RESEARCH ARTICLE
The visual control of landing and obstacle avoidance in the fruit fly
Drosophila melanogaster

Floris van Breugel¹,* and Michael H. Dickinson²
¹California Institute of Technology, Mail Code 138-78, Pasadena, CA 91125, USA and ²Department of Biology, University of Washington, Box 351800, 24 Kincaid Hall, Seattle, WA 98195, USA
*Author for correspondence (floris@caltech.edu)

Accepted 8 February 2012

SUMMARY
Landing behavior is one of the most critical, yet least studied, aspects of insect flight. In order to land safely, an insect must recognize a visual feature, navigate towards it, decelerate, and extend its legs in preparation for touchdown. Although previous studies have focused on the visual stimuli that trigger these different components, the complete sequence has not been systematically studied in a free-flying animal. Using a real-time 3D tracking system in conjunction with high speed digital imaging, we were able to capture the landing sequences of fruit flies (Drosophila melanogaster) from the moment they first steered toward a visual target, to the point of touchdown. This analysis was made possible by a custom-built feedback system that actively maintained the fly in the focus of the high speed camera. The results suggest that landing is composed of three distinct behavioral modules. First, a fly actively turns towards a stationary target via a directed body saccade. Next, it begins to decelerate at a point determined by both the size of the visual target and its rate of expansion on the retina. Finally, the fly extends its legs when the visual target reaches a threshold retinal size of approximately 60°. Our data also let us compare landing sequences with flight trajectories that, although initially directed toward a visual target, did not result in landing. In these ‘fly-by’ trajectories, flies steer toward the target but then exhibit a targeted aversive saccade when the target subtends a retinal size of approximately 33°. Collectively, the results provide insight into the organization of sensorimotor modules that underlie the landing and search behaviors of insects.

Supplementary material available online at http://jeb.biologists.org/cgi/content/full/215/11/1783/DC1

Key words: insect, flight control, Drosophila, obstacle avoidance, landing behavior, target orientation, saccade.

INTRODUCTION
Deciding where and when to land, and subsequently performing a successful landing, is arguably the most critical aspect of flight behavior for most flying animals. Despite this importance, landing has been subject to much less research compared with other aspects of flight behavior. This is likely due to the difficulties of enticing insects to land in specific locations where they can be carefully observed. Unlike take-off, which begins at a fixed location and takes place within a relatively small spatial volume, landing consists of a complex sequence of different behavioral modules separated in space and time. An animal must orient towards a particular sensory feature, alter its wing motion to change its speed and posture, extend its legs and then make contact with the substratum.

Previous studies of landing have focused on the visual stimuli that trigger and regulate landing behavior in a variety of insects including hoverflies (Syritta pipiens) (Collett and Land, 1975), houseflies (Musca domestica) (Borst and Bahde, 1986; Brätenberg and Taddei-Ferretti, 1966; Perez de Talens and Taddei-Ferretti, 1970; Borst, 1990; Wagner, 1982), blowflies (Calliphora eurythrocephala) (Goodman, 1960; Eckert, 1983), bees (Apis mellifera) (Srinivasan et al., 2000; Evangelista et al., 2010), the milkweed bug (Oncopeltus fasciatus) (Coggshall, 1972) and fruit flies (Drosophila melanogaster) (Tammero and Dickinson, 2002b; Wittekind, 1988). Furthermore, electrophysiological recordings exist for neurons believed to be associated with landing and collision avoidance (locusts, Locusta migratoria (Rind, 1990; Gabbiani et al., 1999), blowflies (Taddei-Ferretti and Chillemi, 1981)). The fruit fly, D. melanogaster, is well suited for studies of landing behavior because its small size permits the analysis of long flight sequences within a controlled laboratory setting. This makes it possible to study landing behavior from the moment a visual target first influences an animal’s flight motion to the point of touchdown. In addition, the visual system of Drosophila has been extensively studied (Borst et al., 2010), largely due to the genetic tools that are uniquely available in this species (Simpson, 2009).

Although the free flight landing sequences of Drosophila have not been studied explicitly before, several behavioral modules that are likely to represent components of the behavior have been studied extensively. Flying Drosophila exhibit a robust orientation reflex to vertical contrast edges known as fixation (Götz, 1968; Götz, 1987) (see also Reichardt and Poggio, 1976), which was first identified in mosquitoes (Kennedy, 1939). Although the functional relevance of this tethered flight phenomenon is not clear, free flight experiments suggest that fixation might serve to lead flies towards salient visual objects (Maimon et al., 2008) and thus could represent the earliest component of a landing sequence. Further, Drosophila and other flies often exhibit a flight pattern characterized by relatively long segments of straight flight, interspersed with rapid turns called saccades (Collett and Land, 1975; Wehrhahn et al., 1982; Tammero and Dickinson, 2002a). If these saccades are directed...
Fig. 1. (A) Free flight arena equipped with 3D tracking system and high speed video camera with automated focus system. (B) Definition of visual parameters used throughout the paper. Retinal size \((\alpha)\) is defined as the angle subtended by the post on the fly’s retina (see Eqn 1). Post angle \((\phi)\) is defined as the azimuthal angle of the center of the post from the fly’s flight path. Turn angle \((\psi)\) is defined as the angular change in the fly’s heading over the course of a saccade (see Fig 3). This term is synonymous with saccade amplitude.

MATERIALS AND METHODS

Animals
Experiments were performed on 3–5 day old female fruit flies, D. melanogaster Meigen, from a laboratory stock descended from a wild-caught population of 200 mated females. Flies were deprived of food, but not water, for 2–6h prior to the start of the experiment in order to motivate flight. For each experimental trial, we introduced a group of 12 flies to the corner of the arena within a small test tube. The flies were then free to move throughout the flight arena for a period of 12–24h, during which time data were collected automatically. A wet KimWipe® in one of the corners of the flight arena provided the flies with water for the duration of the experiment.

Flight arena
We performed all experiments in a 1.5×0.3 × 0.3 m working section of a wind tunnel (Fig. 1) that has been described previously (Budick and Dickinson, 2006; Maimon et al., 2008; Straw et al., 2010). In the current experiments, the wind tunnel was switched off so that the internal air was still. To provide the flies with visual contrast, we projected the floor and two long sidewalls with a static black and white checker pattern (checker size 3 cm, 11.5 deg retinal size at 15 cm distance) using a Lightspeed Designs DepthQ projector (Bellevue, WA, USA) with the color wheel removed (120Hz update rate, 360Hz frame rate, mean luminance of 50 cd m⁻²). The two shorter walls of the chamber, consisting of the fine mesh screens of the upstream and downstream ends of the wind tunnel, were not illuminated. The ceiling of the chamber was transparent acrylic.

We tracked the 3D position of individual flies within the chamber using a real-time tracking system, described in detail elsewhere (Straw et al., 2011). The 6-camera system generated an estimate of fly position at 100 frames s⁻¹ with a median latency of 39 ms. For the purposes of tracking, the arena was backlit with an array of near-infrared (850 nm) LEDs. The cameras were equipped with long-pass filters (Hoya R-72) so that the camera images were not contaminated by the checkerboard pattern that was displayed in visible wavelengths.

Experiment protocol
In order to observe the flies’ response to a conspicuous visual object, we placed a 15 cm tall, 1.9 cm diameter post in the center of the

toward certain features, they too should be considered an early component of the landing sequence. Although past studies have shown that visual cues play a large role in triggering saccades and influencing their course direction (i.e. left vs right) (Heisenberg and Wolf, 1979; Tammero and Dickinson, 2002a; Bender and Dickinson, 2006; Stewart et al., 2010), there is not yet definitive evidence that Drosophila make directed saccades, such that they turn precisely to the angular position of a particular visual feature.

Once a fly starts approaching an object, it will receive an expansion cue, which has been shown to elicit a robust collision-avoidance response (Tammero and Dickinson, 2002b; Bender and Dickinson, 2006; Stewart et al., 2010). In order to land, however, the animal must override this reaction and maintain a collision course, reducing its flight speed such that it can touch down safely. One free flight study of houseflies suggests that visual cues are responsible for triggering this deceleration phase prior to landing (Wagner, 1982).

Tethered flies exhibit a robust leg extension reflex in response to an expanding visual stimulus (green bottle flies (Goodman, 1960), houseflies (Borst and Bahde, 1986; Borst, 1986), fruit flies (Tammero and Dickinson, 2002a; Wittekind, 1988)). Although this reflex has previously been termed ‘the landing response’, it only represents one component of landing behavior and its position in the complete free flight landing sequence is not known. Each of the elements of the landing sequence, including saccade generation, deceleration and leg extension, has been shown to be visually mediated (Goodman, 1960; Wagner, 1982).

In this study, we examined the landing behavior of freely flying Drosophila from the point when they can initially resolve a visual target to the moment of touchdown. The analysis was possible in part because of an automated 3D tracking system that allowed us to collect a large number of landing trajectories, as well as a real-time focus-following system that permitted the capture of high temporal and spatial resolution images during the final stages of this behavior. Our dataset also enabled us to explicitly compare landing sequences with sequences in which flies initially flew towards the target but then steered away from it. The results suggest that landing sequences begin with a body saccade directed toward the vertical edge of a visual target. Flies then begin to decelerate at a point determined by both the retinal size of the target and its rate of expansion. Finally, flies extend their legs when the visual target subtends a critical angle. The nature of these triggering mechanisms normally ensures that a fly begins to slow its approach and then extends its legs in time for touchdown. In cases in which flies steer toward a target, but then do not land, the initial orienting behavior is followed by an aversive saccade that is triggered when the target subtends a critical angle. Collectively, the results indicate how a complex behavioral cascade may emerge from a temporal sequence of separated sensorimotor modules.

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arena. The top of this post reached to half the height of the arena. We used two different types of post: a solid black post (matte black spray paint on a smooth aluminium cylinder) and a black and white checkered post (5 mm checkers, 5 deg retinal size at a distance of 5.7 cm, printed on white paper and tightly wrapped around an aluminium cylinder). We also collected data in the absence of a post. Because both visual inspection and statistical comparisons of the data suggested that the results were only marginally influenced by post texture (solid black vs checkered, see supplementary material Fig. S3), we pooled both data sets for the bulk of our analysis unless otherwise noted.

Trajectory reconstruction and analysis
All analyses of flight trajectories were done using custom-designed software written in Python (www.python.org). Each trajectory was treated as an independent sample, as the tracking software was not able to maintain fly identities over the extended period of our experiments. As a result, it is impossible to tell how many individual flies contributed to our analysis (the possible range is 29–348). Our tracking system logs all locomotor behavior within the arena including bouts of flying and walking. The data presented are derived from 29 experimental runs and 3 controls, which generated a total of 81,252 trajectories. Further details of the experimental database are provided in Table 1.

Each trajectory was smoothed to remove digitization errors using a simple forward/reverse, non-causal Kalman filter. Unless otherwise noted, the control data from the no-post trials were culled and analyzed in the same way as the data collected with the post, using an imaginary post with the same dimensions and in the same position as the real post. For our analysis, we only considered trajectories that started at a distance greater than 10 cm away from the post, and approached to within 3 cm of the post. Furthermore, except for the no-post controls, we removed trajectories in which the flies flew above the top of the post at any point within our region of interest. This procedure was taken to maximize the likelihood that we were examining flight behavior that was influenced by the presence of the post. These criteria removed the large majority of the original trajectories, which were often short sections of either flying or walking. As we did not collect as much data under the no-post control arrangement, we did not require the control trajectories to be below the (not present) post height. Because of the visual symmetry of the upper and lower halves of the wind tunnel in these experiments, this difference in processing of the no-post data is unlikely to influence our results. Further, very few of our conclusions depend on an explicit comparison with the no-post data.

We used a simple algorithm to automatically classify trajectories as either ‘landings’ or ‘fly-bys’. Trajectories that ended within 1 cm (~4 body lengths) of the post with a velocity of less than 6 mm s⁻¹ were labeled as landings; all others were labeled as fly-bys. These soft criteria helped in preventing erroneous classifications. Furthermore, visual inspection of the raw data in Fig. 2 shows that our criteria were sufficient to properly segregate landings and fly-bys.

Table 1. Raw trajectory statistics

<table>
<thead>
<tr>
<th>Post type</th>
<th>No. trials</th>
<th>Total trajectories</th>
<th>Mean no. trajectories per trial</th>
<th>Minimum no. trajectories per trial</th>
<th>Maximum no. trajectories per trial</th>
<th>Total no. trajectories after culling</th>
<th>% Landing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black</td>
<td>14</td>
<td>25,393</td>
<td>1813</td>
<td>4</td>
<td>5611</td>
<td>578</td>
<td>32%</td>
</tr>
<tr>
<td>Checkered</td>
<td>15</td>
<td>45,908</td>
<td>3060</td>
<td>269</td>
<td>14,499</td>
<td>608</td>
<td>6.00%</td>
</tr>
<tr>
<td>No post</td>
<td>3</td>
<td>9951</td>
<td>3317</td>
<td>275</td>
<td>9951</td>
<td>266</td>
<td>NA</td>
</tr>
</tbody>
</table>

Fig. 2. Flight trajectories in the presence of a post, classified as fly-bys (n=300 trajectories) and landings (n=177). The trajectories for fly-bys represent a subset of the total data set of n=1065. The thick red overlays on each trace indicate the portions of the trajectories that were classified as the last saccade each fly made prior to its nearest approach to the post, which is the focus of our subsequent analysis. See Fig. 3 and Materials and methods for our definition of a saccade. The thick blue overlays indicate all other saccades. The dotted line in the bold fly-by trace indicates the portions of trajectories after the flies’ closest approach to the post. These portions were omitted from the rest of our analysis because it was unlikely a fly’s behavior was influenced by the post after this point. r, post radius.
bys. Data from the no-post controls were also identified as pseudo-landings (trajectories that intersected the 3D volume of the an imaginary post with identical dimensions to the real one) and pseudo-fly-bys (all other trajectories). All landing sequences were analyzed from start to finish. Fly-bys were only analyzed from the beginning of the trajectory until the point just prior to the first saccade following the closest approach to the post (see Fig. 2). This procedure was necessary to eliminate the portion of the sequence in which the fly was flying away from the post and thus unlikely to be responding to it.

Flight trajectories were described using a number of variables calculated in each frame, including distance to the post (measured to the post surface), ground speed, acceleration, heading (calculated as the tangent to the velocity vector) and angular velocity. Except where otherwise noted (e.g. as in Fig. 2, right), all values were calculated as projected in the x–y plane, thus ignoring changes in altitude. In order to focus our analysis on experimental parameters that can provide insight into possible sensory processes, we used the following variables, defined relative to the fly’s position (see Fig. 1B). Turn angle (ψ) is the angular change in the fly’s heading over the course of a saccade. Post angle (ψ) is the angle between the fly’s heading and the vector to the post. Retinal size (α) is the angle subtended by the post on the fly’s retina, which is calculated as:

$$\alpha = 2\sin^{-1} \frac{r}{d},$$

where r is the radius of the post and d is the distance from the fly to the center of the post.

### High speed imaging

To examine the landing and fly-by behavior near the post with greater spatial and temporal resolution, we mounted a high speed camera (Photron SA1, San Diego, CA, USA) looking down, approximately 30 cm above the post (see Fig. 1), equipped with a 105 mm Nikon macro lens (Nikon USA, Melville, NY, USA). We operated the camera at 5000 frames s⁻¹ with a resolution of 1024×1024 pixels. To overcome the depth of field limitations imposed by the limited available lighting and the large magnification needed to resolve the flies’ legs, we designed an automated motorized focus-following system. The custom-built system used the real-time elevation measurements from our 3D tracking system to automatically adjust a friction belt connected to the manual focus ring of the lens. This system allowed us to capture sharp video of flies at any elevation in the flight arena. The camera was post-triggered whenever a fly came to within 1 cm of the post (capturing both landings and close fly-bys).

One initial limitation of our focus-following system was that because of the distortion from our lens we could not focus through the top of the cylindrical post to visualize a clean circular section at any point along the height of the post. To solve this problem, we machined a gently tapering post (1.9 cm at the base and 1.3 cm at the top). This tapered shape made it possible to see the moment of touchdown along the entire length of the post without obstructions from the top. To account for the effect of the slight change in diameter of the post in these high speed experiments, we used the diameter of the post at the altitude of the fly when calculating the retinal size of the post. This slight modification in our analysis is reasonable, given that trajectories did not vary significantly with altitude. Furthermore, we replicated all analysis using a fixed value for the diameter equal to the mean diameter of the post, but found no significant difference in the results.

### Analysis of saccades

The free flight trajectories of fruit flies are characterized by relatively long straight segments and short rapid turns, called saccades (for example, see Fig. 3B,C). We focused much of our analysis on these saccadic flight segments, which we define as the portions of a trajectory during which the angular velocity exceeds a threshold of 300 deg s⁻¹. To justify both the particular threshold we used to define saccades and our decision to focus on them, we performed an extensive analysis of the angular velocity of all the trajectories we collected (in the presence of the post), and a subsequent analysis of the segments we labeled as saccades (Fig. 3).

The distribution of angular velocities of freely flying flies is well approximated by the sum of a Gaussian distribution (μ=0 deg s⁻¹, σ=85 deg s⁻¹) and a log-normal distribution (mean μ=300 deg s⁻¹, variance σ=2.3 deg s⁻¹) (Fig. 3A). These results are similar to those published on tethered flies (Mayer et al., 1988; Bender and Dickinson, 2006) and as in those studies we take this as evidence for two distinct flight modes: noisy straight flight (described by the Gaussian distribution) and active saccadic turns (described by the log-normal distribution). Although the precise shape of the distribution is to some extent a function of the filtering used to calculate the angular velocity, we did not find any significant difference in the shape when angular velocity was calculated directly from the heading (Fig. 3C, blue trace) or a Kalman estimate (Fig. 3C, black trace). The distribution shown in Fig. 3C comes from the Kalman-estimated angular velocities, which we also use in all subsequent analyses to eliminate measurement noise, such as the transient seen in Fig. 3C.

We define saccades as the portions of trajectories in which there is a >95% probability that the point lies within the log-normal distribution shown in Fig. 3A, a classification that corresponds to an angular velocity threshold of 300 deg s⁻¹. This is similar to the thresholds used in prior work in free flight [300 deg s⁻¹ (Tammero and Dickinson, 2002a)] and magnetically tethered flight [350 deg s⁻¹ (Bender and Dickinson, 2006)]. The amplitude of these saccades, referred to hereafter as turn angle, does not vary by more than ±10 deg within a range of saccade threshold choices from 150 to 450 deg s⁻¹ (Fig. 3D).

The saccades we observed ranged in amplitude from 20 to 270 deg (Fig. 3E), and are well described by a log-normal distribution with a mean of 40 deg and scaling factor of 2.3 deg. Although these turns only comprise approximately 20% of the flight time (Fig. 3G), they account for roughly 80% of all net navigational changes in heading (Fig. 3F). The turn angle is also tightly correlated with peak angular velocity (Fig. 3H), which closely matches prior results found in tethered flies (Bender and Dickinson, 2006). This shows that flies do not perform turns of arbitrary amplitude at constant velocity, and suggests that each turn is an isolated maneuver that can be analyzed independently of the sequences that precede and follow the turn. Although it is possible that flies actively adjust their heading during the remaining flight segments, analyzing these aspects of flight is beyond the scope of this paper. We did not find a significant correlation between turn angle and horizontal flight speed (R²=0.02), or between angular velocity and flight speed (R²<0.001).

### Procedures for analyzing landing behavior

To study the onset of deceleration in landing flies we followed each trajectory backwards in time, starting from the point of landing, and defined the first negative to positive crossover of acceleration (defined as the derivative of flight speed in the x–y plane) as the point of deceleration initiation. For the subset of our landing data for which high speed imaging was available, we scored leg extension...
where $y$ and $x_1$ determine whether relationships between two continuous variables, and $d$ determines whether or not a fly turned after initiating deceleration, see Fig. 8. In these analyses, $x_2$ was represented as a boolean variable (0 or 1). We used the statistical program R (R Development Core Team, 2011) and the Python wrapper rpy2 (Gautier et al., 2011) to fit the linear model to the data (R command lm):

$$y = a_1 x_1 + b_1 + b_2 + a_{1:2} (x_1; x_2),$$

where $a_1$ and $b_1$ are the slope and intercept of the regression between our primary variables ($y$ and $x_1$), $b_2$ is the intercept due to the third variable ($x_2$), and $a_{1:2}$ is the slope due to the interaction between $x_1$ and $x_2$. Essentially, this is analogous to running an analysis of covariance, but allowing for interactions between the covariate $x_1$ and the categorical variable $x_2$. To show whether the impact of $x_2$ was significant, we report a pair of P-values $P(x_2=b_2, P(x_1;x_2)=a_{1:2})$, where $b_2$ corresponds to the intercept due to $x_2$ and $a_{1:2}$ corresponds to the slope due to the interaction between $x_1$ and $x_2$; t-tests tests were performed using the statistics sub-module of SciPy (Jones et al., 2001–), a Python module. We define a threshold of $\alpha=0.01$ to be significant, and $0.01<\alpha<0.05$ to be marginally significant.

**RESULTS**

**Description of landings and flybys**

Excluding trajectories that were above the level of the post, we analyzed a total of 1224 flight trajectories (Fig. 2) (in addition to 194 no-post controls; supplementary material Fig. S1). Flight speeds (measured at a distance of 10 cm from the post) for landing and flyby trajectories were similar in all our experimental conditions with a mean of 0.33±0.12 m s⁻¹ (see Table 2 for details).

In the trajectories that were classified as fly-bys (Fig. 2, $n=1065$), flies exhibited a turn away from the post when they were roughly 3 cm away from the object. This avoidance behavior is clearly

Fig. 3. Changes in turn heading are primarily accomplished using body saccades (defined as flight sequences with angular velocity ($\omega$$>$$300$ deg s⁻¹)]. (A) Histogram of angular velocity ($\omega$) at all time points for all trajectories ($n=1224$, $N=352,680$). The distribution is well approximated by the weighted sum (S, magenta) of a Gaussian distribution (G, black, mean=$\mu=0$ deg s⁻¹, variance=$\sigma=85$ deg s⁻¹) and a log-normal distribution ($L$, red, mean=$\mu=300$ deg s⁻¹, variance=$\sigma=2.3$ deg s⁻¹) such that $S=0.8G+0.2L$. (B) A typical free flight trajectory, seen from above, with red portions indicating saccades. (C) Angular velocity of the trajectory in B, without smoothing (blue) and as a Kalman estimate (black). The sharp transient in angular velocity at t=2.2 is due to a measurement error; such events are eliminated by the Kalman filter. (D) Changes in the $\omega$-threshold used to classify saccades have little effect on measurements of turn angle ($\psi$). The relative change in $\psi$ is plotted as a function of the saccade threshold; box plots indicate mean and first and last quartiles. (E) Distribution of net change in heading of each saccade segment ($\Delta \psi$) (red, $N=5635$) compared with each non-saccade segment ($\Delta \psi$) (black, $N=8897$) for all trajectories ($n=1224$). The distributions are well approximated by a log-normal distribution (red, $\mu=40$ deg, $\sigma=2.3$ deg), and an exponential distribution (gray, $\lambda=0.075$). (F) Approximately 80% of all net changes in heading occur during saccades. The distributions show the ratio of the sum of $\Delta \psi$ to the sum of $\Delta \psi+\Delta \psi_\text{sacc}$ for each trajectory. We tested three definitions for the $\omega$-threshold used to define a saccade: 200 deg s⁻¹ (blue), 300 deg s⁻¹ (red) and 400 deg s⁻¹ (green). The associated curves are smoothed representations of the distributions calculated using a 3rd order 0.4 Hz Butterworth filter. (G) Saccades account for approximately 20% of the flight time. The histograms show the ratio of time a fly was saccading to total trajectory time for each trajectory. The color scheme and curves are defined as in F. (H) Peak angular velocity vs turn angle for all saccades, plotted as a heat map with a logarithmic color scale.
manifest as a zone of exclusion around the post in the top down view of Fig. 2. Within the trajectories classified as landings (Fig. 2, n=177), we observed two general patterns: flies that flew straight towards the post, and those that performed a saccade at some point within 10 cm of the post. The flies that landed did not show any preference for flying near the top of the post (on average flies landed 6.3±3.4 cm below the top of the post; see Fig. 2, right). This shows that under these experimental conditions flies are not more likely to land at the top of an object as previously suggested based on their preference for flying at the level of horizontal edges (Straw et al., 2010).

Saccade results
Because the most significant changes in direction are made during body saccades (see Materials and methods, and Fig. 3), we focused our initial analysis on these behaviors. Of particular interest is the last saccade flies perform prior to their nearest approach to the post, which for landing flies corresponds to the moment of landing. For all of the following analysis we focused exclusively on these saccades (the red overlays in Fig. 2). For our initial analysis we grouped landings and fly-bys together. In the absence of the post, relatively few flies performed a saccade when the retinal size of the imaginary post exceeded 25 deg, whereas in the presence of the post we saw a distinct peak near 35 deg (Fig. 4C). This suggests that the saccades flies make when in the vicinity of the post are likely a response to the post, in particular when the retinal size exceeds 25 deg. Prior to making a saccade, the post angle distributions in the experiments done in the presence of the post and in the absence of the post are similar (Fig. 4A). The fact that the mean post angle is near 0 deg in both cases is presumably a result of the geometry of our rectangular flight tunnel, which favors longitudinal flight. The post angle after turning, however, is clearly different in the post vs no-post conditions (Fig.4B), suggesting that the presence of the post influences the turn angle of the flies. We further confirmed this by convolving the distribution of saccade turn angles (Fig.3E) with the post angle prior to turning, yielding a unimodal distribution (data not shown) that is clearly different from the multimodal distribution shown in Fig.4B. In order to examine the influence of the post on saccade behavior in more detail, we focused only on those saccades made when the retinal size of the post exceeded 25 deg.

The post angle distribution after flies make a turn suggests that there are two independent behaviors governing these actions (Fig. 5). One group turns such that they are headed away from the post (described by Gaussian distributions with μ=±140 deg, σ=50 deg); the other group turns such that they are headed towards the post (described by a Gaussian distribution with μ=0 deg, σ=40 deg). These distributions are each separated by more than twice the common standard deviation, confirming that this is indeed a multi-modal distribution (Behboodian, 1970). These two groups correspond surprisingly closely with the independently classified landing and fly-by trajectories (Fig. 5C). This result justifies our subsequent analysis in which we treat the behavior of saccades made by landing and non-landing flies independently.

To determine in what way the post influences the saccades made by landing and non-landing flies, we examined the relationship between the post angle prior to performing a saccade and the subsequent turn angle. If flies always made saccades directly towards the post we would expect them to make a turn roughly equal in magnitude to the post angle, whereas turns directed away from the post would fall above or below that line. For the saccades prior to landings, these points lie along a line with slope close to one (Fig. 6A), suggesting that the flies were turning towards the post. This is not surprising, because in order to land on the post the flies’ last saccade prior to landing must necessarily have been directed towards the post. Indeed, we see a similar regression in the pseudo-landing flies from the no-post control experiments (supplementary material Fig.S2A). In the presence of the post, however, flies tended to make their last saccades much closer to the post than the control flies performing a ‘pseudo-landing’ in the absence of a post (Fig. 6C; supplementary material Fig.S2C). Because we have already demonstrated that the saccades made when the retinal size of the post exceeded 25 deg were likely influenced by the post (Fig. 4), it is conceivable that the landing flies were in fact directing their saccades towards the post; we will revisit this hypothesis more rigorously later in our analysis.

In contrast, the non-landing flies tended to make aversive saccades when they were close to the post (Fig. 6B), at a mean retinal size of 33±17 deg (Fig. 6D). As expected, there are no obvious trends in the no-post control data for pseudo-non-landing flies (supplementary material Fig.S2C). Although some of the non-landing flies exhibited a final saccade towards the post, these were all done at a much greater distance from the post. To examine the aversive saccades more closely, we again set a threshold on the retinal size of the post at 25 deg (which corresponds to a distance of approximately 3 cm). These saccades – the last saccades non-landing flies made prior to their nearest approach to the post – are strongly correlated with post angle, as evidenced by the two nearly parallel linear regressions for left and right turns (Fig. 7). The data are colored blue and red according to left and right turns, respectively. The small clusters of lightly shaded points (with a post angle close to ±90 deg) correspond to shallow turns towards the post when the flies were flying past the post. The separation between these clusters and the rest of the turns made in the same direction suggest that they are not governed by the same behavioral algorithm, and were thus excluded when we calculated the regressions. In fact, these clusters appear to be associated with the data corresponding to turns in the opposite direction. For example, the light red points (shallow left turns) may be an extension of the dark blue points (right turns).

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Post type</th>
<th>No. trajectories</th>
<th>Speed (m s⁻¹) (μ±σ)</th>
<th>Total length (s) (μ min.; max.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fly-bys</td>
<td>All</td>
<td>1047</td>
<td>0.32±0.12</td>
<td>3.03 (0.37; 24.99)</td>
</tr>
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Visual control of landing in flies

Landing behavior

Of all the trajectories in which a fly came to within 3 cm of the post, 14% landed on the post (n=1224). In order for a fly to safely land it must decelerate to a safe flight speed and extend its legs in time for touchdown (although not necessarily in that order). To examine the deceleration behavior we estimated the point at which a fly started to decelerate prior to landing on the post (see Materials and methods). We initially restricted our analysis of deceleration to those trajectories where flies did not perform a saccade after initiating deceleration. When these points are plotted as a function of each fly’s instantaneous speed and the log of the retinal size of the post, the data fall along a straight line (purple points, Fig. 8A,B). Thus, flies that are flying fast begin to slow down when they are farther away from the post compared with flies that are flying slowly.

Fig. 4. The post influences saccades performed in the vicinity of the post. (A) Prior to turning, flies show a qualitatively similar distribution of post angle in the presence (black, n=1012) and absence (green, n=148) of the post. (B) After turning, flies show a qualitatively different distribution of post angle in the presence (black) and absence (green) of the post. (C) Flies show a qualitatively different distribution for the retinal size at which they make their last saccade in the presence (black) and absence (green) of the post. In all panels the associated shading shows smoothed representations of the distributions calculated using 3rd order 0.3 Hz Butterworth filters.

Fig. 5. Saccades near the post are described by two independent behaviors, corresponding to landing and not landing. (A) Post angle after turning for all saccades made in the presence of the post when the retinal size exceeded 25 deg. (B) The histogram shows the same data as in A, but after the distribution has been reflected about the central axis and added to the original. The symmetric distribution is bi-modal and is well approximated by a linear sum of a two Gaussian distributions shown in blue (μ=0 deg, σ=40 deg) and orange (μ=±140 deg, σ=50 deg). (C) The two Gaussian distributions from B are repeated, and the histograms from B are segregated independently into landings (blue) and fly-bys (orange).
data show that some flies began to decelerate as far away as 10–20 cm from the post, a retinal size of 5–10 deg, which is equivalent to one or two ommatidial acceptance angles. In contrast, we did not find a significant correlation between deceleration initiation and retinal size for fly-bys \((R^2=0.031, n=142)\) or pseudo-landings in the absence of the post \((R^2=0.153, n=82)\). This suggests that the deceleration behavior seen in Fig. 8A is a unique hallmark of landing behavior.

If we now relax the requirement that flies do not turn after initiating deceleration, we see that these points also fall along a straight line (blue points, Fig. 8B). Furthermore, the regressions for turning and non-turning flies are very similar (Fig. 8B). Statistically, the slopes of the regressions are not significantly different from one another \(P(Y_1; X_2)=0.10\) and the differences in intercepts are only marginally significant \(P (X_2)=0.06;\) see Materials and methods). Because this deceleration pattern is uniquely indicative of landing behavior, the saccades performed after initiating deceleration were likely made with the intention of landing, and thus were intentionally directed towards the post.

To study leg extension in free flight we used a high speed video camera mounted directly above the post, equipped with an automated motor-driven focus-following system (see Materials and methods). Because of the limitations of high speed image capture (e.g. long downtimes between trigger events to allow for data transfer), we were only able to collect high speed imagery for a small subset of landings \((n=36)\). As suggested in previous tethered flight studies, we observed leg extension to be a highly stereotyped, all-or-nothing behavior (Fig. 8E). We determined the point of leg extension and initial touchdown for each video by visual inspection (see Materials and methods). In contrast to the start of deceleration, leg extension appears to be independent of flight speed, and unimodally distributed about retinal size \((61±22 \text{ deg})\). The final stage of deceleration took place after touchdown (which we defined as the first point of contact between a fly’s legs and the surface of the post). After touchdown, the flies decelerated from an average of 7.1 cm s\(^{-1}\) (±3.2 cm s\(^{-1}\), \(n=30)\) over the course of roughly half a body length \((1 \text{ mm})\). This would correspond to a constant deceleration of 2.9 m s\(^{-2}\) or roughly 0.3 g.

**Crash landings**

In observing the high speed sequences, it is clear that a sizable percentage \((35.7\%)\) of the landings were crashes in which the head or wings collided with the post before the fly extended its legs. In the cases of wing crashes (Fig. 9D), the fly’s wing struck the surface of the post and in nearly all cases the fly rotated towards the post, extended its legs, and ended up landing successfully. Head-on crashes (Fig. 9C) also resulted in leg extension in nearly all cases, but the end result appeared to depend on flight speed. Slower flies tended to recover quickly and land, whereas the faster ones bounced off the
Fig. 7. Flies make targeted body saccades away from the post and saccade amplitude is independent of turn direction. Saccade turn angle is plotted as a function of post angle for saccades performed by non-landing flies. The data shown are the same as in Fig. 6C, but with the omission of data points where the retinal size is less than 25 deg (see Fig. 4 for justification). The two lines show linear regressions for left turns: \( \psi = 2.68 \phi + 155 \) deg \((R^2 = 0.25, n = 342)\) and right turns: \( \psi = 2.47 \phi - 149 \) deg \((R^2 = 0.27, n = 270)\). Assuming bilateral symmetry in the behavior, the regression becomes: \( \psi = 2.58 \phi - \text{sign}(\phi) 152 \) deg \((R^2 = 0.259, n = 565)\). The light colored points represent shallow saccades towards the post when the post was close to 90 deg on either side of the fly. For reasons discussed in Results, these points were omitted when calculating the regressions. The histograms at the top show the distribution of left and right turns. The associated shading shows a Gaussian distribution \((\mu = 25 \text{ deg}, \sigma = 40 \text{ deg})\). The histograms on the right show the distribution of turn angle for left and right turns. The associated shading shows a Gaussian distribution \((\mu = 90 \text{ deg}, \sigma = 60 \text{ deg})\). The units are occurrences, and the black bars show the distributions associated with the light colored points, which were omitted when calculating the colored histograms.

DISCUSSION

In this study, we examined the landing behavior of *Drosophila* by analyzing their flight behavior in the presence of a conspicuous vertical post. Landings appear to consist of a temporal sequence of three distinct behaviors. First, flies actively turn towards the visual target *via* saccades that are directed toward the center of the post (Fig. 6A). The flies next begin to decelerate at a point that is a function of both their speed and the retinal size of the post (Fig. 8A,B), although in some cases deceleration is initiated prior to turning towards to the post (Fig. 8B). Finally, flies extend their legs just prior to touchdown when the post subtends an absolute size of approximately 61±22 deg on their retina (Fig. 8D). In contrast, flies that do not land make a targeted saccade away from the post when it subtends a retinal size of approximately 33 deg (Figs 6, 7).

Attractive and aversive saccades

The tendency for flies to fly towards prominent visual features, such as high contrast edges and posts, was first documented by Kennedy for tethered mosquitoes (*Kennedy, 1939*), and has been studied thoroughly in tethered (*Götz, 1968; Götz, 1987*) and free-flying *Drosophila* (*Maimon et al., 2008*). Over time, this so-called fixation behavior could be achieved *via* either smooth tracking, according to the model proposed by Reichardt and Poggio (*Reichardt and Poggio, 1976*), or a series of directed saccades (or both, as proposed by Land *et al., 1992* and observed in humans). Achieving target tracking through saccadic maneuvers has been proposed for hoverflies when visual targets lie out side their optical fovea (*Collett and Land, 1975*) as well as for houseflies chasing conspecifics (*Boeddeker et al., 2003; Boeddeker and Egelauff, 2005*). To our knowledge, our data provide the first evidence that *Drosophila* make targeted body saccades towards and away from visual features, although many tethered flight studies have suggested that they saccade in the direction of a visual target (*Heisenberg and Wolf, 1984*). Although subtle, this is an important distinction in that in order to perform a targeted saccade the magnitude of the turn – and not just the direction – must depend on the retinal position of the object prior to the turn.

Whereas the saccades directed towards the post do not seem to be triggered by specific target size, the distribution of aversive saccades suggests a trigger threshold of roughly 33 deg (Fig. 6D). This corresponds quite closely with data from a previous study in the same apparatus, using a different-sized post (1.27 cm diameter, 30 cm tall) (*Maimon et al., 2008*). Another study using magnetically tethered *Drosophila* (free to rotate about their yaw axis) reported earlier than for the black post \((P<0.001, \text{ supplementary material Fig. S3F})\). The second substantial difference is in the intercept of the linear regression associated with the turn angle of aversive saccades (supplementary material Fig. S3A,B). The regressions suggest that in the presence of the checkered post flies make a smaller turn (by approximately 40 deg) compared with those made in the presence of the black post \([P(\psi) = 0.03, 0.001, \text{ for left and right turns, respectively}]\). See supplementary material Fig. S3 for full statistical details.

Although neither deceleration nor leg extension is strongly correlated with post contrast (supplementary material Fig. S3C,D), the percentage of trajectories that ended in the fly landing in the presence of the checkered post (7.4%, \(n=662\)) was much lower than for the solid black post (29%, \(n=637\)). Of these landings (for which we had high speed data) a much higher percentage were crash landings in the presence of the black post (38.5% of landings on the black post, \(n=29\), were crashes) compared with the checkered post (18.5% of landings were crashes, \(n=27\)).
that flies exhibit aversive saccades in response to expanding squares when the retinal size reaches approximately 60°, with an estimated neural processing delay of about 50 ms (Bender and Dickinson, 2006). Electrophysiological recordings in locusts (Gabbiani et al., 1999; Gabbiani et al., 2001) as well as hawkmoths (Wicklein and Strausfeld, 2000) also support a triggering mechanism for aversive maneuvers that depends upon an absolute angular threshold. This retinal size threshold model, which is independent of contrast, also would explain why we did not observe a significant difference in the aversive saccades in experiments using the black and checkered posts.

The simplest implementation of a neural mechanism for achieving targeted body saccades would make use of the assumption that the fly’s body and head are oriented in the direction in which it is flying. By further analyzing the high speed video that we collected during our experiment we found that flies do not, in fact, always orient their bodies in the direction in which they are flying, even during straight flight segments, resulting in a slip angle that ranges between 0 and 50° (Fig. 10). The resolution of our video was not sufficient to resolve head motion, so it is possible that the flies partially corrected for this slip by adjusting the position of their head. Alternatively, the slip angle could be partly responsible for the variance in the observed turn angles we measured (Fig. 6A, Fig. 7).

Landings

The combination of free flight 3D tracking in a large volume and focus-following optics on a high speed camera enabled us to observe the complete landing sequence of freely flying Drosophila from approach and deceleration to leg extension and the final moments of touchdown. Despite the wide variety of approaches (Fig. 2), many of which show intermittent targeted body saccades towards the post, flies exhibit a clear pattern in when they initiate deceleration prior to landing (Fig. 8A,B). This pattern depends on a combination of their speed and distance to the post. However, it is very unlikely that the fly can accurately measure either its ground speed or its distance to the post directly. Given the constraints of the visual and mechanosensory systems available to the fly, it is more likely that they use a measure of the retinal size of the post (which is correlated with distance) and the rate of expansion (which is correlated with ground speed). For this reason, we re-plotted the linear fit from Fig. 8B in terms of the retinal size of the post, α (as defined by Eqn 1), and its retinal expansion velocity, Ω (Fig. 9):

\[ \Omega = \frac{d\alpha}{dt} = \frac{-2s(\gamma / d^2)}{\sqrt{1 - (r / d)^2}}, \]  

where \( s \) is the flight speed in the \( x-y \) plane, \( r \) is the radius of the post and \( d \) is the distance from the fly to the center of the post. This retinal size-dependent expansion threshold model (RSDET)
Visual control of landing in flies can be visualized by considering the approach trajectories of flies flying at constant velocity toward the post, plotted in the $\alpha - \Omega$ plane (Fig. 11). A fast flying fly crosses this threshold, and thus starts to decelerate, at a greater distance from the post than a slow flying fly. From the perspective of the fly, a relatively low rate of expansion is sufficient to trigger deceleration when an object size is small, whereas a higher rate of expansion is required when the retinal size of an object is large. Note that this model is independent of the actual physical size of the object, but by combining measures of $\alpha$ and $\Omega$, deceleration would not, for example, be triggered by a physically large, but distant object (because $\Omega$ would be too small). This principle is nearly identical to the rate of relative retinal expansion velocity model (RREV), previously proposed by Wagner for houseflies (Wagner, 1982). The RREV model states that insects should begin decelerating when the ratio of retinal expansion velocity to the retinal size of an object reaches a critical threshold:

$$ RREV = \frac{1}{\alpha} \Omega. $$

Wagner further simplified this definition as:

$$ RREV' = -2 \frac{1}{d}, $$

where $d$ is the distance to the center of the post and $s$ is the flight speed. Note, however, that this simplified definition is derived by making some approximations that are only valid when the distance to the object is much greater than the object’s radius. However, in many of the trajectories we recorded, flies initiated deceleration only after they were quite close to the post, at distances of the same order as the radius. Thus, although the RSDET and RREV models are fundamentally identical (both are a measure of the expansion relative to retinal size) and are probably experimentally indistinguishable, we will keep the terminology distinct for the sake of mathematical clarity.

Using the above approximation, the RREV model is formally the inverse of the time-to-contact ($\tau$), that is, the time before the fly will collide with an object assuming that it is indeed on a collision course and flying at constant velocity:

$$ RREV' = \tau^{-1}. $$

For reference, without any approximations the time-to-contact can be calculated as:

$$ \tau = \frac{-2 \sin \alpha / 2}{\Omega \sqrt{1 - \sin^2(\alpha / 2)}}. $$

Because of this relationship, the RREV model has been referred to as the time-to-contact model (Gabbiani et al., 1999). The time-to-contact model, using a time-to-contact threshold value of about 120 ms, can be made to fit our RSDET model quite closely up to retinal sizes of 80 deg (Fig. 9). Note that once flies are close enough to the post for it to reach a retinal size of 80 deg they have typically
already initiated deceleration (Fig. 8B), so comparing performance of either model beyond this point is not particularly meaningful.

Although the time-to-contact model may be an intuitive way of thinking about the time course of a trajectory, we prefer not to use this terminology because neither of two critical assumptions, constant velocity and a direct collision course, is valid for the flies' behavior. Furthermore, there is no need for the fly to actually calculate a time to contact when a simple retinal size-dependent expansion threshold calculation is sufficient. The three models, RSDET, RREV and time-to-contact, are all fundamentally the same with regard to the sensory inputs they use and the behaviors they predict.

Once the fly has started to decelerate it needs to control its speed such that it will reach a safe touchdown velocity prior to landing. This is not a trivial calculation, as there are no experimentally supported hypotheses for how a fly might accurately measure the distance between itself and a physical object. Previous work on honeybees landing on flat horizontal surfaces suggests that they use a simple controller that holds the rate of retinal expansion constant, elegantly guaranteeing that they reach a flight speed of nearly zero just before touchdown (Srinivasan et al., 2000). However, our data for fruit flies landing on a vertical post are not consistent with this model (e.g. when speed is plotted with respect to distance in a linear scale, we do not see a linear relationship between these two parameters). This should not be surprising, because the two experimental paradigms are fundamentally different (both in geometry and animals).

As the retinal size of an object and its derivatives are the only optical cues directly available to the fly, the most biologically plausible controller would use some combination of retinal size, rate of expansion and the rate of change of expansion. In Fig. 12, we show that both rate of retinal expansion ($\Omega$) and the rate of change of the rate of retinal expansion ($\dot{\Omega}$), could, in principle, be used to safely decelerate prior to impact without requiring a measurement of ground speed, object distance or a priori knowledge of how large the object is. In both cases, $\Omega$ is first put through a threshold function (Eqn 8), where the threshold ($\zeta$) is defined by the solid purple curve in Fig. 9:

$$\Omega_{z,k} = \max(\Omega_k - \zeta, 0).$$  

(8)

The discrete time control models for $\Omega$ (Fig. 12B) and $\dot{\Omega}$ (Fig. 12C) are defined by Eqns 9 and 10, respectively:

$$s_{k+1} = s_k - K_{\Omega} \Omega_{z,k},$$  

(9)

$$s_{k+1} = s_k - K_{\dot{\Omega}} \dot{\Omega}_{z,k},$$  

(10)

where $s$ is the flight speed in the x-y plane, $K_{\Omega}$ is the gain for $\Omega$, and $K_{\dot{\Omega}}$ is the gain for $\dot{\Omega}$. In order for Eqn 10 to be stable in the final moments of landing, we need to add the requirement that $\dot{\Omega}_{z,k}$ is greater than or equal to zero. These models, which match the general trend of the observed data, are provided only as proofs of concept that such controllers could be employed by the fly given the limited sensory information available to it. Future experiments will be needed to test whether or not flies actually use such algorithms.

The next stage of landing – leg extension – has been subject to more prior work than the rest of the landing sequence because of the ease of studying it in tethered flight preparations. Several hypotheses for the underlying neural mechanism that trigger leg extension have been proposed. One idea is that flies use the same sort of retinal size threshold trigger that is used for the expansion avoidance response. This model is supported by several studies on tethered flying Drosophila, which extend their legs at a fixed retinal size of about 50 deg with a neural processing delay of approximately 50 ms (Wittekind, 1988; Tammero and Dickinson, 2002b). Leg extension behavior in houseflies and blowflies, however, is
inconsistent with the retinal size threshold, because they will extend their legs in response to sinusoidal gratings expanding within a grating mask of fixed size (Borst and Bahde, 1986; Wehrhahn et al., 1982). The authors of these studies proposed a spatio-temporal integration model, in which flies integrate motion energy until a certain threshold is reached (Borst and Bahde, 1986). Note that because multiple pathways could trigger leg extension, these two hypotheses are not mutually exclusive. Alternatively, a fly could react to a sudden change in luminosity in its visual field, referred to as the temporal contrast model. This model has been proposed for triggering escape responses in stationary Drosophila (Holmqvist and Srinivasan, 1991; Trimarchi and Schneiderman, 1995) as well as leg extension responses in blowflies (Goodman, 1960), but does not elicit turning or leg extension in Drosophila (Tammero and Dickinson, 2002b). Finally, flies could use the ‘time-to-contact’ model, or the more general RSDET model that we proposed above as the trigger for deceleration.

Because we do not see any correlation between leg extension and flight speed, and thus rate of expansion (Fig. 8D), it is unlikely that either the spatio-temporal integration model or the RSDET model is responsible for triggering leg extension in free flight. The most parsimonious hypothesis for explaining the leg extension behavior we observed is a retinal size threshold model. The retinal size we measured for this threshold (61±22 deg, n=36) is remarkably close to a previously published result from tethered flies of about 50 deg (Tammero and Dickinson, 2002b).

However, it is unlikely that the leg extension trigger is as simple as a retinal size threshold, as many of the non-landing flies experience retinal sizes of approximately 60 deg, yet very few extended their legs (we did, however, observe some examples of non-landing flies extending their legs as if in preparation for landing). The additional requirement that the extent of the object needs to be centered on the field of view might prevent unnecessary leg extension during fly-bys, as they will typically have turned away from the post by the time it subtends 60 deg (Fig. 6D). This idea is consistent with psychophysical tuning curves from tethered flies, which show that leg extension is triggered by expansion centered on the fly’s retina, but not by lateral expansion (Tammero and Dickinson, 2002b).

The final stage of landing – touchdown – appears to be a stereotyped open-loop process, likely done without visual feedback. We did not find any indication that flies orient their bodies (and thus legs) in relation to the surface of the post, a behavior that has been observed in honeybees (Evangelista et al., 2010). Because honeybees weigh of the order of 200 times more than a fruit fly, and they often need to make more challenging landings, such as on flowers swaying in the breeze, it is not surprising that their landing sequence is more complex. The time between leg extension and touchdown is less than 50 ms for about 1/3 of the landings we observed (Fig. 13). This is such a short time frame (equal to the visual processing delay found in other experiments described earlier) that it is unlikely that this aspect of landing is under tight visual control. In the majority of touchdowns we observed that one of the two front legs would touch the post before the other. Because the legs were spread out, this asymmetric touchdown creates a moment arm that automatically orients the fly to the normal of the post surface.

**To land, or not to land?**

What factors determine a fly’s choice to land or not? Is the decision dictated solely by sensory experience, or does the animal’s internal state play a role? In other words, if two different flies started with the same exact initial sensory conditions, would they be likely to follow similar trajectories? A simple explanation for whether a fly lands or not would be that certain visual cues ultimately lead to landing while others lead to aversive maneuvers. We term this

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**Fig. 12.** Potential control models for deceleration. The purple trace shows the observed point of deceleration, repeated from Fig. 8B. (A) Observed speed vs retinal size traces, duplicated from Fig. 9A. Four arbitrary trajectories at different initial velocities are highlighted for clarity. Using the same initial conditions from the observed data in A, we simulated the time course of trajectories using two kinds of deceleration controllers: (B) \( s_{\alpha+1} = s_{\alpha} – 3500 \times \Omega_{C,k} \), (C) \( s_{\alpha+1} = s_{\alpha} – 170,000 \times d(\Omega_{C,k})/dt \), where \( \Omega_{C,k} \) is defined by Eqn 8. See Discussion for more details.

**Fig. 13.** Time elapsed between leg extension and touchdown is less than 100 ms for the majority of landings (n=36).
Crashes

Our focus-following system, which enabled us to capture the final moments of landing, revealed that 35.7% of landings were crashes (these crashes were excluded from the data shown in Fig. 8). Because our tracking system was unable to maintain fly identity over the course of our experimental runs, we cannot rule out the possibility that there are simply some individuals that are bad fliers, and we plan to address this question in the future. For the analysis in this paper we assumed that all flies behave similarly.

The result that the majority of crashing flies initiate deceleration at the appropriate time according to the RSDET model is of particular interest. It is not that the flies failed to decelerate; the problem appears to be that they did not decelerate fast enough. According to our proposed models for velocity control prior to landing, deceleration is controlled by some combination of the rate of expansion and the rate of change of expansion (Fig. 10). If the flies are able to measure expansion sufficiently well to trigger deceleration, why were they unable to use that measure to control their deceleration? One hint comes from the observation that flies crashed into the solid post more frequently than they crashed into the checkered post. It would make sense for the measure of expansion from the checkered post to be more accurate, as there are more contrast edges to use for calculating motion. However, perhaps a more important error in the crash landings than insufficient deceleration is the failure of these flies to extend their legs. If they were able to detect the presence and size of the post in order to initiate deceleration, why did they not extend their legs in time? One possible explanation for this is that leg extension may only be triggered if the flight speed is below some threshold. This hypothesis is supported by Fig. 8D and Fig. 9B, which suggest a threshold of approximately 0.2 m s\(^{-1}\). We plan to address these hypotheses in future experiments.

Post texture

Although subtle, the differences in behavior in the presence of the checkered and solid black posts deserve comment. The most apparent difference in behavior correlated with post texture was the fact that far fewer flies landed on the checkered post compared with the solid black post (Tables 1, 2). More experiments will be necessary to get a full understanding of why this is the case, but our current hypothesis is that under our experimental conditions, at distances beyond which the flies could resolve the individual checkers on the checkered post (~5–10 cm), the checkered post may not have been as conspicuous as the black post. This would have caused fewer flies to be attracted to, and thus land on, the checkered post. Furthermore, as flies show such a strong preference for navigating towards conspicuous vertical patterns, it would not be too surprising if they adjusted their behavior in the presence of such visual features by increasing flight speed. Together with the reduced saliency of the checkered post hypothesis, this would explain the slight difference in mean flight velocities we observed in landing flies in the presence of the black post (0.39±0.13 m s\(^{-1}\)) compared with the checkered post (0.32±0.13 m s\(^{-1}\)).

We also found that non-landing flies turn, on average, at a retinal size of 10 deg earlier in the presence of the checkered post (P(X2)=0.03 and 0.001 for left and right turns, respectively; see supplementary material Fig. S3 for complete statistical details). This suggests that the aversive saccade maneuvers are, to some degree, a function of object contrast. We found the same trend for leg extension, although the statistics are less convincing (P=0.08). These observations are in agreement with the similarly subtle results found in tethered flies (Bender and Dickinson, 2006), and favor a model in which the internal contrast of the object, and not just the position and expansion rate of its edges, influences the underlying visual processing. This may, at first, appear to be at odds with the contrast-independent retinal size threshold that we and others propose as the trigger for both aversive saccades and leg extension, but there could easily be two (or more) pathways for triggering these behaviors. For example, aversive saccade maneuvers can be elicited by wide field expansion (Tammero and Dickinson, 2002a). Alternatively, the circuitry that somehow tracks the expansion of edges might nevertheless be sensitive to internal motion. Indeed, a system using exclusively a retinal size threshold would have functional limitations, as it would cause a fly to either extend its legs or initiate an aversive saccade when a physically large, but very distant object reached the appropriate retinal size. By incorporating some sort of expansion threshold in addition to the retinal size threshold, these unnecessary triggers could be prevented. This addition to the model could explain the slight dependence on contrast we observed.

CONCLUSION

In conclusion, our findings suggest that flies have an internal state that guides their decision of whether to land or not. In both cases, flies actively turn towards the far edge of the post when the post is far away. Flies that do not land make targeted body saccades away from the post once it reaches a critical retinal size threshold of 33±17 deg. Landing flies, however, continue to make targeted body saccades towards the far edge of the post and eventually start to...
decelerate when a retinal size-dependent expansion threshold is reached, followed by leg extension, which is triggered by a fixed retinal size threshold of 61±22 deg, and finally touchdown (Fig. 14).

LIST OF SYMBOLS AND ABBREVIATIONS

- \( d \): distance to the center of the post
- \( n \): no. trajectories
- \( N \): no. data points (100t data points for each trajectory, where \( t \) is the duration of the trajectory in \( s \))
- \( r \): post radius
- \( \Omega \): retinal expansion velocity (deg \( s^{-1} \)), see Eqn 3
- \( RSDET \): retinal size-dependent expansion threshold
- \( \phi \): post angle, see Fig. 1B
- \( \psi \): angular velocity
- \( \alpha \): retinal size (deg), see Eqn 1 and Fig. 1B
- \( \tau \): time-to-contact
- \( \zeta \): expansion threshold, see Fig. 9
- \( \Omega \): retinal expansion velocity (deg \( s^{-1} \)), see Eqn 3
- \( \varphi \): angular velocity
- \( \psi \): angular velocity

ACKNOWLEDGEMENTS

The authors gratefully acknowledge Dr Andrew Straw, who wrote the 3D tracking software used for our experiments, Sawyer Fuller for building the wind tunnel apparatus, and Will Dickson and Peter Polidoro for their help in building the automated follow-focus system used for the high speed video recordings.

REFERENCES


Pseudo-Landings

Pseudo-Fly-by's
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<td>Turn after dec. initiation</td>
<td>Slope</td>
<td>Intercept</td>
<td>$R^2$</td>
<td>N</td>
</tr>
<tr>
<td>------------</td>
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<td>-------</td>
<td>-----------</td>
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<tr>
<td>Black</td>
<td>False (purple)</td>
<td>–0.21</td>
<td>0.22</td>
<td>0.82</td>
<td>111</td>
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<tr>
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<td>–0.19</td>
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<td>–0.13</td>
<td>0.2</td>
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