Eye movements and target fixation during dragonfly prey-interception flights

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Abstract The capture of flying insects by foraging dragonflies is a highly accurate, visually guided behavior. Rather than simply aiming at the prey’s position, the dragonfly aims at a point in front of the prey, so that the prey is intercepted with a relatively straight flight trajectory. To better understand the neural mechanisms underlying this behavior, we used high-speed video to quantify the head and body orientation of dragonflies (female Erythemis simplicicollis flying in an outdoor flight cage) relative to an artificial prey object before and during pursuit. The results of our frame-by-frame analysis showed that during prey pursuit, the dragonfly adjusts its head orientation to maintain the image of the prey centered on the “crosshairs” formed by the visual midline and the dorsal fovea, a high acuity streak that crosses midline at right angles about 60° above the horizon. The visual response latencies to drifting of the prey image are remarkably short, ca. 25 ms for the head and 30 ms for the wing responses. Our results imply that the control of the prey-interception flight must include a neural pathway that takes head position into account.

Keywords Dragonfly · Eye movement · Flight · Image fixation · Vision

Introduction

The interception of prey insects in flight is an essential element in the dragonfly’s behavioral repertoire. Dragonflies of the family Libellulidae spend much of their days perched, only taking off to capture small insects as they fly overhead. Remarkably, they do not fly directly towards their prey, but rather aim at a point in front of the prey, so that they intercept the prey with a relatively straight flight trajectory (Olberg et al. 2000). This interception strategy is highly successful; Baird and May (1997) reported a capture rate of 76% in their study of foraging females (Pachydiplax longipennis) and in our S-VHS video study of males of various Libellulid species foraging from pond’s edge we saw only a single miss in 38 flights, a success rate of 97% (Olberg et al. 2000). Prey capture flights are usually quite short, often less than 200 ms from takeoff to contact with the prey item. These short flights leave little time for evasion, and in our field studies we have never observed obvious evasive maneuvers by the prey insect.

Prey interception is guided by the visual system. Of special interest for this study is a distinct region of the compound eye, with ommatidial facets much larger than those in the rest of the eye, covering the dorsal surface of the eyes. Dominated by blue and UV photoreceptors (Labhart and Nilsson 1995), this region is well adapted for foraging on insects against blue sky. The dorsal ommatidial axes are nearly parallel, so that most of the dorsal surface of the eye is directed at very narrow upward and forward crescent, a “fovea” about 20° in height and intersecting visual midline about 60° above the horizon (Fig. 1). Within the dorsal fovea small inter-ommatidial angles (Sherk 1978) result in resolution of ca. 15 min of arc (or even less for moving objects, Rowe 1987)
In earlier work (Olberg et al. 2000) we proposed the following simple hypothesis to explain prey interception: during pursuit the dragonfly steers so as to maintain the prey at a constant bearing, resulting in a collision course with the prey. This interception strategy, termed “proportional navigation,” would allow the dragonfly to intercept prey without any information about the prey's distance. The strategy would only require steering to minimize retinal slip of the prey's image. Target-selective descending neurons (TSDNs) that could provide this control have been described (Olberg 1986; Frye and Olberg 1995).

The simplest way in which proportional navigation could be implemented by the flying dragonfly would require that the dragonfly's head be rotationally stabilized during pursuit. Such visual stabilization has been well documented in free flying blowflies (van Hateren and Schilstra 1999). If the dragonfly's head were stabilized relative to the visual environment, small movements of the target’s image on the retina would indicate changes in the absolute angle from the dragonfly to its prey. The TSDNs would respond to such movements and send compensating instructions to the flight motor. By minimizing the drift of the target image in this way, the dragonfly would intercept its prey.

The above scenario depends heavily on the rotational stabilization of the head relative to the visual environment. In this study, we used high resolution, high-speed video to examine the orientation and movement of the head before and during prey pursuit. Our goal was to determine whether the head was rotationally stabilized during prey capture flights. Furthermore we sought to understand the role, if any, of the dorsal fovea in monitoring prey movements.

Materials and methods

Flight cage

Adult dragonflies do not normally forage in captivity and quickly starve even when their laboratory cage is loaded with flying insect prey. This problem was overcome with an outdoor flight cage whose mesh walls and ceiling admitted full sunlight, including UV. The flight cage was constructed of 1.9 cm copper pipe (2.9 m square and 2.5 m high) covered with polyethylene/polypropylene aquatic netting (US Netting, Erie, PA). The 0.5 cm gauge of the netting allowed small insects, such as mosquitoes and midges to pass freely through the cage walls providing natural prey for the captive dragonflies. The cage was located in a courtyard, providing shelter from wind but receiving full sunlight during the videotaping period, generally from 9 a.m. to 12:30 p.m. Perches constructed of wood or Styrofoam were dispersed within the cage and a ca. 1-m diameter plastic pool and potted plants were added to provide water and shade.

Typically 6–8 female dragonflies Erythemis simplicicollis (family Libellulidae) were netted in the wild and introduced into the flight cage. By the following day the dragonflies showed behavior indistinguishable from that seen in the field, perching and periodically taking off after small flying insects. Male dragonflies were not used because they did not forage in the flight cage.

To elicit prey capture flights, we moved 2 mm white glass beads above the perched dragonfly. The white beads were just as attractive as black beads and much easier to see in the video. To restrict the behavior as much as possible to a single plane, we moved the bead above the animal and in the same plane as the animal, normal to the camera’s field of view. During the first summer, the beads were affixed with 5 min epoxy to the end of a fine (75 μm) tungsten wire, approximately 75 cm in length. This wire was fine enough to be nearly invisible to our eyes and stiff enough to produce small jerky movements similar to those of small flying insects. The tungsten wire was attached to a stiff steel wire (1.6 mm diameter) 50 cm in length with epoxy and this steel wire was inserted into the hollow end of a 1.1 m fishing rod that was manipulated by hand. During the second summer the bean was affixed to the center of a fine...
nylon monofilament fish line stretched between the ends of a Y-shaped fork of bamboo. This more rigid mounting gave us better control of the beetle’s movements. We believe that the fish line was not visible to the foraging dragonflies, because they occasionally collided with it in flight. We found no difference in the response of the dragonflies to the two different methods of bead presentation.

We found that the animals became habituated to our experimental conditions and after several capture attempts stopped taking off after our artificial prey object. In a few cases a small insect was applied to the bead; this provided a reward to the foraging dragonfly and reduced the behavioral habituation to the bead stimulus. Because of this habituation, we usually released the dragonfly after 2–3 days of videotaping and replaced them with fresh animals.

Video

High-speed video clips were captured with a Redlake Motion Pro 2000 (Redlake MASD LLC, Tucson, AZ, USA) camera with an Elicar 90 mm macro lens, which provided a 12 cm field at 1 m. We placed the camera from 0.5 to 1.5 m away from the perching animals. To aid in our analysis of head position, we designed and oriented the perches to encourage the dragonflies to perch either aligned with and towards the camera or at right angles to the axis of view. Because dragonfly foraging flights are invariably upward, we positioned the camera with the dragonfly at the bottom of the camera’s field of view. The camera was connected to an Acme KB-108-1 field computer running Microsoft Windows 2000 and Redlake MIDAS software for capture at 500 frames per second and 1,280 × 1,024 pixel resolution.

Analysis

Video clips were digitized frame-by-frame by hand, using the Redlake MIDAS analysis software. The coordinates were then exported to Microsoft Excel spreadsheets for analysis. For each clip we digitized the bead position, center of the head and two other points on the head. In side shots, we also digitized the point at the tip of the tail. Twelve of the clips were digitized a second time by a different person with the results that were always within a few pixels on one another.

To calibrate approximate distances we used average dimensions of *Erythemis* females, 6 mm head width or 41 mm body length. Because we found about 3% variability in the length of the animals we measured and because the animal was not always oriented precisely head-on or at right angles to the camera-viewing axis, we estimate that our distance calibrations are only accurate within about 5%.

Head orientation

One of our goals in this project was to determine whether the dragonfly uses its dorsal fovea to fixate the prey during pursuit. When viewed from the side the front and back of dragonfly’s head appear to be bounded by nearly straight lines, and we used those lines to estimate the direction of view of the center of the fovea. To do this we viewed isolated *Erythemis* heads from directly above using a dissection microscope and axial illumination. We rotated the head, mounted on a goniometer for angle measurements, and observed the pseudopupil until the center of the fovea was directed straight up. We identified the center of the fovea as the region with largest pseudopupil; the entire fovea was about 22° wide, extending about 11° forward and backward from the center along the dorsal midline. We then photographed the head from the side and measured the angles of the front and back of the head (Fig. 1). In three animals we found that the center of the fovea was approximately 34° (33.5°, 34°, 36°) forward from the line of the back of the head and 19° (17.3°, 19.5°, 20.3°) forward from the line of the front of the head. Given the 3° variability in our angle measurements and also our uncertainty in assigning a precise line to the front or back of the head, especially in images somewhat blurred by motion, we estimate that our measurements are only accurate to within about 5°.

Results

In this study we obtained high-speed (500 frames/s) video clips of 128 pursuit flights by *Erythemis simplicicollis* females. Forty-eight of these were views directly from the front (n = 33) or directly from the side (n = 15), and we analyzed these 48 clips for head position before and, if possible, during pursuit flights. We estimate that these 48 clips represent about 25 different individual dragonflies. The 48 clips include data from both means of bead presentation; the results from the two methods were indistinguishable from one another. In this report we use the term “prey” to refer to the stimulus, a white bead. The bead was usually presented within about 15 cm of the animal and sometimes as close as 5 cm, resulting in short pursuit-flight durations, typically less than 200 ms (mean 168 ms; range 62–480 ms). These flight durations were similar to the average duration of 184 ms measured in naturally foraging dragonflies (Olberg et al. 2000).

In this high-speed video study we confirmed the conclusion of an earlier field study (Olberg et al. 2000) that dragonflies use an interception strategy, i.e., the dragonfly’s flight course is aimed at a point in front of its intended prey. In almost all cases, when the prey maintained consistent
flight speeds and direction, the dragonfly’s flight path was nearly a straight line to the point of interception (Fig. 2a–c).

Straight flights such as those shown in Fig. 2a–c do not arise from a ballistic strategy in which the dragonfly flies along a predetermined interception flight track. Flight tracks in which the prey changed direction (Fig. 2d–f) showed that the dragonfly reacts to changes in the prey’s trajectory with changes in its own flight path (Fig. 2d–f).

Behavioral response latencies

Circuitous flight tracks such as those in Fig. 2d–f allowed us to estimate the latency of the dragonfly’s reaction to changes in the direction of its prey. In some flights, we could distinguish exaggerated wing strokes before prey induced turns (Fig. 3a, lower inset). The latency measured from prey deviation to wing correction ranged from 26 to 42 ms (mean = 29 ms, s = 6.4, n = 6). We measured an average latency of 38 ms (s = 5.1, n = 16) to an observable course correction after abrupt changes in prey direction. The annotated flight track shown in Fig. 3 illustrates a wing-response latency of 28 ms resulting in a visible turn in the flight track 36 ms after the prey turn.

A second method confirms and refines our behavioral latency measurements. Rather than determining behavioral latency by inspection of wing movements or by flight path deviation, which requires an accurate assessment of the cue used by the dragonfly, we examined the x-coordinate of the dragonfly and prey locations over time. For example, in Fig. 3b a plot of the x component of the two paths illustrates graphically the dragonfly position lagging behind the prey position. The highest correlation between these two paths (0.916) occurred with a latency of only 28 ms, very close to the 29 ms average wing response latency measurement.

Head orientation

During pursuit, the dragonfly’s head was precisely oriented with respect to the prey. In 18 cases we were able to quantify the dragonfly’s head angle during the pursuit flight. Seven of these were viewed from head-on allowing us to determine the direction of view of the visual midline (Fig. 4a), and 11 of these were from the side, allowing us to determine the direction viewed by the dorsal fovea (Fig. 4b–c). With only one exception, we found that the dragonfly oriented its head during flight to maintain its target on or very near the “crosshairs” formed by the intersection of the visual midline with the dorsal foveal band.

Two features of the top trace in Fig. 4a suggest that the rotation of the head to fixate the prey on midline includes a predictive component to prey tracking. Firstly the head rotation at takeoff continues along the same slope (i.e., angular velocity) that the prey moved about 26 ms earlier. Thus the eye traces the path that the prey would have taken had it not reversed direction. The change of direction of the head rotation lags behind the change of direction of the prey by about 26 ms. Secondly, as the prey swings back to the left during the later part of the trace, the head angle follows the prey angle with no obvious time lag.

The histograms of Fig. 5 show that during most of the pursuit the dragonfly is kept within about 10° of midline and 10° of the foveal center. Examples with the prey moving forward (Fig. 5c) and backward (Fig. 5d) above the dragonfly reveal no obvious bias in the foveal tracking of

Fig. 2 Six flight tracks. Open circles indicate prey location with larger open circles every 10th frame (20 ms). Filled diamonds indicate center of dragonfly head with large filled circle every 20 ms. Large circles of dragonfly and prey correspond in time; the first circle indicates positions in first frame in which legs lose contact. Gray lines at lower end of dragonfly trace show position and length of body at takeoff (animal viewed head-on in c, d, f). Plus signs at a–c and f indicate head and prey locations at capture. Calibration bars = 2 cm. a–c. Dragonfly follows straight-line interception course. (clips 6-29a, 7-8a, 7-8b). d–f Dragonfly turns in response to changes in prey direction (clips 8-20u, 6-24c, 7-29b)
the prey. There may be a slight difference in tracking between cases in which the dragonfly flies forward and cases when it flies backward in pursuit. The median angle between prey and fovea during forward flight is $-4.3^\circ$, indicating that the center of fovea is aimed behind the bead relative to flight direction. The median angle between prey and fovea during backward flight is $3.1^\circ$, indicating that the center of fovea is again aimed somewhat behind the bead relative to flight direction. These slight skews notwithstanding in the accumulated histograms (Fig. 5a, b), as well as in each of the histograms of different pursuit scenarios (Fig. 5c–f), the bead is kept within $10^\circ$ of the center of the crosshairs at least 85% of the time.

Of the 18 clips analyzed for head orientation during flight, only one (Fig. 6) did not follow the pattern established by all the others, suggesting that other visual pursuit strategies are available to the foraging dragonfly. In this instance the dragonfly was viewed from head-on as it flew precisely sideways in pursuit of the prey. For most of this pursuit the dragonfly kept its head nearly in level, rather than rotating the head to fixate the prey on midline (Fig. 6b). We could not ascertain whether the prey’s image was maintained on the lateral region of the dorsal fovea, but the head position as viewed from the front was consistent with this possibility.

Discussion

Three principal points emerge from this high-speed video study of dragonfly prey interception. (1) The dragonfly steers an interception course, leading its prey, (2) during pursuit the dragonfly’s head rotates freely with respect to the rest of the body to fixate the prey’s image on the “cross-
hairs” formed by the intersection of dorsal foveal band with visual midline, (3) the behavioral latency in response to the movement of the prey image is remarkably fast, typically less than 30 ms. In this report we have focused on relatively short pursuit flights (usually 5–15 cm), because we could accurately measure head orientation only with close-up camera views. However, short flights such as these are not uncommon in foraging *Erythemis* females. They are not restricted to such short forays, however; we also observed them taking off after prey at a distance of 0.5 m or more.

Points (1) and (2) above imply that the dragonfly is not usually flying in the direction viewed by the midline dorsal fovea. Instead, the dragonfly’s flight course is directed at a point in front of the prey’s movement, while the head rotates to keep the target fixated. These results then require us to modify our earlier hypothesis (Olberg et al. 2000) for the control of interception flight. We had hypothesized that the dragonfly would stabilize its head, and thus its eyes, on the visual environment, responding with compensatory flight corrections to any drift of the prey’s image on the retina. In this way the prey’s image would be stabilized on the eye and the flight would describe an interception course. In a landmark study of head and body positions and orientations of blowflies in free flight, van Hateren and Schilstra (1999) showed that head is rotationally stabilized relative to the visual environment with rapid head saccades accompanying course changes. However, in the blowfly study flies were not actively orienting to an object, as were the dragonflies.

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**Fig. 4** Fixation of the prey image on midline and dorsal fovea. *Open circles* indicate angle from the dragonfly head to the prey. *Filled diamonds* indicate direction of view of midline (a) or dorsal fovea (b, c). *Dashed line* indicates 0 ms, the time of takeoff. a Head orients in flight to maintain the prey image near visual midline (clips 7-22i, 7-8b). b, c Head orients to maintain the prey image near the center of the fovea when the prey moves forward (a clips 7-29c, 6-29a) or backward (b clips 7-29a, 7-22e) relative to the dragonfly.

**Fig. 5** Histograms showing distribution of midline or fovea angles relative to the angle to the prey. Visual angle is subtracted from prey angle in each frame, and histogram of each clip is normalized to 100%. Normalized histograms are averaged. a Angle to prey is centered on visual midline in head-on clips. b Angle to prey is centered on fovea in the accumulated sideways clips. Positive values in b–f indicate that the prey angle is behind the center of the fovea. c, d Subsets of the sideways clips with target moving forward (dotted arrow, c) or backward (dotted arrow, d) relative to the animal show no obvious bias. e, f Subsets of the sideways clips with the animal flying forward (dotted arrow, e) or backward (dotted arrow, f) show no obvious bias.
It is clear from the results we report here that the movement of the prey's image elicits rotation of the head as well as Xight steering and that the head rotation is slightly faster than the wing response. A diagram of the neural connections underlying interception (Fig. 7) must therefore include two pathways, one controlling head position and one eliciting Xight turns. While we have much evidence showing that the TSDNs constitute the major pathway for target-directed flight steering (Olberg 1986; Frye and Olberg 1995), we have not identified the neurons that control target-directed head rotation. One possible scheme would have the TSDNs controlling both head and wing movements. However, for the majority of the TSDNs we think this is unlikely for the following reason. In order to stabilize the prey image on a specific region of the eye, neuronal control of head movements must include precise position information (Land and Collett 1974). Most of the TSDNs show distinct directional sensitivity to target movement, but their responses do not vary systematically for target movements at different locations within their receptive fields, making them unlikely candidates for precisely fixating the prey. Two of the TSDNs, however, could reasonably have a role in rotating the head to keep the target on the foveal midline. These neurons (DIT1 and MDT4-Olberg 1986; Frye and Olberg 1995) have small receptive fields with their centers neatly centered on the dorsal foveal midline (Frye and Olberg 1995). Whether stimulation of these two neurons produces head rotation is still to be determined. It is equally possible that centering of the prey image on the dorsal foveal midline simply brings these neurons to bear on the task of flight control.

With both the head and wings responding to target-image movement, the coordination between head and wings is essential for orientation control. Thus a pathway must exist which transmits information to the wings about head rotation relative to the thorax (Fig. 7). A group of multimodal neurons that are directionally sensitive to head rotation are known to provide input to the wings. In an earlier study (Olberg 1981) we suggested that these neurons form the pathway for rotational stabilization of the flying dragonfly, and that one of their functions was to produce wing torque tending to realign the thorax with the head. These neurons, which were termed “self movement detectors” (Olberg 1981), could, in principle, continue to provide steering input to the wings while the image is well stabilized on the fovea.
Eye specialization

Our results provide evidence for the role of the dorsal foveal band in prey interception. It has been known for a long time that the dorsal ommatidia of the dragonfly show a remarkable degree of specialization, not only in their spectral sensitivity (Labhart and Nilsson 1995), but also in their large lens diameters and small inter-ommatidial angles (Sherk 1978; Horridge 1978), properties that result in a high acuity fovea (see Horridge 2005 for review). Various authors (Sherk 1978; Sauseng et al. 2003) have suggested that this region could be important in prey capture, since dragonflies invariably attack their prey from below, placing the prey on the upward-facing retina. Sherk (1978) also suggested that the precise alignment of these facets and their underlying rhabdomes could endow them with sensitivity to the pattern of polarization in the sky above, which could be useful in orientation and navigation. These suggested functions are not mutually exclusive.

There are many examples of specialized eye regions serving behavioral functions in insects. One of the best-known examples is the male-specific acute zone of the fly eye. This region is located on visual midline and about 20°-30° above the horizon (Land and Eckert 1985). Male houseflies pursuing females keep the image of the female on this acute zone at least 80% of the time (Wagner 1986). Furthermore, male-specific neurons in the lobula of the optic lobe are directionally selective for small target movement, precisely the properties appropriate for controlling tracking behavior (Gilbert and Strausfeld 1991).

Although there are some parallels between the tracking flight in male flies mediated by the male-specific acute zone and the prey pursuit flight in dragonflies mediated by the dorsal fovea, there are also fundamental differences. Although tethered flies rapidly rotate their heads in all planes to follow moving gratings (Gilbert et al. 1995), during tracking flights the male’s body appears to remain mostly in line with the head, which is directed towards its quarry, another fly. Dragonflies show no tendency to align their bodies towards their prey. The head is rotated to place the prey’s image on the foveal midline, but the orientation of the rest of the body is highly variable. The direction of flight relative to the body can as easily be backwards or sideways as forward, but it is always in a direction that leads the prey for interception (Olberg et al. 2000). In this way the dragonfly pursuit is more similar to the interception flights of some hoverflies (Collett and Land 1978) than to the tracking flights of houseflies.

The dragonfly’s dorsal fovea is probably also used for estimating the distance, and therefore the size of a potential prey item (Olberg et al. 2005). Perched dragonflies typically bob their heads upward in response to an object passing above them (Kirmse and Lässig 1971; Miller 1995; Sauseng et al. 2003). This movement usually results in the object’s image passing across the dorsal foveal band. The rocking head motion includes a significant translational component (Olberg and Seaman, unpublished) that could allow the dragonfly to extract distance information based on motion parallax, a possibility discussed in detail elsewhere (Olberg et al. 2005). The pre-flight head movements also include fixation of the prey image on the foveal midline, several examples of which can be seen in Fig. 4.

Response latencies

The higher spatial and temporal resolution in this study allowed us to refine our estimates of the latency between detecting and responding to object image motion. In an early study (Olberg et al. 2000), based exclusively on evaluating dragonfly and prey flight tracks, we estimated this latency to be between 33 and 50 ms, somewhat higher than the average latency of 29 ms that we report in this study. The remarkable speed of this visual reflex may account for the impressive success rates of foraging dragonflies. Baird and May (1997) measured a success rate of 76% in foraging Pachydiplax longipennis, and we found an astonishing combined capture rate of 97% in short flights of Erythemis simplicicollis and Leucorrhinia intacta (Olberg et al. 2000).

Perhaps not surprisingly, the visual reflexes of dragonflies foraging in outdoor sunlight are much faster than would be predicted from electrophysiological studies in the laboratory. The shortest visual latency measured in descending interneurons in the cervical connectives was 45 ms. The descending interneurons synapse onto thoracic pre-motor or motor neurons, which must then excite muscle, increasing appreciably the estimate for latency based on lab measurements.

The role of prediction in prey interception

Whether the goal is to catch a ball, avoid a moving projectile, or grab a flying insect out of the air, it is important to be able to predict where a moving object will be some time in the future. This ability has been investigated in a variety of vertebrate animals and especially in humans (see Regan et al. 1998 for review). The head movement plotted in the top trace of Fig. 4a suggests that the dragonfly is able to predict the future position of its prey. The first head rotation in this trace shows a simple tracking response to the prey’s movement with a visual latency of about 26 ms. However, after the prey is again fixated in flight (at about 60 ms) the image is held on midline with no obvious response latency. This might suggest that the head movement is now governed by the angular velocity, rather than the position, of the moving image. Responding to the velocity of the prey’s image would allow the dragonfly to predict its future position (Adelman et al. 2003).
The predictive ability of the dragonfly’s visual response is also seen in its choice of initial takeoff direction. The flight tracks in Fig. 2a–c, show that the takeoff direction is quite an accurate prediction of the line that the dragonfly should take to intercept its prey. Like the prediction controlling head orientation, determination of the best line for interception is based on the angular velocity of the prey’s image (Olberg and Henry, unpublished). The interplay between target fixation and prediction of future target position underlies a far more sophisticated mechanism for prey interception by dragonflies than we previously proposed (Olberg et al. 2000).

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