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Prey pursuit and interception in dragonflies

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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 · θ_E error angle · θ_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.,

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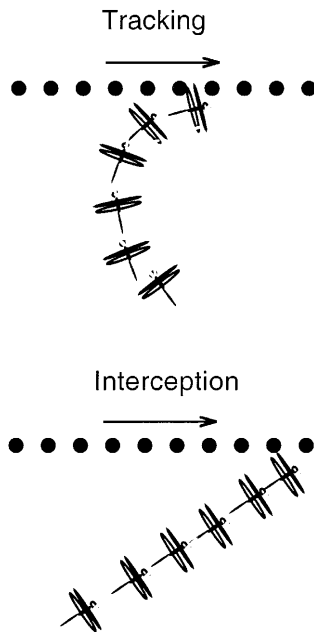


Fig. 1 Two alternative strategies to catch a flying insect, as described in text (after Collett and Land 1978)

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 (θ_E). 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 (θ_A). 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, actual 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*, *Pachidiplex 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

directly toward them in flight (Fig. 2). In no case did we observe the spiraling flight path which would indicate that the dragonfly is aiming at the prey's perceived position.

How do dragonflies steer a course that intercepts the prey's flight path? A simple strategy for steering an interception flight path is for the dragonfly to steer so as to maintain its prey at a constant retinal position. If the dragonfly's flight speed exceeds that of its prey, and if the prey's bearing is less than 90° from straight ahead, this strategy will always yield a collision course. Thus, we hypothesize that the dragonfly steers during pursuit to minimize drift of the prey image on the retina.

The above hypothesis predicts that if we measure the angle of the prey on the dragonfly's retina during pursuit (θ_E), that angle will be less than 90° from straight ahead, and that the angle will remain constant. To estimate the angle of the head, we extended a line through the abdomen, measuring θ_E relative to that line (Fig. 3a). That measurement, however, is based on the assumption that the dragonfly's head position is tightly coupled to its abdominal position, an assumption which is almost certainly not true. Therefore, we also measured θ_A , the angle from the dragonfly's head to the prey relative to the horizon (Fig. 3b).

Plots of θ_E and θ_A revealed that θ_A deviated far less than θ_E (Fig. 4). To quantify this we measured the average change in each of the angles during 13 prey-pursuit

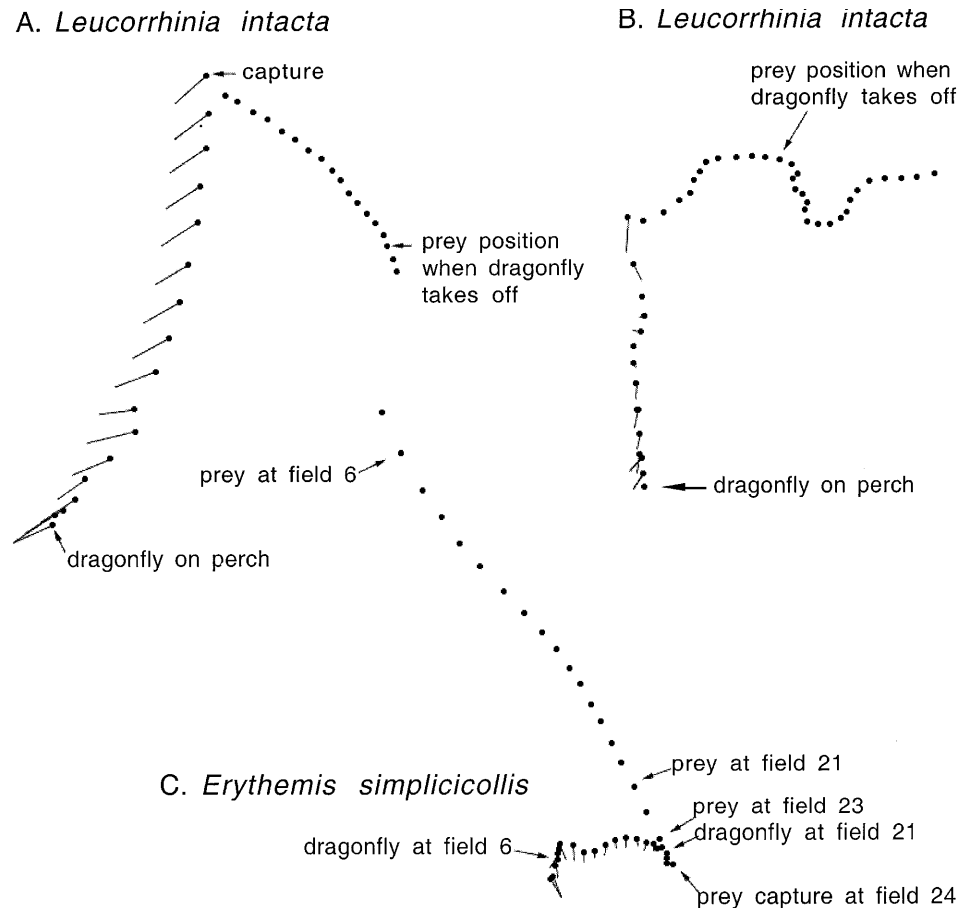
flights (we excluded the final field before prey capture in which very large angular changes were the rule as the dragonfly positioned itself to catch the prey). The average change in the θ_A per field was 2.8° , far less than the 8.0° average change in θ_E . These results suggest that, if the dragonfly is steering in flight to minimize retinal slippage of the prey image, the head is being rotationally stabilized with respect to the visual world.

Our data are consistent with the hypothesis that dragonflies intercept their prey by keeping the absolute angle to the prey constant, i.e., by steering flight to minimize drift of the prey image on the retina. This hypothesis implies that the pursuit flight is under the control of visual feedback, rather than being a ballistic act. A test of this prediction is to examine whether the pursuing dragonfly responds when the prey turns. We found that turns of the prey were generally answered by turns of the dragonfly with a latency of two or three video fields (33–50 ms, Fig. 5).

Estimation of prey distance

We do not yet know the basis for the dragonfly's decision to begin prey pursuit. The high success rate of foraging flights implies that the dragonfly must in some way estimate the distance of potential prey items. We did

Fig. 2A–C Three examples of prey capture flights. *Filled circles* indicate prey positions and *filled circles with tails* indicate dragonfly positions. *Arrows* indicate prey and dragonfly position at the start of the pursuit flight. Plotting interval: 16.7 ms. **A** *Leucorrhinia intacta*. Duration of prey capture flight = 283.3 ms (17 fields). **B** *L. intacta*. Duration of flight = 216.7 ms (13 fields). **C** *Erythemis simplicicollis*. Prey does not appear on video until field 5. Dragonfly is moving away from the camera. Last view of prey before capture is field 23. Duration of flight: 400 ms (24 fields)



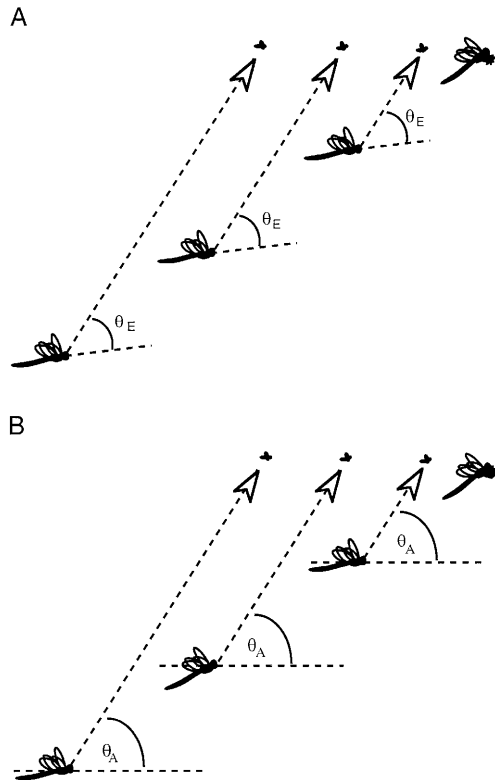


Fig. 3A, B Alternative hypotheses for producing interception flight tracks. **A** Steering to maintain a constant error angle (θ_E). Error angle is measured relative to the longitudinal axis of the animal. **B** Steering to maintain a constant absolute angle (θ_A). Absolute angle is measured relative to the horizon

not observe dragonflies taking off after distant, flying birds even though their angular subtense on the eye might well match that of a nearby dipteran. We considered two possible mechanisms for estimating prey distance: (1) use of motion parallax information produced by head movements; or (2) use of the time-course of the prey's angular velocity.

Head movements

Perching dragonflies often perform rapid head movements as flying objects pass by. In addition to head rotation, our videos reveal that these head movements have a large translational component, with contributions from the legs, from neck flexion, and from movement of the highly mobile prothoracic segment. Translational head movements are known to provide distance information in locust (Collett 1978). In the dragonfly, distance information provided by head movements, coupled with the visual angle of the object, could form the basis for the decision to take off. Our data, however, suggest that dragonflies do not require head movements to estimate prey distance. We analyzed head movements in 64 successful prey-capture flights in *L. intacta*, *E. simplicicollis*, *S. vicinum*, and *P. longipennis*. In 43 successful captures there were no prepar-

atory head movements before take off. In the other 21 successful captures, the latency from head movement to take off was highly variable (one to six video fields, 16.7–100 ms, before take-off).

Time-course of prey angular velocity

Distant flying objects such as birds or airplanes maintain a relatively constant angular velocity on the retina, and nearby flying objects display a sharp increase and decrease in angular velocity as they pass overhead (Fig. 6; in this illustration we have selected typical flight speeds for the bird and the insect). Although, by itself, the velocity profile does not uniquely specify the size and distance of a passing object, a “spike” in angular velocity could be a cue which alerts the animal to a nearby flying insect. We found a spike in angular velocity in each of the 18 flight tracks in which we could detect prey position for at least six fields before take-off (Fig. 7). In 15 of the 18 flights, the spike occurred at least 33 ms before take-off (mean time from peak to take-off = 71.3 ms, SD = 40.1 ms, $n = 15$).

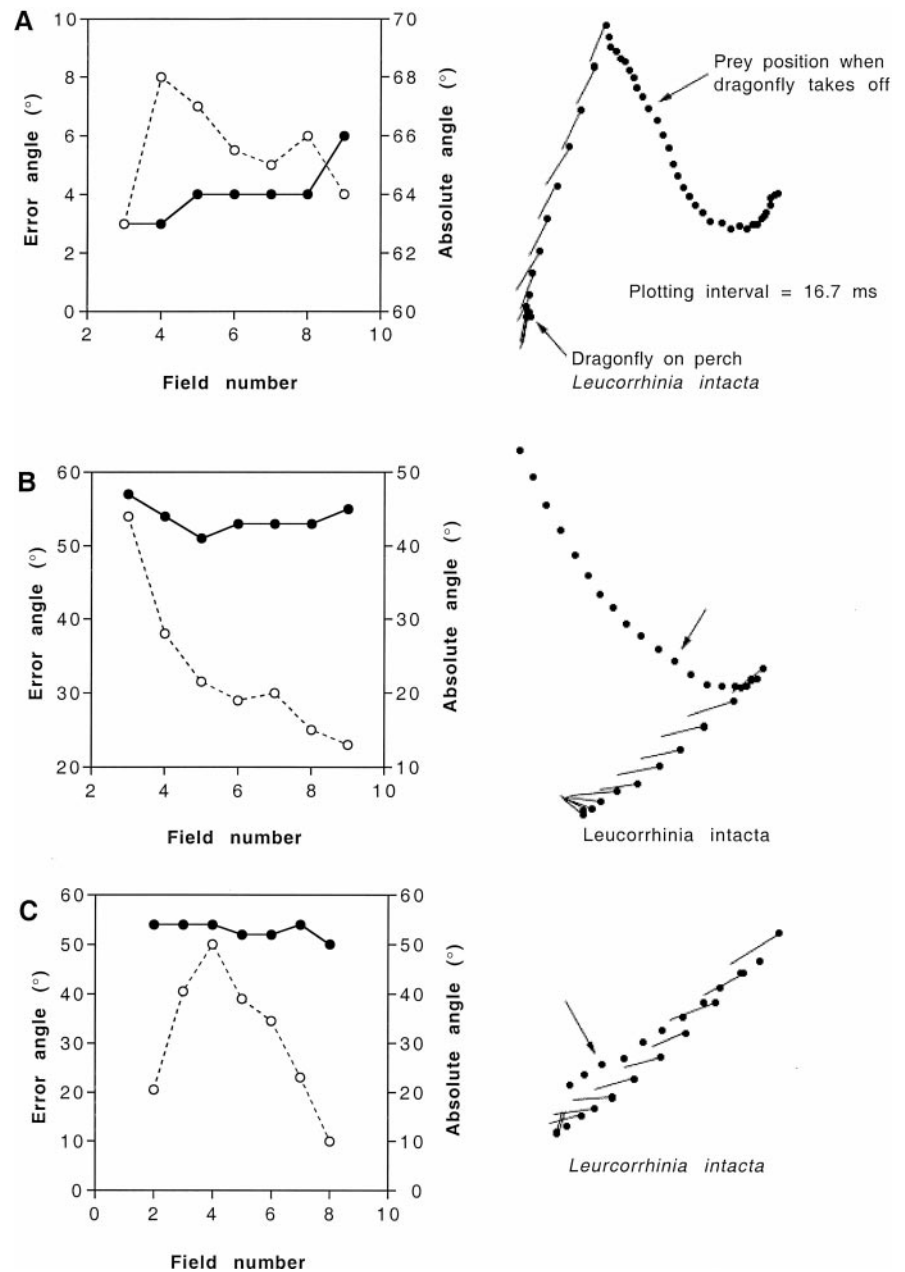
Discussion

Prey-pursuit flight tracks indicate that dragonflies intercept their prey in flight. In this way their pursuit strategy is different from that described for other insects, such as flies (Land and Collett 1974) and beetles (Gilbert 1997). In general these insects direct their chases toward the currently perceived position of their quarry. In contrast, dragonflies direct their flight paths to a point in front of the prey, predicting the flight path.

The interception strategy outlined here for dragonflies is analogous to that adopted by humans (baseball players) approaching a fly ball (McBeath et al. 1995). The fielders' tactic apparently consists of restricting retinal slip to an upwardly projecting straight line (McBeath et al. 1995). This strategy results in a curved path to the point of the catch. Outfielders are, of course, restricted to the plane of the ball field, whereas flying dragonflies operate in three dimensions. Therefore, dragonflies can steer to minimize retinal slip in all directions. If the prey flies in a straight line, this strategy results in a straight approach. This closed-loop strategy means that for both humans and dragonflies, the pursuer does not head for a known point of interception, but rather knows how to get to that point simultaneously with the arrival of the flying object. In humans, catching a flying object is clearly a learned strategy. In dragonflies the interception strategy is more likely “hard wired” into the nervous system. When the adult dragonfly first emerges from its aquatic nymphal world, it is able not only to take off and fly, but also to orient to objects in space, such as a convenient perch.

The appeal of our hypothesis of minimizing retinal slip in order to intercept flying prey is that it is well

Fig. 4 Analysis of absolute angles (*closed symbols*) and error angles (*open symbols*) to prey for three sample flights (A–C). Absolute angle is held more constant than the error angle during prey-capture flights



matched to the visual properties of the TSDNs, the neurons which probably guide prey pursuit. These neurons respond exclusively to the movement of small objects. TSDN receptive fields are large (Frye and Olberg 1995), making precise localization of the object unlikely. TSDN responses to object movement, however, are highly directionally selective (Olberg 1986). Thus, they are well suited for stabilizing prey images on the retina during pursuit.

Our video sequences have been exclusively from freely foraging dragonflies in the field. This approach has led to three major limitations in our study. The first is that we have resolved the prey-pursuit flights in only two dimensions, i.e., in a plane perpendicular to the axis of the video camera lens. We could only analyze flight

tracks in which the prey were visible because they flew roughly at right angles to the camera and at about the same distance as the dragonfly upon which the lens was focused. Thus, we cannot claim that our picture of the foraging flights is a complete one. However, the conclusions we have drawn have been consistent, whether they came from flights in which we had a sideways view or flights in which we had a longitudinal view. Clearly, however, our calculations of absolute and angular velocity represent minimal estimates of these values, and our angular measurements represent only the angles measured in the vertical plane upon which the three dimensional flight track is projected.

A second limitation in our study is that we could not resolve head position during prey pursuit. Our hypothesis

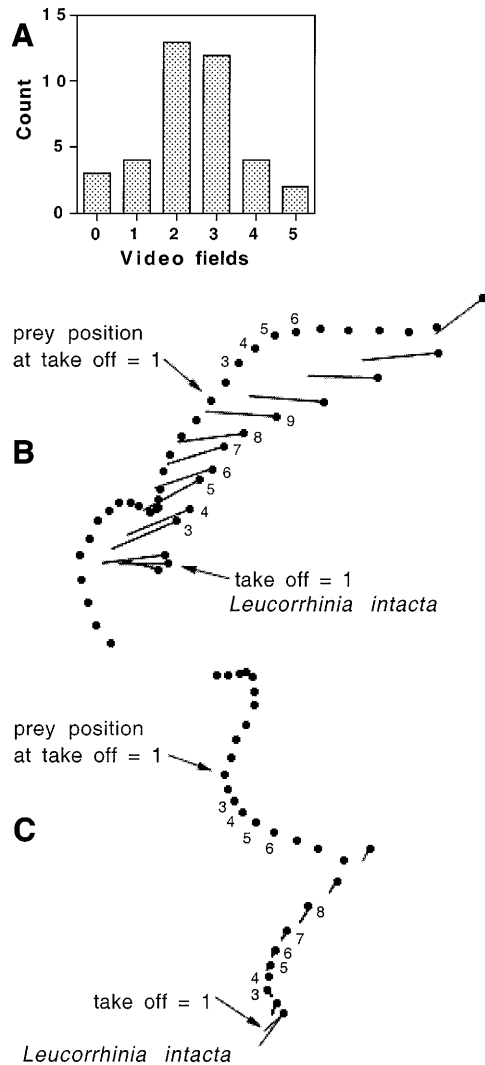


Fig. 5 **A** Time (video fields) elapsed for a dragonfly to change flight direction after the prey turns ($n = 38$ prey turns from 36 prey pursuits). We defined a turn in the prey or dragonfly flight as a point deviating from a line drawn through the three previous prey or dragonfly positions. **B** Example of response of the dragonfly to prey turns. In this flight track, the prey (filled circles) completes a turn from field 4 to 6. The dragonfly (filled circles with tails) responds to the turn at field 6 and completes the turn at field 8. This is a 33.3-ms (two video fields) turning latency. **C** Example of response of the dragonfly to prey turns. The prey completes a turn from field 2 to field 3 and from field 4 to field 5. The dragonfly responds to the first turn at field 4 and the second turn at field 6, each with a 33.3-ms turning latency

involves minimizing image drift on the retina. Clearly any rotation of the head will contribute to image drift. We found that absolute angle to the prey appears to be held constant while the error angle, as measured using the abdominal axis, changes. This suggests that the dragonfly stabilizes its head against rotation during the prey capture flight. Optomotor stabilization of the head rotational position is a common feature among animals with sophisticated visual systems. Head stabilization in the roll plane during flight has been demonstrated in a variety of insects including locusts (Hensler and Robert 1990), blowflies (Hengstenberg et al. 1986) and drag-

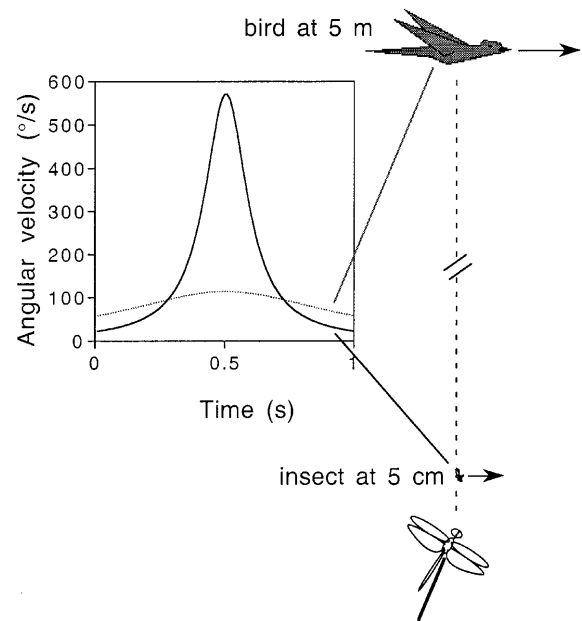


Fig. 6 A sharp rise and fall in angular velocity could be used as a cue to discriminate between nearby small objects (insects) and distant large objects (birds). Graph shows the angular velocity ($^{\circ} s^{-1}$) for a 2.5-mm insect, 5 cm away, flying at 50 cm s^{-1} and for a 25-cm bird, 5 m away, flying at 10 m s^{-1} . Each object makes a 3° visual angle on the retina of the dragonfly

onflies (Stange and Howard 1979). Furthermore a tethered dragonfly in flapping flight turns its head in the yaw and pitch planes also, to follow the rotation of a surrounding striped drum while it does not follow the movement of small dark targets on a white drum (Olberg 1978).

The third limitation in our study is our use of standard video format, which provides only 60 fields s^{-1} , to study a very high-speed behavior (mean duration 184 ms). With our temporal resolution of 16.7 ms, we are almost certainly missing important components of the behavior.

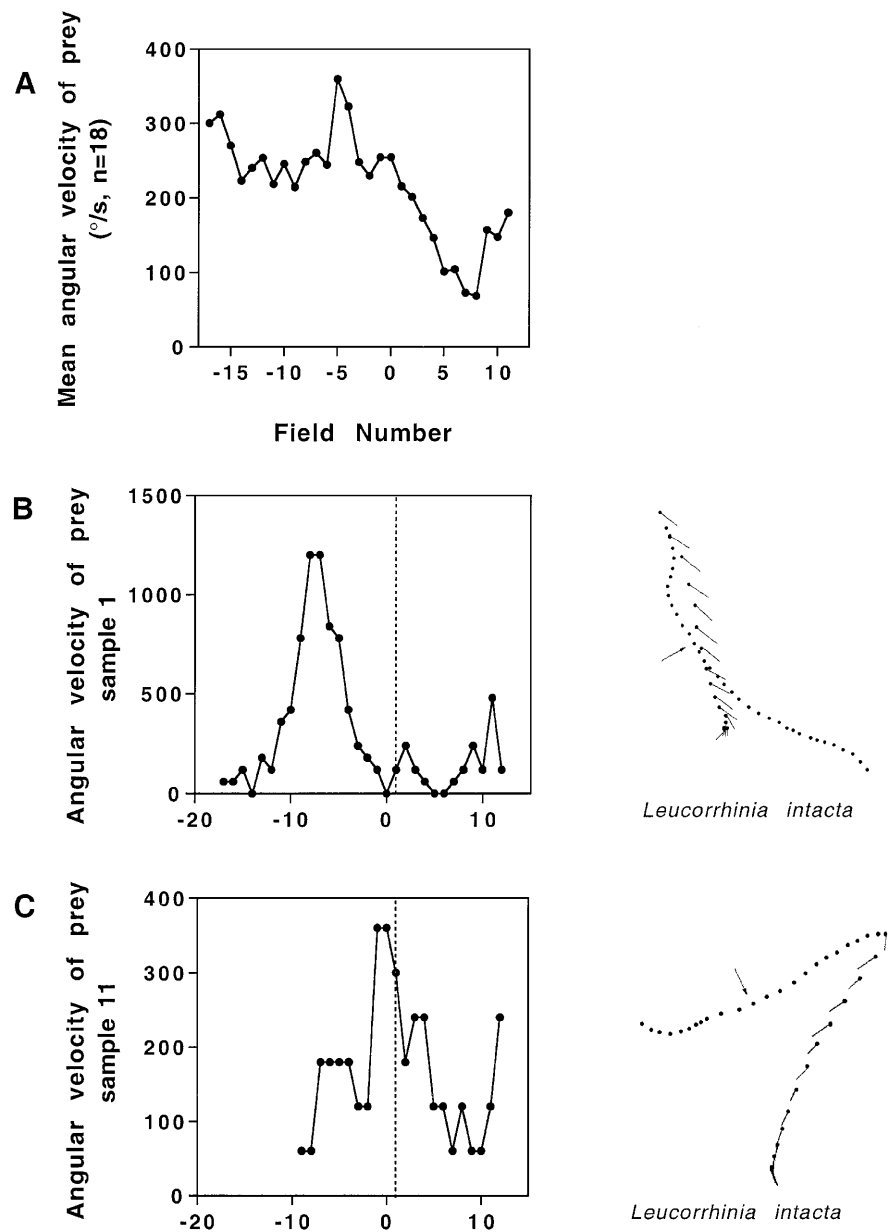
The above limitations point to the need to elicit prey pursuit in a controlled setting, using a stimulus that we can manipulate and high-speed video for greater temporal resolution. We are currently developing such a system, because it is prerequisite to performing an adequate test of our hypothesis for the mechanisms underlying prey pursuit.

The decision to take off after prey

Information about the distance of a passing flying object is critical to a foraging dragonfly. In its absence the dragonfly would take off after large, far-away objects as readily as to nearby small insects. The high foraging success rates which are reported here and elsewhere (Baird and May 1997) confirm that dragonflies do not make that mistake.

Motion parallax elicited by head movements could provide information about prey distance before take-off

Fig. 7A–C Angular velocity of the prey before and after take-off. Field 1 is always the first frame where dragonfly is off the perch, as represented by arrows in the flight tracks. **A** Mean angular velocity from 18 *L. intacta* flight tracks. **B** Angular velocity of prey in a single prey pursuit by *L. intacta* (sample 1 of the mean plotted in **A**). In this prey flight the angular velocity reaches a peak of $1200^{\circ} \text{ s}^{-1}$ at fields -6 and -7 , just as the prey passes over the perched dragonfly. *Dashed line* on graph and *arrow* on prey flight track indicate first frame after dragonfly leaves perch. **C** Angular velocity of prey in a single prey pursuit by *L. intacta* (sample 11 of the mean plotted in **A**). In this prey flight, the angular velocity reaches a peak of $360^{\circ} \text{ s}^{-1}$ at fields -1 and 0 , just as the prey passes over the perched dragonfly.



(Wallace 1959; Kirmse and Lässig 1971; Sobel 1990; Miller 1995). Such use of head movements to provide motion parallax for distance estimation has been demonstrated in grasshoppers (Collett 1978; Eriksson 1980), and in mantids (Rossel 1983; Walcher and Kral 1994). However, our study suggests that such movements are not required for the take-off decision. An alternative explanation for head movements is that they perform a preparatory function, serving to pre-align the head of the perched dragonfly with the target and in the intended flight direction.

Another possible distance cue available to the perched dragonfly is the time-course of the angular velocity of a passing object, as diagrammed in Fig. 6. Although the velocity time-course of a passing object does not uniquely specify its distance, within biologically rea-

sonable limits a nearby passing insect will produce much greater angular accelerations than a larger object such as a bird whose angular size matches that of the insect. The spike in angular velocity associated with the passage of the nearby insect could be a cue for initiating pursuit. This hypothesis can be tested by manipulating acceleration of a small object moved in a circular path around the dragonfly. Our hypothesis predicts that the dragonfly will take off after the object if acceleration and deceleration are added, but not if the object is moved at a constant velocity.

It seems likely that additional, as yet undescribed, mechanisms enhance the dragonfly's ability to estimate the distance of passing objects. Our recent recordings of TSDN responses at varying distances suggest that, near visual midline, the dragonfly may use the binocular

disparity of the images on the two compound eyes to determine distance (R.M. Olberg and L.M. Stanek, unpublished observations).

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