Prey pursuit and interception in dragonflies

Abstract  Perching dragonflies (Libellulidae; Odonata) are sit-and-wait predators, which take off and pursue small flying insects. To investigate their prey pursuit strategy, we videotaped 36 prey-capture flights of male dragonflies, Erythemis simplicicollis and Leucorrhinia intacta, for frame-by-frame analysis. We found that dragonflies fly directly toward the point of prey interception by steering to minimize the movement of the prey’s image on the retina. This behavior could be guided by target-selective descending interneurons which show directionally selective visual responses to small-object movement. We investigated how dragonflies discriminate distance of potential prey. We found a peak in angular velocity of the prey shortly before take-off which might cue the dragonfly to nearby flying targets. Parallax information from head movements was not required for successful prey pursuit.

Key words  Dragonfly · Prey capture · Insect vision · Flight · Visual pursuit

Abbreviations  TSDN target-selective descending interneuron · $\theta_E$ error angle · $\theta_A$ absolute angle

Introduction

Visual detection, localization, and interception of moving objects in space requires highly sophisticated visual systems found only among arthropods, mollusks and chordates. A superb example of visually guided interception is the capture of flying insect prey by dragonflies. Dragonflies of family Libellulidae are, for the most part, sit-and-wait predators, perching on the ground or on vegetation and periodically taking off after small insects as they fly by. Once in flight, dragonflies swoop upwards from underneath their flying prey, grabbing the prey with their outstretched legs. They are very effective predators, with capture rates as high as 97% (this study). Our research is aimed at determining the neural basis of this rapid and highly accurate, visually-guided behavior.

In dragonflies, visual information about moving objects such as flying prey is transmitted from the brain to the thorax by a small group of identified interneurons. We have found eight bilateral pairs of large, feature-detecting interneurons, called target-selective descending neurons (TSDNs) which project to the thoracic ganglia from the brain (Olberg 1981, 1986; Frye and Olberg 1995). TSDN-receptive fields are located in the forward and upward quadrant of visual space, i.e., in the direction of the prey immediately before capture. Two TSDN pairs, with receptive fields along the visual midline, are highly selective for small (1–4°) objects. The remaining six pairs, most with larger receptive fields, respond over a wide range of object sizes. All but one pair are strongly directionally selective. Electrical stimulation of individual TSDNs is sufficient to produce steering movements of the outstretched wings (Olberg 1983). Thus, TSDNs probably function in steering flight toward moving objects, such as prey.

How can a small group of interneurons direct a complex and highly precise behavior such as prey pursuit? To answer this question we need detailed knowledge of the behavior itself.

Interception of moving objects using visual cues is a behavior which has been studied in variety of animals, including humans. Collett and Land (1978) described two alternative strategies which might be employed to catch a flying insect, which they describe as “tracking” versus “interception”. In the first strategy, tracking, the pursuer aims at the perceived location of the target, i.e.,
it steers to minimize the deviation of the image of the object from straight ahead. If the pursuer flies faster than the pursued, this strategy will lead to a spiraling flight track ending in capture (Fig. 1a). Most insects which have been studied use this simple strategy to pursue moving objects, whether those objects are conspecifics (Land and Collett 1974; Wagner 1986; Land 1993a, b), prey (Gilbert 1997), or other objects (Zhang et al. 1990), and whether the objects are in the air or on the ground. In the second strategy, interception, the pursuer flies in a relatively straight line which intersects the projected flight path of the target (Fig. 1b). Male hoverflies (Eristalis or Volucella) exhibit an interception flight path in their pursuit of females. Rather than aiming at the female’s current position, the male hoverfly aims at a point in front of her, flying along a relatively straight course which will intersect her flight path. The algorithm used by the male for interception requires a female target of a known size and flight speed (Collett and Land 1978).

How do dragonflies approach their prey? In an attempt to learn more about this behavior we videotaped dragonfly prey-capture flights in the field for frame-by-frame analysis of their flight tracks. Our analysis of these flight tracks was aimed at answering several questions. Does the dragonfly direct its flight toward the position of the prey or does it intercept the prey? What visual signals of prey position and movement does the dragonfly receive and how does it respond to those signals during the pursuit flight? We found that, like male hoverflies, dragonflies intercept flying insect prey, even though, unlike female hoverflies, that prey varies in size and flight speed. We offer a simple hypothesis as to how dragonflies manage to intercept their prey.

**Materials and methods**

We analyzed 36 prey-capture flights of male Erythemis simplicicollis and Leucorrhinia intacta, sit-and-wait predators which take off after passing prey. Prey-capture flight sequences were recorded on a Panasonic S-VHS Camcorder AG-450 along the shore of a nearby lake (Collins Lake, Scotia, N.Y.) or along an abandoned canal site (Vischer’s Ferry, Clifton Park, N.Y.) between the hours of 11:00 a.m. and 5:00 p.m. Our best results came from sunny, windless days. Small flying insect prey were often visible as white dots against the relatively dark background of distant vegetation. However, in some cases we placed a 1-m² piece of black cloth on a wood frame behind the foraging dragonfly, allowing us to see prey items more easily. Video sequences were replayed through a Panasonic AG-7350 editing deck and captured field-by-field (60 fields s⁻¹) on a Power Macintosh 8500 with video card, using Adobe Premiere software. Individual fields were transferred to graphics software files (Adobe Photoshop or Aldus Superpaint) for reconstruction of the flight tracks and for measurement of angles and distances.

In our analysis we were able to obtain the following information:
1. The coordinates of the dragonfly and the prey.
2. The error angle of the dragonfly (θ₂). This was defined as the angle between the longitudinal axis of the dragonfly and the line drawn from the center of the head of the dragonfly to the prey (Fig. 3a).
3. The absolute angle of the prey (θ₁). This was defined as the angle between the line drawn from the center of the head of the dragonfly to the prey position and a horizontal line (Fig. 3b).
4. The distance between the dragonfly and prey. Because the distance from the camera to the dragonflies varied, we used the following procedure to estimate distance. We measured the greatest length of the animal as it appeared on the tape. We then defined that number of pixels as equal to the average length of the males of the given species, values obtained from Needham and Westfall (1975). Actual distances may have been less because the axis of the dragonfly may never have been precisely in a plane perpendicular to the axis of the camera. However, true distances may also have been greater because the dragonfly and the prey were seldom precisely in the same plane and we could not take the third dimension into account.

To study head movement before prey pursuit, we filmed separate, close-up videos of the head of perched and actively foraging Sympetrum vicinum, Pachydiplax longipennis, L. intacta, and E. simplicicollis (64 events recorded).

**Results**

To understand the role that the TSDNs might play in prey pursuit, we videotaped 36 prey-capture flights of male dragonflies, E. simplicicollis and L. intacta (family Libellulidae), for frame-by-frame analysis (60 fields s⁻¹, 16.7-ms resolution). Of these flights, 35 (97%) ended in successful captures, judged by obvious chewing motions after the return to the perch. Only video segments of L. intacta (n = 19) were used for analysis of prey behavior before the dragonflies began pursuit. The observed prey-capture flights were brief (mean prey pursuit duration = 184 ms, SD = 73 ms, n = 28).

Prey-pursuit flight tracks

Our analysis of prey-capture flight tracks indicates that dragonflies intercept their prey, rather than steering