Report

A Simple Vision-Based Algorithm for Decision Making in Flying *Drosophila*

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Summary

Animals must quickly recognize objects in their environment and act accordingly. Previous studies indicate that looming visual objects trigger avoidance reflexes in many species [1–5]; however, such reflexes operate over a close range and might not detect a threatening stimulus at a safe distance. We analyzed how fruit flies (*Drosophila melanogaster*) respond to simple visual stimuli both in free flight and in a tethered-flight simulator. Whereas *Drosophila*, like many other insects, are attracted toward long vertical objects [6–10], we found that smaller visual stimuli elicit not weak attraction but rather strong repulsion. Because aversion to small spots depends on the vertical size of a moving object, and not on looming, it can function at a much greater distance than expansion-dependent reflexes. The opposing responses to long stripes and small spots reflect a simple but effective object classification system. Attraction toward long stripes would lead flies toward vegetative perches or feeding sites, whereas repulsion from small spots would help them avoid aerial predators or collisions with other insects. The motion of flying *Drosophila* depends on a balance of these two systems, providing a foundation for studying the neural basis of behavioral choice in a genetic model organism.

Results

Free Flight

To test whether flies respond differently to large and small visual objects, we placed a long post (31 cm high; 1.27 cm diameter), a short post (1.27 cm high, 1.27 cm diameter, suspended centrally with thin nylon monofilament), or no post at the center of an enclosed tunnel and tracked the trajectories of *Drosophila melanogaster* with a multicamera system (Supplemental Experimental Procedures available online) (Figure 1A). The main result of these experiments was that flying flies tended to steer clear of the small object, whereas they flew much closer to the long vertical post (Figure 1B, left and center). Trajectories in the long- and short-post conditions differed qualitatively from the case in which no object was present in the arena (Figure 1B, right), indicating that the animals were actively attracted to the long post and repulsed by the short one.

Flies rarely landed on the long post and instead turned away just before contact to avoid collision. Preliminary evidence suggests that flies are more likely to land on long posts if these objects are associated with an attractive odor (data not shown). However, under the conditions used in these experiments (i.e., in the absence of odor) flies would often revisit

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the long object, turning away each time as they approached within 1–2 cm (Figure 1B, center, dark trace). This avoidance elicited by the long post at short distances is consistent with a previously characterized collision-avoidance reflex [4] that is triggered when an expanding object subtends ~60° on the retina [4]. The conflict between long-distance attraction and short-distance avoidance of the long post is manifest in residence probability functions as a small, 1- to 2-cm-diameter exclusion zone within a larger zone of attraction (Figure 1B, center). However, the expansion-avoidance reflex cannot explain the considerably larger exclusion zone around the short post (Figure 1B, left). Inspection of individual trajectories (Figure 1B, left, dark trace) indicates that the flies reacted to the small post at a greater distance, and thus a smaller angular size, than in the long-post case.

We calculated the minimum Euclidean distance between each trajectory and the central 3D coordinate of each post. As expected from inspection of individual trajectories, flies approached closer to the center of the long post than the short post (Figure 1C; rank sum test, $p = 4.2 \times 10^{-5}$). At distances less than ~7 cm from the small post, at which point it subtends over 10°, there was a strong decay in the probability of approach (Figure 1C, arrow). The larger exclusion zone around the smaller object is also manifest in plots of residence probability as a function of distance from the x-y center of the arena (Figure 1D). Consistent with the minimum-Euclidean-distance analysis, these probability distributions showed that flies avoided a larger area around the short post (rank sum test, $p < 0.0001$). To more fairly compare the long- and short-post data, we only considered sample points within a middle z slice through the tunnel (15 cm thick) in these, and all subsequent, quantitative analyses.

What behavioral algorithms explain these free-flight results? One trivial possibility is that the flies took off closer to the long post than the short post but otherwise flew randomly within the arena. However, we found that the start locations of trajectories were consistent across the three experimental conditions (Figure S1), indicating that any differences in flight distribution must be due to the animals' behavior once airborne. During flight, behavioral reactions to the long and short post might be either directional (i.e., taxis) or nondirectional (i.e., kineses) [11]. A directional mechanism would involve explicitly steering toward or away from the objects, whereas a nondirectional mechanism would involve a change in translational speed or the rate of turning as a function of distance to the objects.

We found that nondirectional mechanisms could not fully explain the observed differences in residence probability (see Supplemental Data and Figure S2). To test for the presence of directed responses, we extracted two angular metrics for each sample point (Figure 2A), both determined after collapsing the data to the horizontal plane and assuming that the flies' heads were oriented in the direction of flight. (The extent to which the bodies or heads were not aligned with the direction of flight [12] will add noise to the results but should not bias them on average one way or the other.) "Post angle" is defined as the angle of the post relative to the tangent of the flight trajectory. This metric serves as a coarse estimate of the angular position of the post on the
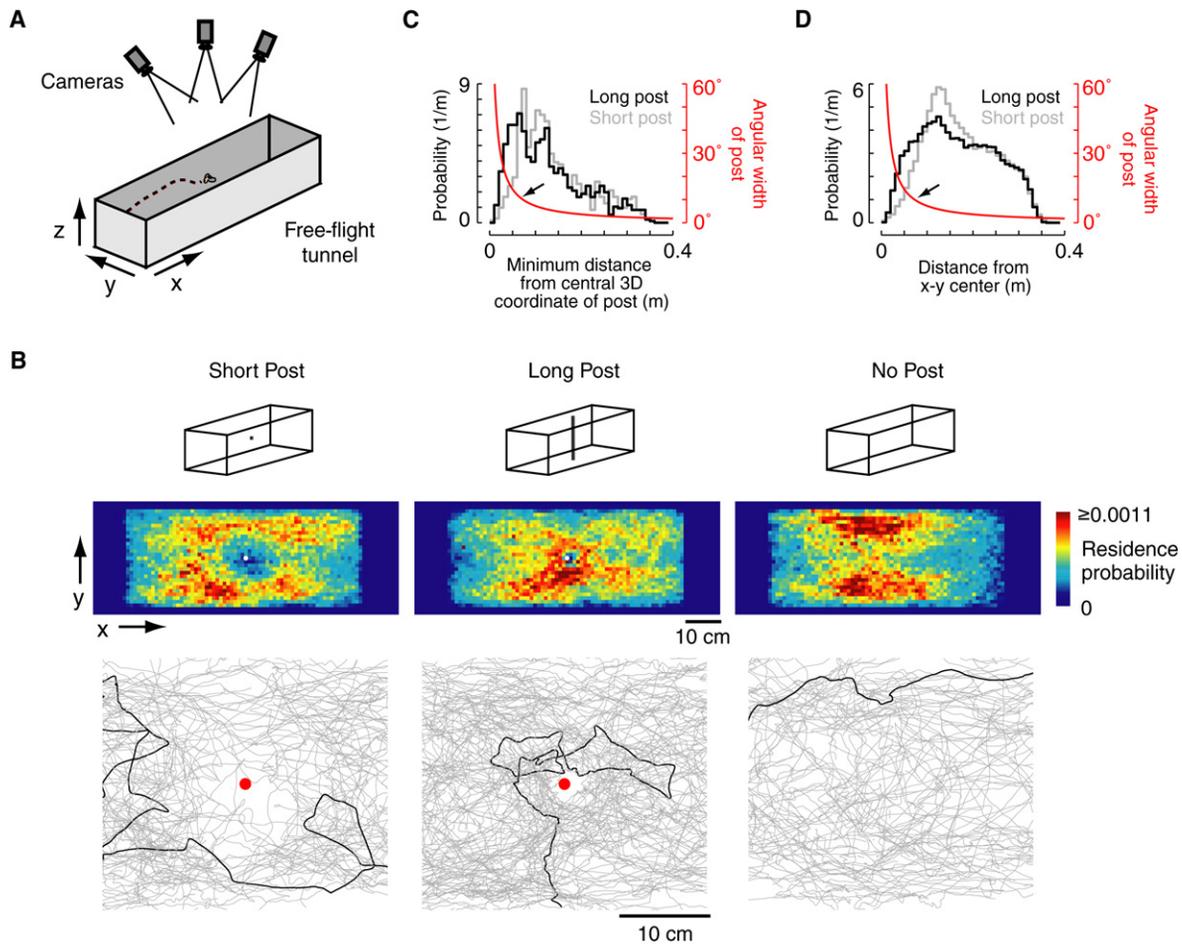
Figure 1. Flies in Free Flight Aggregate near a Long Post and far from a Short Post

(A) Arena.

(B) Residence probability and free-flight trajectories. A short post, a long post, or no post was placed at the center of the arena. In pseudocolor, we show residence probability histograms of the flight trajectories (1 cm² bins). Below, we plot raw trajectories in gray with one representative trace highlighted in black. Trajectories had to be longer than 3 s to be included in the residence probability analysis and 40 s or longer to be included in the raw-trace panel. White and red dots indicate the location of the posts, to scale.

(C) Distributions of the minimum 3D distance between flight trajectories and the center of the long post (n = 962) or short post (n = 715). The red curve depicts how the angular size of the small post, or width of either post, changes with distance from the object.

(D) Distributions of data points as a function of distance from the x-y center of the arena. The long post contains 426,879 sample points. The short post contains 314,232 sample points. The arrow in (C) and (D) indicates distance where small post subtends 10°. For (C) and (D), we analyzed trajectories >3 s long and only considered sample points in a 15-cm-thick middle z slice.

fly's retina. "Turn angle" is defined as the change in flight direction between consecutive samples. We averaged our calculation of turn angle within a 30 ms time window starting 30 ms after our determination of post angle. This delay was used because freely flying flies are known to react to visual stimuli within this time frame [13]. Plotting turn angle as a function of post angle, we observed that the flies actively turned away from the short post (Figure 2B, top). That is, with the post on the left (positive post angles), the animals turned right (negative turn angles), and vice versa. An aversive turn response was evident as far as 14 cm away from the short post, and such a finding could readily explain the exclusion zone in the residence probability functions (Figure 1B, left panel). At a distance of 14 cm, the small post subtended an angle of ~5° on the retina, indicating that the flies could respond to stimuli whose angular size was on the order of a single photoreceptor's acceptance angle. Note that with no post in the tunnel, there was also a weak tendency for the flies to turn

away from the center of the arena (Figure 2B, bottom), possibly explaining why the flies accumulated near the walls in the no-post condition (Figure 1B, right). However, this background response, probably due to the visual surround of the arena, was substantially smaller than the small-post response.

The long post elicited measurable turn responses as well, particularly 2–6 cm away from the object (Figure 2B, center). In this case, however, the functions were more complicated, presumably because they combined the effects of at least two visuomotor reflexes: fixation and looming-dependent collision avoidance. Fixation was evident from the positive slope of the response function at zero post angle, which indicates a stable equilibrium that kept the flies turning toward the object. At post angles of ± 40°–80°, the responses reversed, indicating that flies also steered away from the posts at these close distances. The functions indicated two additional stable equilibria at ± 90°, suggesting that some flies briefly orbited around the long post in a circular arc. Although we did find
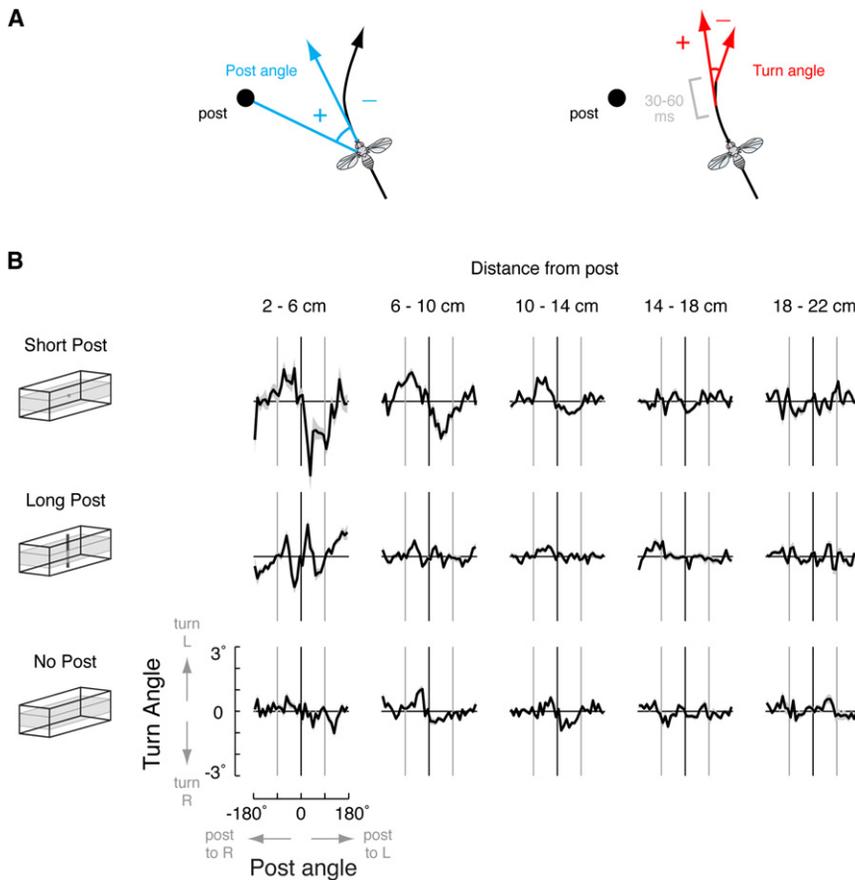
A

B

Distance from post

Figure 2. Flies Actively Turn toward a Long Post and away from a Short Post in Free Flight

(A) Angle definitions. The post angle refers to the angle of the post on the fly's retina (+ post on the left, − post on the right). The turn angle refers to the change in the direction of heading between consecutive samples, averaged 30–60 ms after calculating the post angle (+ left turns, − right turns).

(B) Mean "turn angle" as a function of "post angle" (10° bins) at various distances to the objects. Each plot averages ~40,000 sample points (min: 10,200; max: 67,540; mean: 46,673) from ≥30 flies (with pseudoreplication) (Supplemental Experimental Procedures). Standard errors are shown as gray regions around each curve. In the no-post condition, we calculated the distance to where the post would have been at arena center.

Tethered Flight

We measured the steering behavior of tethered, flying *Drosophila* in response to visual stimuli presented on an LED display [14, 15] (Figure 3A and Supplemental Experimental Procedures). Flies viewed a 15° wide vertical stripe of variable height (8°–94°). Our initial measurements were conducted under closed-loop conditions, in which the animal itself controlled the angular velocity of the visual stimulus. The fly's turn response was measured optically with a wing-beat analyzer [14], and the signal was used to control the angular velocity of the surrounding visual pattern (Supplemental Experimental Procedures). This closed-loop paradigm simulated purely rotatory flight; when the animal steered left, the stripe rotated rightward on the LED display, and vice versa.
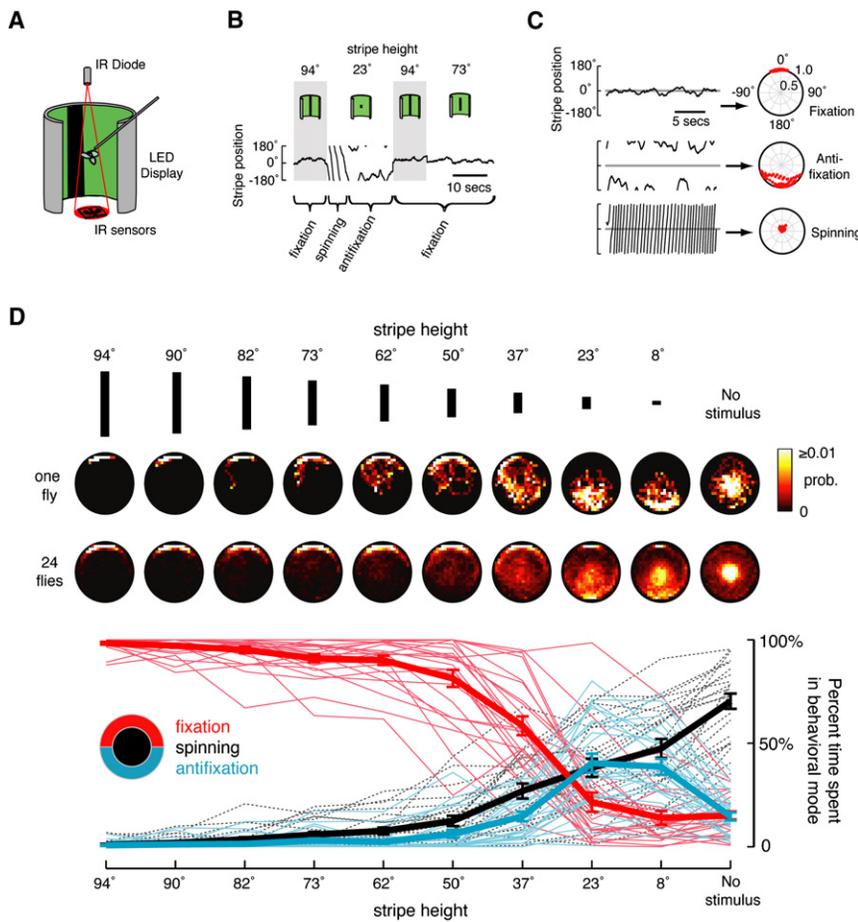
Figure 3B shows stripe position during a closed-loop experiment from a single fly. When presented with a long stripe, the fly stably maintained the stimulus in its line of flight (fixation [7, 8]). When presented with a short stripe, the fly first allowed the stimulus to rotate around the arena for a few seconds (spinning) and then kept the small object directly behind the line of flight (antifixation). Although spinning and antifixation superficially appear as distinct behaviors, it is likely that they are both manifestations of the same aversive reaction. *Drosophila* have a blind spot in the rear which leads to an instability in anti-fixation that often results in a bout of spinning. Like the individual in Figure 3B, flies presented with a short stripe often switched between bouts of spinning and antifixation. Further, the probability of spinning varied as a function of the feedback gain used in the experiment (data not shown), indicating that this behavioral state was strongly influenced by the dynamics of the closed-loop conditions. Despite these subtleties, the closed-loop data, like the free-flight results, indicate that long stripes attract and short stripes repel.

To further quantify the closed-loop data, we converted the time series of stripe positions into a polar format. We processed the data with a boxcar filter that calculated the mean vector orientation of the fly every 200 ms (Supplemental Experimental Procedures). After this transformation, fixation

examples of such trajectories (data not shown), interpretations of these responses must be made with caution. In addition to the fact that the functions in Figure 2 combined the effects of fixation and collision avoidance, flies are known to fixate not on the center but the edges of vertical stripes [10]. Edge fixation becomes an issue when flies are very close to the post, where the angle subtended by the object is large (Figure 1C, red line) and the difference between the center and the two edges of the object is significant. Thus, the accuracy of our post-angle measurements, which were coarse to begin with, decreased further as flies approached close to the object. Despite these caveats, the analysis in Figure 2 clearly indicates that flying *Drosophila* respond to short and long objects in fundamentally different ways.

The data suggest that aversion to small objects is not driven by expansion avoidance, but it is difficult to fully rule out this possibility with free-flight data. In particular, it is possible that expansion-based reflexes operate at a farther distance with the short post compared to the long post because the short post presents four expanding edges, whereas the long post presents only two. Past work in a tethered-flight simulator [4] argues against this explanation in that *Drosophila* behavioral responses are triggered when a small, expanding object reaches an angular size of ~60° [4], whereas in free flight, we observed aversion when the image of the short post was as small as 5°–10°. Nevertheless, to directly determine whether flies are averse to small, nonlooming objects, we conducted tethered-flight experiments in which flies observed stimuli that never expanded but had different shapes.

Figure 3. Flies Fixate Long Stripes, but Antifixate or Spin Short Stripes in Closed-Loop Tethered Flight

(A) Tethered-flight arena. The animal was tethered at the center of a cylindrical LED array. The beating wings produced signals in two optical sensors below the animal.

(B) Raw data from one fly. 0° indicates the bar is directly in front of the fly (+ bar on the left, − bar on the right). 180° and −180° indicates the bars are directly behind the fly.

(C) Polar-plot depictions of the time series data (see Supplemental Experimental Procedures).

(D) Polar-plot probability densities of one fly (top row) and averaged among all 24 flies (second row). We divided the polar plots into three non-overlapping regions (colored icon; Supplemental Experimental Procedures). The percentage of data points that fell into each region indicated the percentage of time the animals spent fixating, antifixating, or spinning each stimulus. These percentages are shown as a function of stripe height. Averaged data (±SEM) are shown with thick lines. Individual-fly data are shown with thin lines.

appears as a band of points at the top of the plot, antifixation appears as a somewhat broader band near the bottom, and spinning corresponds to points near center (Figure 3C). Averaged polar-plot probability densities showed that *Drosophila* fixated long stripes, whereas they antifixated or spun short stripes (Figure 3D).

To estimate the amount of time flies spent fixating, antifixating, or spinning each stimulus, we calculated the percentage of data points that fell in the front, back, or center of each polar plot (Supplemental Experimental Procedures). On average, flies fixated the longest stripe >95% of the time, and they antifixated or spun the shortest stripe >85% of the time (Figure 3D, bottom). A potential concern is that the flies were unable to see the smallest stimuli, whose height approached the interommatidial angle of ~5° [16]. However, control experiments in which the stripe was made invisible (but the angular position of this invisible stripe was still recorded) indicated that the flies did actively respond to even the smallest stimuli. The percentage of time spent antifixating a small stripe was significantly greater than the percentage of time spent antifixating in the control case (23° stripe versus no stimulus: paired t test, $p = 1.8 \times 10^{-5}$; 8° stripe versus no stimulus: paired t test, $p = 2.3 \times 10^{-6}$). Conversely, the percentage of time spent spinning a small stripe was significantly smaller than the percentage of time spent spinning in the no-stimulus control (23° stripe versus no stimulus: paired t test, $p = 2.2 \times 10^{-11}$; 8° stripe versus no stimulus: paired t test, $p = 1.0 \times 10^{-7}$).

Males of many dipteran species chase conspecifics in flight. *Drosophila* mating, however, does not involve aerial pursuit,

suggesting that male fruit flies may also be averse to small spots when flying. We tested males in the identical closed loop paradigm and found that male *Drosophila* are averse to short stripes, much like females (Figure S3).

In a natural scene, any object—such as a vegetative perch or an aerial predator—might appear as either a dark object on a bright background or vice versa, depending on their position with respect to the observer and the sun. Thus, if these reflexes are ethologically relevant, one would predict them to be independent of contrast polarity. For this reason, we repeated our flight-arena experiments after reversing the contrast sign of our stimulus (i.e., bright objects on dark backgrounds). The result was that long stripes attract, and short stripes repel, whether they are dark stimuli on a bright background or vice versa (Figure S4). This contrast invariance suggests that these phenomena are distinct from those briefly described in prior research (p. 206 in [16]); however, they are consistent with a recent analysis that systematically examined the effect of contrast on stripe fixation [15].

To examine the response of *Drosophila* to different-sized objects without the complication of feedback dynamics, we conducted a set of open-loop experiments, in which flies responded to visual stimuli but could not control them. Flies viewed a 15°-wide vertical stripe undergoing a sinusoidal horizontal oscillation (22.5° amplitude; 1 Hz) about a static mean angular position. In different trials, the stripe appeared at one of five angular positions, with one of six heights (8°–94°). The steering responses of a single fly are shown in Figure 4A. This animal turned toward the first two stimuli presented, which were long stripes, whereas it turned away from the third stimulus, a short stripe.

As expected, flies were attracted to long stripes (>67°), but repelled from short ones (<30°) (Figure 4B). We calculated the mean turn response of individual flies in a 4 s window
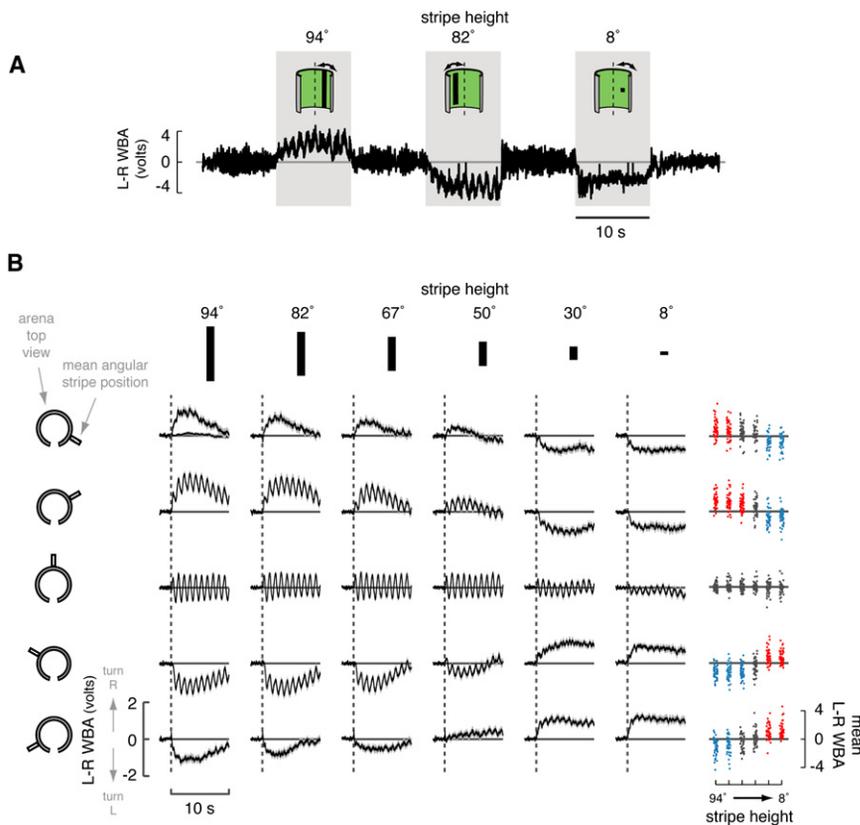
Figure 4. Flies Turn toward Long Stripes and away from Short Stripes in Open-Loop Tethered Flight

(A) Raw turn responses of one fly. Positive deviations of the curve indicate rightward turns; negative deviations indicate leftward turns. Ten seconds of closed-loop stripe fixation alternated with 10 s of open-loop stimulus presentation (gray regions) are shown. "L-R WBA" refers to left minus right wingbeat amplitude.

(B) Averaged turn responses of 44 flies. On a given trial, a stripe was presented with one of six possible heights (columns) and at one of five possible angular positions (rows; −120°, −60°, 0°, 60°, and 120°, top to bottom). The stimulus was on the right for the top two rows, on the left for the bottom two rows, and directly in front of the fly for the middle row. Dotted lines indicate the onset time of the open-loop stimulus. The top-left plot includes the averaged response to the presentation of a blank screen (curve near zero). Standard errors are shown as gray regions around each curve. For each row, we show the distribution of mean values from individual flies to the right (see main text). Distributions significantly different from zero, with positive means, are shown in red; distributions significantly different in from zero, with negative means, are shown in blue (t test, p < 0.01; Bonferroni correction for 30 comparisons). A random jitter was added to each dot's position along the abscissa for better visualization of each distribution.

starting 1 s after stimulus onset (Figure 4B, distributions on right). Long stimuli elicited attractive turn responses that were significantly different from zero; short stimuli elicited repulsive turn responses that were also significantly different from zero (t test, p < 0.01; Bonferroni correction for multiple comparisons). Note that tethered- and free-flight measurements were in quantitative agreement; 8°–30° high stimuli were aversive, whereas longer stimuli were attractive.

The open-loop responses revealed that long-stripe attraction and small-stripe repulsion have different dynamics. When stimuli were presented in the front hemifield, flies tracked the 1 Hz oscillation of the long stripe but responded to only the mean position of short stripes (Figures 4A and 4B, middle three rows). These differences in response dynamics could explain, in part, why closed-loop fixation of long stripes was more precise and why antifixation often led to spinning. Notably, flies did not follow the 1 Hz oscillation of any stimulus presented in the rear hemifield (Figure 4B, top and bottom row). Also, long-stripe attraction decayed with continuous stimulus presentation, whereas small-stripe repulsion remained steady with prolonged stimulus presentation. To characterize whether attraction and repulsion differed in their sensitivity to stimulus speed, we rotated either a long or short stripe around the flies in open loop, at various speeds, and measured the flies' steering responses (Figure S5). Long-stripe attraction was highly direction selective, being most sensitive to fast front-to-back motion [16, 17]. This selectivity is consistent with a system used for orienting toward landmarks; front-to-back motion would indicate drifting off course and thus should trigger a strong corrective response. In contrast, short-stripe repulsion was most sensitive to slow stimulus speeds and exhibited a similar response for both

back-to-front and front-to-back motion. Taken together, these differences in response polarity, dynamics, and direction selectivity suggest that the attractive and aversive reactions are mediated by separable sensory-motor pathways.

Discussion

Observations on free-flying flies (Figures 1 and 2) together with experiments on tethered flies in closed and open loop (Figures 3 and 4) demonstrate that *Drosophila* possess two opposing visuomotor reflexes that explain salient features of the animal's flight behavior. Animals are attracted to long vertical objects, whereas they are repulsed by small objects. The visually guided behaviors detailed in this manuscript are most probably mediated by motion-sensitive neurons downstream of photoreceptors R1–R6. Specifically, in the lobula plate of blowflies, "feature-detecting" cells respond vigorously to elongated vertical contours [18]. The homologs of these neurons might mediate fixation of long stripes in *Drosophila*. In houseflies and hoverflies, other neurons in the lobula plate and lobula respond best to small stimuli [19–21], and the homologs of these cells might underlie small-object aversion in *Drosophila*. Because we did not vary the chromaticity of our stimuli, we cannot exclude the contribution of color as an additional cue that flies use in triggering attractive and aversive flight responses.

Males of many fly species, including houseflies (*Musca domestica*, *Fania cunnicularis*), flesh flies (*Sarcophaga bullata*), and hoverflies (*Syritta pipiens*), chase females as part of courtship [13, 22, 23] (see also [C. Gilbert et al., 2003, Soc. Neurosci., abstract]). Long-legged flies (*Dolichopodidae*) and robber flies (*Asilidae*) prey upon small insects on the wing.

Thus, at least in certain behavioral contexts, some flying dipterans are attracted toward small spots, not repelled. *Drosophila*, however, do not prey on other insects, and courtship does not involve flight. From an ethological point of view, *Drosophila* would do well to avoid any small object in midair, even static objects (Figure 1), because these could only signify a hazard. In contrast, dipterans that chase conspecifics, or hunt while flying, require a more sophisticated algorithm that may, for example, rely on more complex features of object motion or color to differentiate repulsive predators from attractive mates and prey.

Our results indicate that flying flies use a rather simple vision-based algorithm to avoid potentially harmful objects. Might walking flies use a similar strategy? The visual-motor behaviors of walking *Drosophila* are likely to be more complicated because these flies exhibit social behaviors such as courtship and aggression while on the ground. For example, male flies could not chase and orient toward female flies if small objects were aversive to them. A brief report ([24] cited in [16]), suggests that walking *Drosophila* might exhibit a similar behavior as the one reported here for flying *Drosophila*, i.e., attraction to tall stripes and aversion to small spots. However, this behavior is not consistent with studies using "Buridan's paradigm," which show that walking flies respond equivalently to long and short visual objects [25], or an earlier study that did not report either clear attraction to or repulsion by small objects [10]. Collectively, these studies do not present a simple picture of comparable reflexes in walking *Drosophila*, as might be expected from the more complicated suite of behaviors that occur on the ground.

Here, we describe a new visuomotor reflex—small-object repulsion—that has a measurable influence on free-flight behavior. Whereas the neural mechanisms of this reflex remain unknown, the differing responses to long and short objects suggest that the two behaviors may be, at least partly, mediated by different neural circuits (although it is likely that many of the same cells are activated in both behaviors, especially near the sensory and motor periphery). An intriguing possibility is that the visual control of flight in *Drosophila* arises from a handful of partly nonoverlapping sensorimotor neural pathways, including long-object fixation [14], small-object repulsion, expansion avoidance [4, 5, 26], optomotor equilibrium [27], and landing responses [5, 28–30]. These innate behaviors, and potentially others yet to be discovered, could additionally be modified by learning [31]. The molecular tools available in *Drosophila* should allow for a rich, mechanistic description of each individual pathway. More significantly, however, elementary rules governing the interaction of these putative sensorimotor modules may come into sharper focus, thereby allowing for the formulation of a bottom-up, biologically driven theory of behavior.

Supplemental Data

Additional Discussion, Experimental Procedures, and five figures are available at http://www.current-biology.com/cgi/content/full/18/6/464/DC1/.

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