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Report

Visually Mediated Motor Planning in the Escape Response of *Drosophila*

Gwyneth Card[1] **and Michael H. Dickinson**[1,*]
[1]Bioengineering
California Institute of Technology
Pasadena, California 91125

Summary

A key feature of reactive behaviors is the ability to spatially localize a salient stimulus and act accordingly. Such sensory-motor transformations must be particularly fast and well tuned in escape behaviors, in which both the speed and accuracy of the evasive response determine whether an animal successfully avoids predation [1]. We studied the escape behavior of the fruit fly, *Drosophila*, and found that flies can use visual information to plan a jump directly away from a looming threat. This is surprising, given the architecture of the pathway thought to mediate escape [2, 3]. Using high-speed videography, we found that approximately 200 ms before takeoff, flies begin a series of postural adjustments that determine the direction of their escape. These movements position their center of mass so that leg extension will push them away from the expanding visual stimulus. These preflight movements are not the result of a simple feed-forward motor program because their magnitude and direction depend on the flies' initial postural state. Furthermore, flies plan a takeoff direction even in instances when they choose not to jump. This sophisticated motor program is evidence for a form of rapid, visually mediated motor planning in a genetically accessible model organism.

Results

As described previously [4], we used a high-speed video camera to capture the motion of fruit flies in response to a 14-cm-diameter black disk that fell toward the animals along a 50° downward trajectory. Individual flies were loaded into small opaque vials from which they climbed through a narrow tube onto the center of a $5 \times 5\ \text{mm}^2$ platform. We triggered the descent of the black disk and started video capture once a fly had settled on the horizontal surface of the platform. Ninety-six percent of the flies responded to the descending disk by jumping into the air and initiating flight. A typical escape sequence is shown in Movie S1, available online. The mean delay between the start of the stimulus and the onset of flight (measured by the loss of tarsal contact of the mesothoracic legs) was 215 ms ± 42 ms (mean ± SD). Because we do not know when the flies first notice the stimulus, this value represents an upper limit on the time window, within which all of the sensory-motor processing for the escape behavior occurs.

Although the stimulus approached the platform from the same direction in each trial, the azimuthal angle of the stimulus relative to the fly's body axis (θ) varied across trials because the flies settled on top of the platform with different orientations (Figure 1A). To determine whether flies bias their takeoff direction to avoid the threatening stimulus, we measured each fly's initial azimuthal angle heading over the duration of leg extension. As shown in Figures 1B and 1C, flies tended to jump away from the looming stimulus, even when the stimulus approached from directly in front. We tested for bias in our experimental apparatus by dropping the disk from the opposite side of the platform, but we found no positional effect ($p \geq 0.05$, Watson-Williams test). In order to analyze our results with more statistical rigor, we reflected all the rightward approaches across a line of bilateral symmetry and parsed our data into five 36° bins of approach angle (Figures 1D, 1E, and 1F). An analysis with circular statistics [5] indicated that flies jumped backward in response to looming objects in front of them and jumped forward in response to looming objects behind them (binned means not different from $\alpha = 0°$ and 180°, respectively; $p = 0.05$, one-sample test for mean angle). In response to stimuli approaching from the side, however, flies jumped at an angle that was approximately halfway between directly away ($\alpha = \theta + 180°$) and directly forward ($\alpha = 0°$) (binned means at $36 < \theta < 72°$ and $72 < \theta < 108°$ are significantly different from $\alpha = 0°$ and $\alpha = 180°$, $p = 0.05$; Figure 1F). This forward bias is not surprising, given that voluntary takeoffs elicited by either attractive odors or internal cues are almost always in the forward direction (data not shown).

An approaching predator (or, in our case, a falling disk) creates both visual and mechanosensory cues that a fly might use to compute the direction for an escape. To test whether visual cues alone are sufficient, we repeated our experiments with a clear acrylic windshield placed between the falling disk and the takeoff platform [6]. For the five different binned values of stimulus direction, we found no significant difference in behavior in the presence or absence of the windshield ($p \leq 0.02$). We conclude that although mechanosensory cues might still play a role, visual information alone is sufficient for a fly to determine the direction of an approaching threat.

A fly might bias its initial heading by either modulating its leg motion so as to jump away from a threat or, alternatively, jumping forward but then quickly using its wings to steer while jumping. To test between these hypotheses, we repeated our analysis of takeoff direction on flies whose wings had been surgically removed. Ninety-seven percent of wingless flies (35 out of 36) jumped in response to the looming stimulus (see Movie S2). As shown in Figures 1E and 1F, the initial heading of wingless flies was statistically indistinguishable from normal winged flies in all 36° clusters of θ except $0 < \theta < 36°$. Although wing forces might still contribute, these experiments demonstrate that the leg motor system alone is sufficient to bias the direction of takeoff. We also performed the reverse experiment—testing the escape responses of flies with intact wings whose mesothoracic legs (T2) had been surgically removed (Figures 1D and 1E and Movie S3). Although they cannot jump, these flies were also able to escape away from the looming stimulus by "leaning" in the right direction before takeoff. These flies do not jump into the air, but the aerodynamic force created by their wings lifts them off the substratum in a direction determined by their leaning posture. The results were identical to controls in all θ groups except $108 < \theta < 144°$ (Figure 1F). Together with the prior experiments,

*Correspondence: flyman@caltech.edu

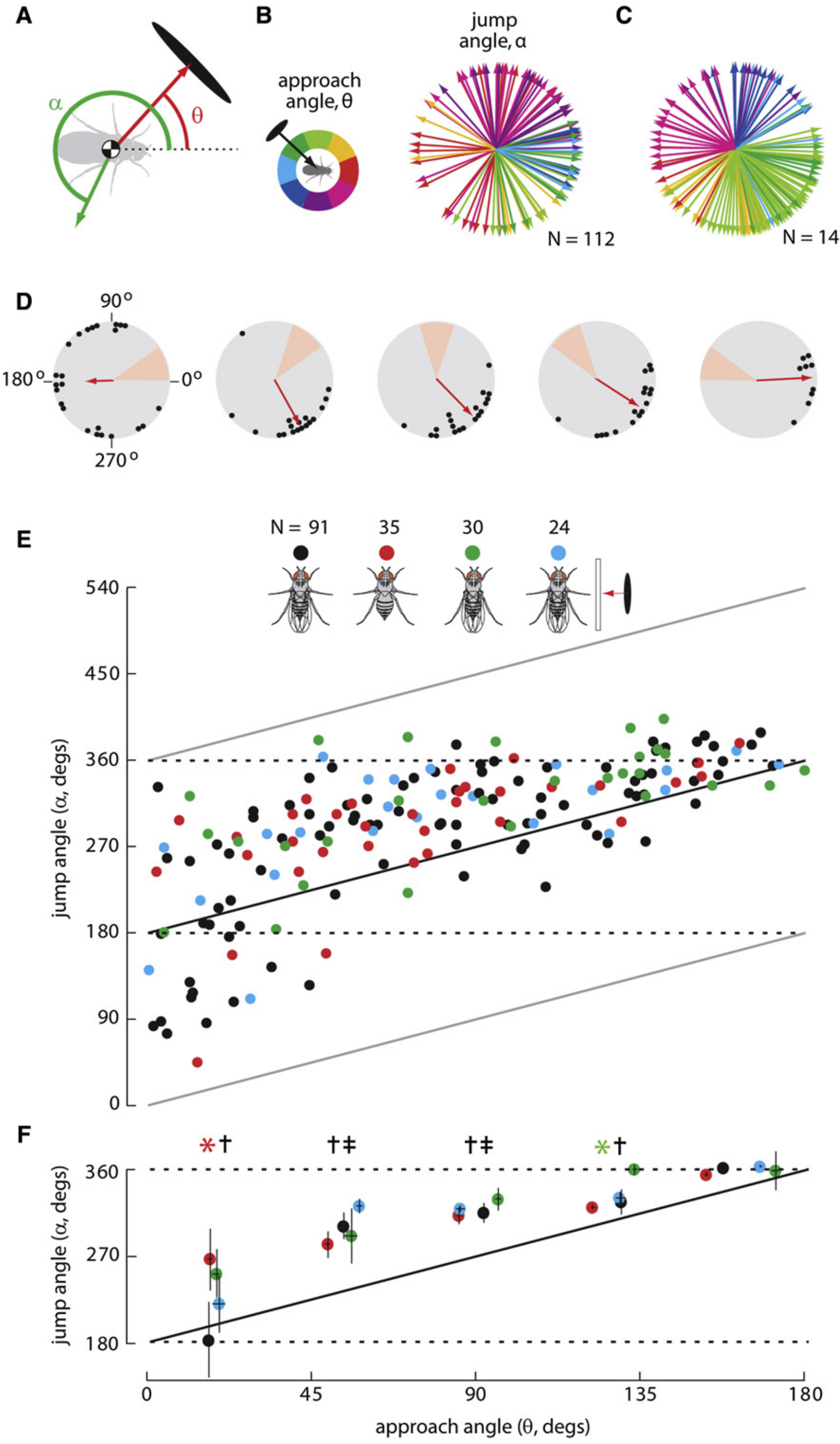

Figure 1. Flies Control Their Escape Direction in Response to a Visual Looming Threat

(A) We measured the azimuthal position of the stimulus (θ) and the direction moved by the fly's center of mass (COM) during the resulting escape jump (α) relative to the initial heading of the fly (indicated by the dotted line).

(B and C) Each arrow shows the direction (α) jumped during one trial and is colored by stimulus direction (θ, see inset). (C) plots data from prism-platform experiments; see Figures 2 and 3.

(D) Assuming bilateral symmetry, we transformed all data to represent responses from left-side approaches ($0^\circ \leq \theta \leq 180^\circ$). We plotted α (black dots in 5° bins) for each of the five 36° ranges of θ (indicated by the light red wedge); the red arrow indicates the circular mean jump direction, and its length is inversely related to data angular dispersion.

(E) A linear representation shows α as a function of θ for different experimental treatments: normal flies (black, as in [D]), flies with wings excised at the wing hinge (red), flies with T2 legs clipped (green), and normal flies behind a clear acrylic windshield (blue). The dashed lines indicate hypotheses for how the data should be distributed if the flies always jump forward ($\theta = 360^\circ$) or backward ($\theta = 180^\circ$), regardless of stimulus direction. Gray diagonal lines show where the data would be expected to fall if the flies always jumped directly toward the stimulus ($\theta = \alpha$). The black diagonal line indicates where the data would fall if the flies always jumped directly away from the stimulus ($\theta = \alpha + 180^\circ$).

(F) Circular means and standard deviations for each experimental treatment, grouped into the same 36° θ bins shown in (D). In each θ group, we compared the mean jump direction under normal conditions (black) to several hypotheses, as indicated by the symbols above each cluster: "†" The circular mean is significantly different from 0° or 360° ($p = 0.05$, one-sample test for the mean angle [5]). "‡" The mean is significantly different from $\theta + 180^\circ$ ($p = 0.05$, one-sample test for the mean angle). "*" The normal fly mean was significantly different from the mean of the other treatment, indicated by color ($p \leq 0.02$, Watson-Williams test [5]).

these results indicate that escaping from looming objects involves a sensory-to-motor transformation in which a visual estimate of the azimuthal orientation of the stimulus is transformed into postural changes that predominantly determine takeoff direction.

To better resolve the postural changes that precede flight, we modified our observational platform by replacing the opaque platform with a right-angle prism (Figure 2A and Movie S4) so that we could image both the side and underside of each fly. Using this arrangement, we could determine the position of the six tarsal contacts and each fly's center of mass (COM) at two time points: before release of the stimulus (t_0) and just prior to takeoff (t_{pre}) (Figures 2A and 2B). Because only the T2 legs provide thrust during takeoff, we chose to measure the position of each fly's COM relative to a coordinate system determined by the line segment connecting the T2 tarsi and that segment's perpendicular bisector (Figure 2B). The results indicate that flies actively reposition their COM away from the direction of the looming stimulus (Figure 2B) and that this orientation accurately predicts the direction of their subsequent jump (Figure 2C). Examples of these behaviors for stimulus approaches from the front, side, and back are provided in Movies S4, S5, and S6.

Our analysis indicates that the COM motions elicited by different stimulus directions are brought about by different combinations of leg placement (lifting the legs and placing

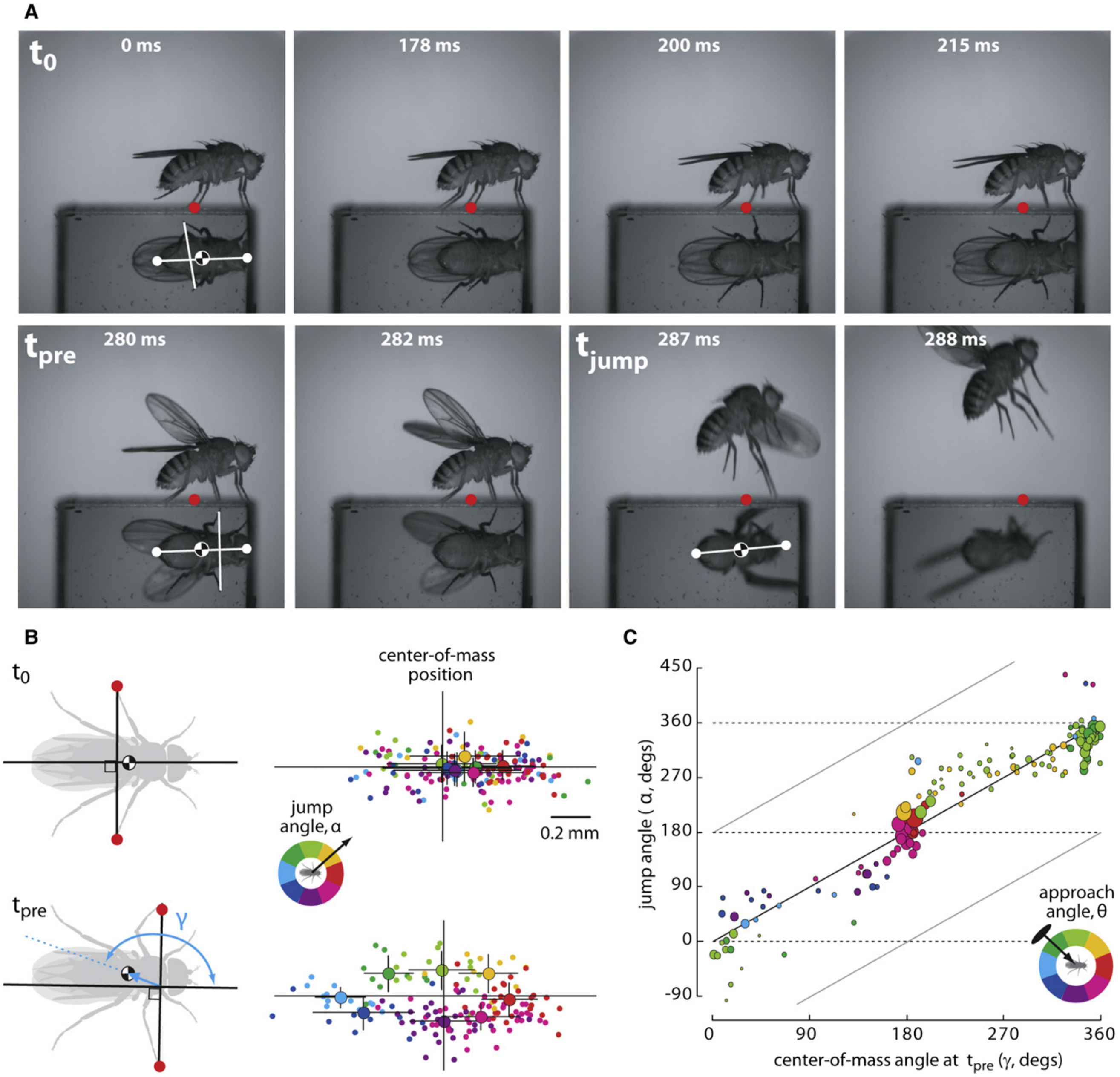

Figure 2. The Relative Position of the COM and T2 Jumping Legs after Preflight Movement Determines Jump Direction

(A) A video sequence with the prism platform shows a typical escape. The looming stimulus approaches from in front of the fly (right-hand side of the images). Time stamps denote milliseconds elapsed since stimulus onset. White dots on the prism image mark the head and abdomen points used to determine the fly's COM (black and white circle) at three time points: stimulus onset (t_0), immediately before the jump (t_{pre}), and the moment of takeoff at the end of the jump (t_{jump}). The red dot marks the contact point of the T2 tarsi with the surface at t_0.

(B) We plot the COM locations ($n = 147$) relative to axes determined by a line connecting the left and right T2 tarsi and a perpendicular line that bisects that segment. Each colored dot represents the location of the COM of a fly during a single trial at t_0 (top) or t_{pre} (bottom). Colors indicate the direction the fly subsequently jumped (α, see inset). Large circles with error bars represent COM position (mean ± SD) for eight clusters of data, parsed according to the jump angle, α (45° bins).

(C) Jump angle (α) as a function of the angle of the COM location at t_{pre} (γ). The size of each point is proportional to the length of the COM vector (γ), and the color indicates the angle of stimulus approach (θ, see inset). Dashed, gray, and black lines are used as in Figure 1E.

them in new locations) and leaning (shifting the body position by altering joint angles without changing tarsal position). The most prominent leg placements were the lateral movements of the T2 legs along an axis parallel to the longitudinal axis of the body, which shifted the COM forward or backward relative to the points of tarsi-ground contact. In contrast, the leaning movements primarily resulted in a sideways relocation of the COM, both in real-world coordinates and relative to the T2 tarsi. The magnitude and direction of both these motions varied strongly with the angular location of the looming stimulus. The functions shown in Figures 3A and 3B amount to maps of the sensory-motor transformation that relates the azimuthal position of the looming stimulus in visual space to a set of motor actions that will determine jump direction. For example, a frontal stimulus position (θ = 0°) elicits a large forward longitudinal motion of the T2 legs, whereas a rear position elicits a small rearward motion of the T2 legs. This visuomotor transformation results in a proper alignment of the COM so that the fly's subsequent jump will carry it away from the looming threat. In contrast, sideward stimulus directions (θ = 90° and 270°) do not elicit lateral motions of the T2 legs, but rather lateral leaning movements that move the COM to an appropriate location for a sideward jump. The efficacy of these leaning movements in biasing jump direction is demonstrated by the performance of animals that are missing the T2 jump legs (Figure 1 and Movie S3).

The sensory-motor transformation that enables flies to jump away from looming threats might consist of a simple feed-forward motor program in which a stimulus arriving from a particular visual direction triggers a particular motor program for leg motion, regardless of the initial posture of the body. Alternatively, the motor program might take into account the fly's postural state before and during the preflight movements. In this case, a fly would not change its orientation if by chance its body happened to be in the correct posture for a directed escape before the threatening stimulus was detected, whereas the movement would be exaggerated if a fly was out of position when it first observed the stimulus. To test whether preflight motor programs compensate for initial posture, we parsed all takeoff sequences into two categories, those in which the COM was (1) anterior or (2) posterior to the line connecting the T2 tarsi (Figure 3C). Within these two groups, we examined cases in which the looming disk approached from within the 90° sectors either in front of or behind the animal and measured the motion of each fly's tarsal contacts and COM in world coordinates (Figure 3C). The results indicate that flies do indeed compensate for the initial posture of the body. The effect of prestimulus posture is most easily seen in the placement of the T2 legs along the anterior-posterior axis in response to stimuli approaching from the front (θ = 0°). If their COM started anterior to the T2 tarsi, flies make a large forward corrective movement with their T2 legs prior to takeoff (Figure 3C). This forward movement of the legs is accompanied by a backward motion of the body. In contrast, if the COM starts posterior to the T2 legs—closer to the "correct" position for a backward takeoff—the flies make small rearward leg movements. Thus, the polarity of the longitudinal leg motion is dependent on the flies' postural state when the stimulus is detected.

We repeated this analysis to examine motor planning for sideways escapes by parsing sequences according to whether each fly's COM was to the (1) left or (2) right of a longitudinal axis that was perpendicular to the line connecting the T2 tarsi (Figure 3D). We then compared cases in which the looming stimulus approached from within the 90° sectors from the left or right of the fly. Although the leg movements in preparation for sideways takeoffs are more complicated than for forward or backward takeoffs, the analysis confirmed that a fly's preflight motor program compensates for initial posture. For example, when the disk approaches from the left, flies with a leftward-biased COM exhibit a large postural change to shift their COM to the right, whereas flies with a rightward-biased COM make a much smaller change in COM position. Further, the data show that the preflight motor program is distributed throughout all thoracic neuropils: Although the motion of the T2 legs tends to be greatest, the pro- (T1) and meso- (T3) thoracic legs also contribute to the preflight postural changes.

We found that the dependence of preflight positioning movements on initial COM position holds at very fine resolution for all stimulus directions. Figure 3E shows vector maps of COM movement from each COM starting position for all eight stimulus directions (see Experimental Procedures). The COM movements in each panel appear to converge on a single location, which we suggest represents the target of the escape motor program for that stimulus direction. This interpretation is supported by the locations of the black dots in each panel of Figure 3E. These points, which are replotted from Figure 2B, are the average COM locations at t_{pre} for trials in which flies jumped within particular 45° sectors. For example, in the top subpanel (light green vector field) in which the stimulus approached from the fly's left, the black dot represents the mean COM location for all jumps in a 45° sector to the right. In this and other subpanels, the movement vectors appear to converge on the COM location that would carry the animal away from the looming stimulus. According to this model, each stimulus position in visual space maps not to a stereotyped motor response, but rather to a COM target location.

A timeline for the various components of the escape behavior, aligned according to the time of takeoff (t_{jump}), is shown in Figure 4B. The first manifestation of the flies' response to the looming stimulus is the positional changes of their T1 and T3 legs. Flies that were grooming at the time the stimulus was released placed their tarsi down on the platform during this period. Approximately 200 ms later, the flies begin to reposition their T2 legs. Just after the T2 legs start to move, flies start to raise their wings in preparation for takeoff. Prior to takeoff, there is a distinct pause in the motion of the T2 legs, which is followed by their rapid extension to power the jump. Throughout the course of these experiments, we observed many cases in which flies displayed early components of an escape without ever jumping. Out of the 147 individuals tested, five flies exhibited both leg and wing motion but never jumped, three flies moved their legs but never raised their wings or jumped, three flies adjusted only their wings but did not jump, and six flies exhibited no motion at all. The most parsimonious explanation for this behavioral timeline is that early components (e.g., motion of front and back legs) are activated by the looming stimulus at lower thresholds, whereas later components (e.g., wing elevation and jumping) are activated at higher thresholds (Figure 4D). The model indicates how a sophisticated motor behavior might be constructed from a simple set of separate motor actions [7].

Discussion

We have shown that in response to a threatening stimulus, *Drosophila* exhibit a set of motor actions prior to flight initiation that are responsible for determining the initial direction of the escape. Within approximately 200 ms, the fly estimates the direction of an approaching visual stimulus and encodes a motor program that will move the body into an appropriate position to jump away from the looming threat. This behavior, which effectively plans the direction of takeoff, occurs approximately 100 ms earlier than all previously identified components of the escape response [4, 8, 9], and it is not reflexively coupled to flight initiation because a fly can prepare for an escape without taking off. The involvement of all six legs indicates that this motor program coordinates leg movements across all three thoracic segments. The dependency of the behavior on initial postural state suggests that the fly uses either efference copy [10] or proprioceptive feedback in generating the leg-movement commands. Leg proprioceptors and associated local

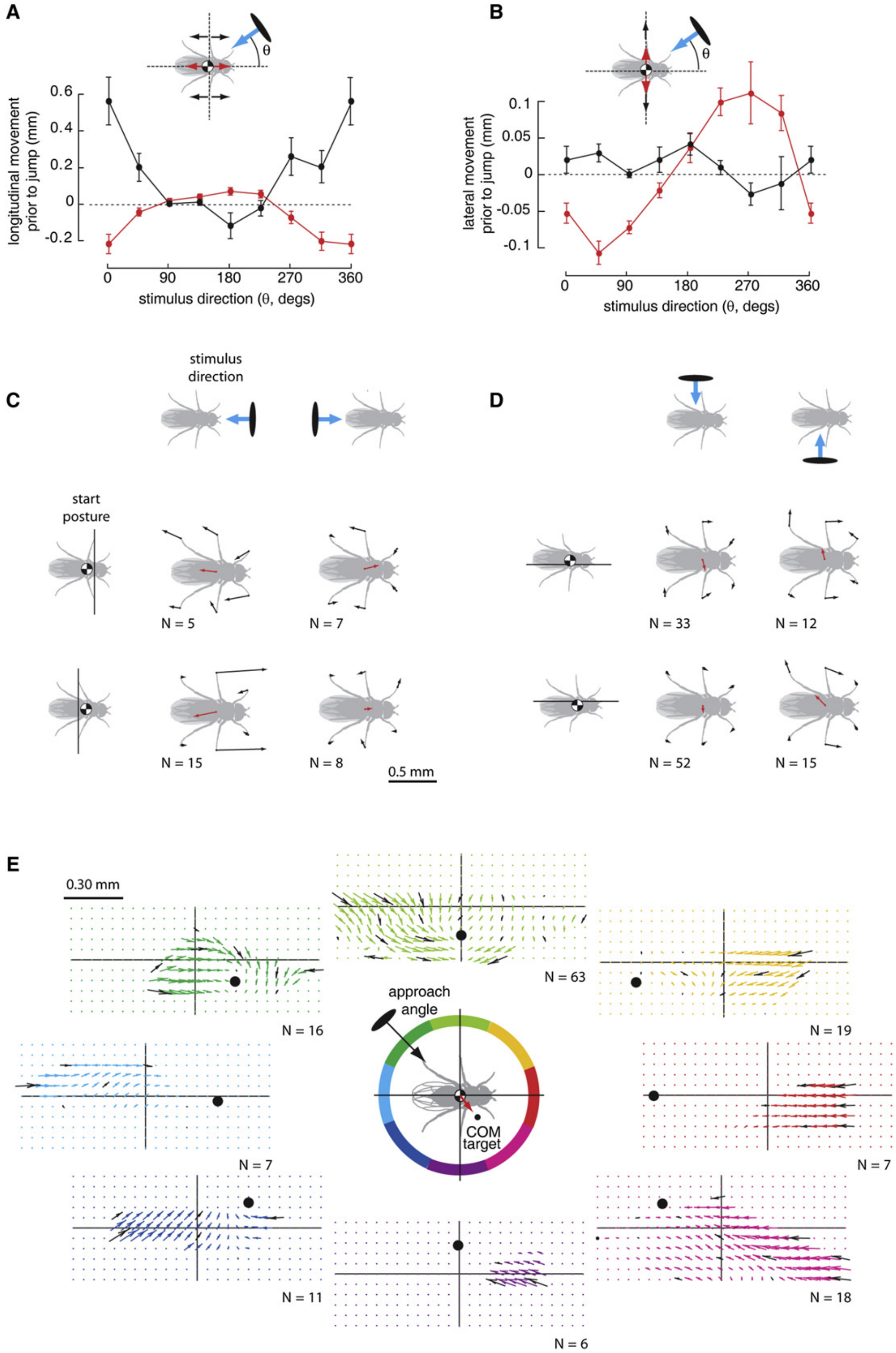

Figure 3. Preflight Movements Vary according to Postural State

(A) and (B) Longitudinal and lateral movements (mean ± SEM) of the T2 legs (black) and COM (red) in world frame, prior to the jump as a function of stimulus direction.

(C and D) Vectors indicate motions of the legs (black) and COM (red) for different starting positions of the COM relative to the T2 tarsi. (C) shows responses to stimuli approaching from a 90° sector either in front of or behind the fly for flies whose COM at t_0 was either behind (top) or in front of (bottom) a line connecting the T2 tarsi. (D) shows responses to stimuli approaching from a 90° sector either to the left or right of the fly for flies whose COM at t_0 was either to the

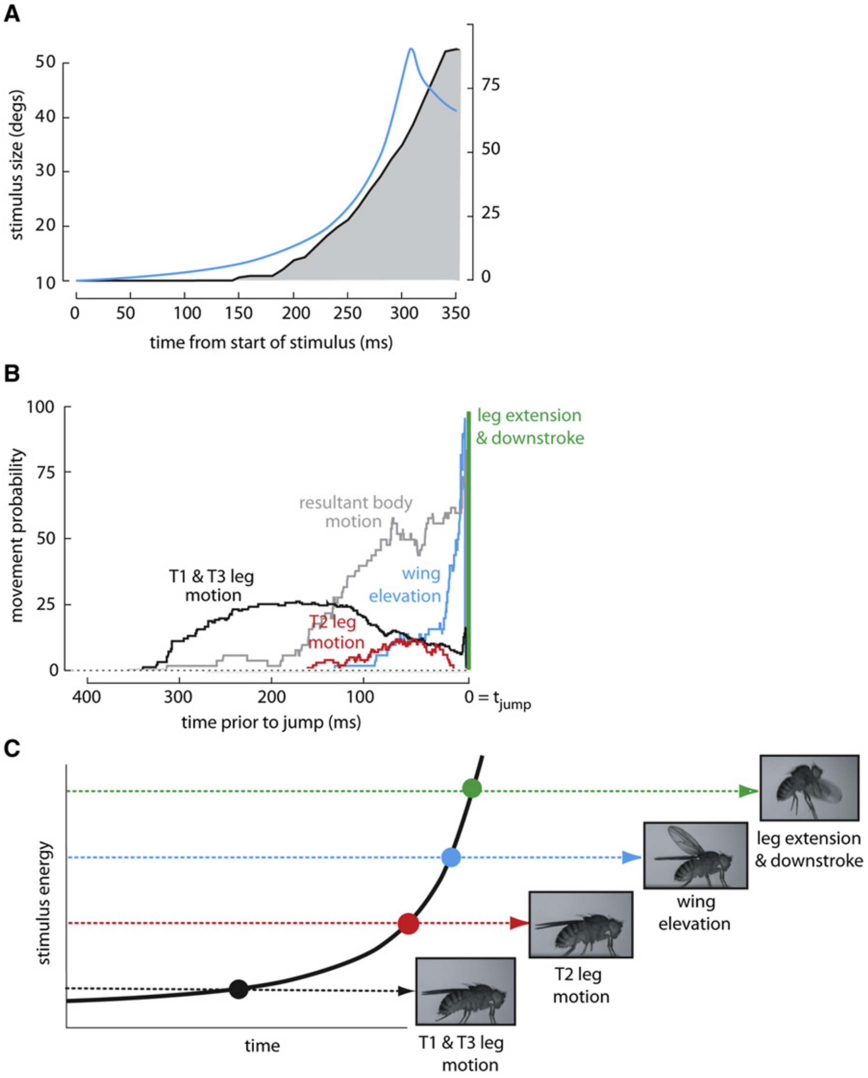

Figure 4. A Simple Model for Preflight Motor Planning

(A) The cumulative probability of takeoff (indicated by the shaded area) in relation to the time course of increasing stimulus size (indicated by the blue line), n = 177.

(B) The probability that a particular part of the fly was moving at time points prior to the jump: T1 and T3 legs (black), T2 legs (red), wings (blue), body (gray), n = 50. The green line indicates the takeoff itself, in which legs extend rapidly and wings stroke downwards.

(C) A simple model for how flies may direct movement of their COM before takeoff. As stimulus energy increases with the increasing visual angle of the looming disk, it crosses the thresholds for different independent motor programs. T1 and T3 leg movement occurs first, indicating that this motor program may have the lowest activation threshold. In a typical backward-jumping sequence, motor commands to reposition the T2 legs are activated next, possibly followed by wing elevation. Finally, when the stimulus energy is very high, rapid leg extension of the middle legs is activated to complete the takeoff sequence.

thoracic circuits might be sufficient to provide such feedback [11], in which case descending commands from the brain might be identical regardless of initial posture. Alternatively, the proprioceptive feedback might project anteriorly to modify descending commands from the brain according to postural state.

A pair of large-diameter interneurons called the giant fibers (GF) [3, 12, 13] are thought to trigger visually mediated escape responses in flies by coordinating the rapid bilateral contraction of leg extensor and wing-depressor muscles [2, 14, 15]. An as-yet-unidentified small-diameter pathway is activated even earlier in the escape sequence to raise the wings prior to takeoff [4, 8, 16]. Neither the GF pathway nor the wing-raising pathway, however, could easily explain the behaviors we describe here. GF activation elicits immediate bilateral leg extension and thus could not activate early events within the escape sequence, and the preparatory leg movements occur with a variable delay prior to wing elevation and are thus unlikely to be triggered by the same pathway (Figure 4). Further, we observed examples of animals shifting leg posture without raising their wings. We conclude that the early planning movements must be triggered by another as-yet-unidentified pathway that conveys visual information to thoracic circuits that control leg motion. This early component of the behavioral sequence presumably increases the effectiveness of escape by directing the animal away from a would-be predator. Such tactics do not guarantee success. For example, a recent comparative study shows how painted redstarts (*Myioborus pictus*) exploit flies' escape behaviors to flush them from the substrate into the air [17]. It is even possible that such a predator might learn to anticipate the direction of the fly's takeoff, although we know of no such evidence.

Some features of this behavior are similar to those that have been described for jumping locusts. Before voluntary jumps, locusts can use motion-parallax cues to aim toward specific visual targets [18]. In response to looming visual objects, locusts exhibit directional "hiding responses," in which they lean their bodies away from the threat to hide behind a post

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left (top) or right (bottom) of the midway point on the line connecting the T2 tarsi. The vectors represent the motion of the legs and COM between two time points: t_0 and t_{pre} (see Figure 2A). Each vector represents the vector mean for the indicated number of trials.

(E) Vector fields for relative COM motion for eight different stimulus directions (see center icon for color code). The origin of each vector indicates a fly's COM at t_0 relative to the T2 tarsi. Black vectors indicate the vector sum of COM movements, measured between t_0 and t_{pre}, over 0.2 × 0.1 mm rectangles centered on the vector origin. Colored lines are interpolated (see Experimental Procedures). Vector length is proportional to movement magnitude. Grid points without vectors are starting locations for which we could not interpolate expected movement given the limited data set. The large black circle in each plot represents a target location to which the fly might move its COM in order to jump directly away from the stimulus, determined on the basis of the data in Figure 2B, which shows the mean location for the COM at t_{pre} for each of the eight relevant jump directions. The number of trials contributing to each vector field is indicated in each panel.

they are grasping [19]. Locusts can also direct their jumps away from looming stimuli [20], although their accuracy is coarser (forward ± 50°) than that reported here for flies, which can direct their jump in any direction, including backward. The greater accuracy of flies is probably due to the fact that they use agile middle legs to jump, rather than powerful hind legs, and thus need not overcome as much of a biomechanical bias to jump forward as do locusts [21]. Both locusts and flies direct their jumps with leg and body motions prior to leg extension. However, in locusts these postural adjustments occur after the start of cocontraction of the extensors and flexors of the femur-tibia joint, whereas the comparable movements of flies are the earliest components of the escape sequence. This sequence of aiming the jump prior to leg extension is possible because flies do not need to cocontract the muscles of their jump legs to store energy before takeoff. With respect to the flies' ability to adjust their escape motor program on the basis of initial position, there is no evidence that locusts compensate for their postural state in planning for jumps. However, locusts do exhibit load compensation [22] in their directed grooming movements [23], indicating that their targeted leg motions do make use of proprioceptive feedback.

Collectively, the results from studies on flies and locusts suggest that the insect central nervous system is capable of transforming particular azimuthal positions in visual space to a set of spatially targeted trajectories in motor space (Figure 3E). We propose that this information is utilized by the motor system through a set of independent descending pathways with different thresholds of activation (Figure 4B). A similar model has been suggested for the responses of locusts to looming stimuli, in which an unknown pathway activates early cocontraction of the jumping legs, whereas the descending contralateral movement detector (DCMD) may trigger subsequent events in the jump sequence [24]. In structure, the fly's escape behavior fulfills the criteria for motor planning, which is considered a hallmark of vertebrate cortex [25]. Comparative neuroanatomical studies of insects suggest that such transformations may take place within the central complex [26], a set of evolutionarily ancient midline neuropils in the arthropod brain. In the future, it will be of interest to dissect this behavior with the genetic and physiological approaches that are available in *Drosophila*.

Experimental Procedures

We used 3-day-old female *Drosophila melanogaster* from a laboratory culture as described in [4]. In other animals, we excised the T2 legs near the femur-coxa joint. We used high-speed video cameras (Photron, San Diego, CA) to record images at 5400 frames per second. The falling-disk stimulus and the methods for calibrating the high-speed video camera are described in [4], with the exception that flies emerged onto a flat 5 mm^2 plastic platform in the current study. The starting position of the disk was 420 mm from the center of the platform. The disk radius was 70 mm and accelerated toward the fly at an angle of 50° relative to horizontal. The disk fell toward the center of the platform for 250 mm (for a period of 300 ms) before it was stopped by a foam block. In some trials, this platform was replaced with a 5 mm^2 right-angle prism to enable imaging of the ground contact of all six tarsi. The entire imaging area was surrounded by backlit white cloth.

For each sequence, we marked the location of the fly's head and the end of its abdomen in the video frame 1.85 ms before the middle legs began to extend (t_{pre}) and in the frame when the tarsi first left the ground (t_{jump}). For data taken with the prism platform, we also marked the contact points of all six legs with the ground at t_{pre} and t_{jump}, and we marked body and leg points at stimulus onset (t_0). The fly's COM is well approximated by the halfway point between the head and abdomen. The fly's prestimulus heading vector was determined from the orientation of the head-abdomen line at t_{pre} (Figure 1) or t_0 (Figure 2). The jump direction was determined from the vector spanning the COM position at t_{pre} to the COM position at t_{jump}. The leg and COM movements shown in Figures 3C and 3D are the vectors oriented from the tarsal contact point (or COM) location at t_0 to the new contact point (or COM position) at t_{pre}. To make the vector fields shown in Figure 3E, we found the vector representing each fly's t_0-to-t_{pre} COM movement relative to the T2 tarsi. We then binned these vectors according to the COM location at t_0. Grid spacing for the bins was 0.2 mm in the longitudinal direction (x) and 0.1 mm in the lateral direction (y). We then interpolated these binned COM movement vectors to a finer mesh with 0.5 × 0.5 mm spacing by using a standard implementation of Delaunay triangulation in Matlab (The MathWorks, Natick, MA).

All statistical measures were taken with procedures appropriate for circular data [5]. To assess the significance of our results in Figure 1, we analyzed the distribution of jump directions for each experimental group (normal, clipped-wing, clipped-leg, and wind-blocked) in each of the five 36° bins for stimulus direction (θ). We used two tests for circular data to compare our results. To compare the observed mean jump direction to the hypothesis that the fly jumped forward ($\mu_a = 0°$) or away from the stimulus ($\mu_a = \theta + 180°$), we used the one-sample test for mean angle, which is analogous to the one-sample t test for linear data. The hypothesis that the observed mean direction, μ_o, is the same as a hypothesized mean direction, μ_a, was tested by determining whether μ_o was within a 95% confidence interval around μ_a. To compare mean jump directions between experimental conditions (e.g., normal flies versus clipped-wing flies), we used the Watson-Williams test, which calculates the probability that two experimental groups are sampled from one population with a single mean. The reported p value in Figure 1F is the probability that the observed variance in the two sample populations has occurred by chance. We consider $p \leq 0.05$ to indicate that the two populations have significantly different means.

Supplemental Data

Supplemental Data include six movies and can be found with this article online at http://www.current-biology.com/cgi/content/full/18/17/1300/DC1/.

Acknowledgments

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