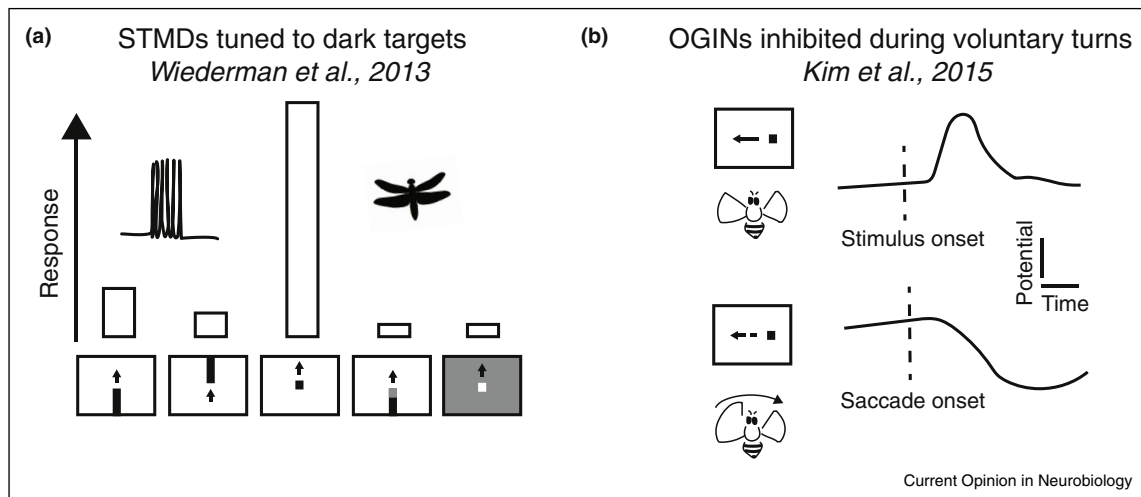
Neural responses to biologically relevant target motion. **(a)** Dragonfly STMDs are tuned to the motion of dark targets and give no response to otherwise identical leading or trailing edges, to a dark target followed by an even darker edge, or to a bright target against a dark background [38]. **(b)** 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••].

edges, or by bright targets (Figure 3a, [38]). This makes neuroethological sense since dragonflies aim to contrast prey against the sky [31]. Killer flies, however, attack white flies and dark fungus gnats against both dark and light backgrounds [2••], suggesting that there must be tweaking of their target detection circuitry compared with dragonflies. Dragonfly STMDs temporally correlate a dark contrast change followed by a bright contrast change [38], as when a dark target traverses a bright background (Figure 3a). This could be enabled by the parallel peripheral OFF and ON channels that have been described in *Drosophila* [9]. By instead correlating ON with a delayed OFF input, killer flies could theoretically generate target sensitivity to bright targets, but confirmation still awaits.
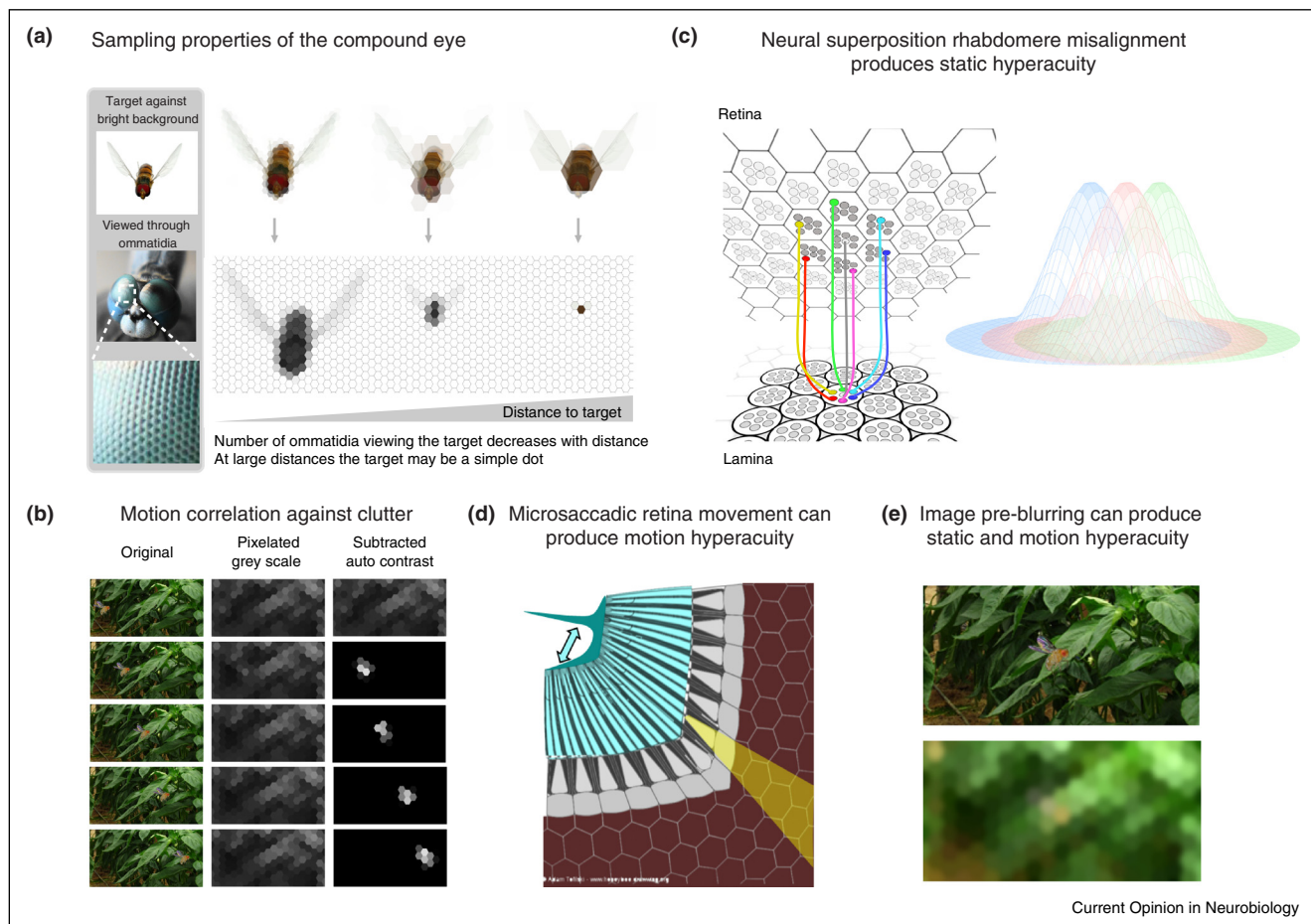
A well-known issue in visual coding is that when turning stationary features in the surround move across the retina (bottom panel, Figure 3c). Such retinal motion should be ignored during voluntary turns, via for example, an *efference copy* [39], but until recently direct evidence has remained scarce. Recent data show that the speed of corrective head movements in dragonflies (ca. 4 ms) are consistent with the presence of an efference copy [18••]. The second, more direct example, comes from recently described fruit fly optic-glomeruli interneurons (OGINs), which respond with a strong depolarization to object motion (top panel, Figure 3c) across a large part of the visual field [40••]. OGINs are suppressed by a hyperpolarizing input during intended turns (bottom panel, Figure 3c, [40••]), thus providing direct electrophysiological evidence for an efference copy. It will be exciting to see if efference copies in more vicious predators show faster inhibition dynamics.

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

Figure 4

(a) Sampling properties of the compound eye

Target against bright background

Viewed through ommatidia

Distance to target

Number of ommatidia viewing the target decreases with distance
At large distances the target may be a simple dot

(c) Neural superposition rhabdomere misalignment produces static hyperacuity

Retina

Lamina

(b) Motion correlation against clutter

Original | Pixelated grey scale | Subtracted auto contrast

(d) Microsaccadic retina movement can produce motion hyperacuity

(e) Image pre-blurring can produce static and motion hyperacuity

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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). **(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.drawwing.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 [2••]), hoverflies (neuronal [51]), and robber flies (behavior [15]).

Conflict of interest statement

Nothing declared.

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Papers of particular interest, published within the period of review, have been highlighted as:

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