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## A simple strategy for detecting moving objects during locomotion revealed by animal-robot interactions

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### Abstract

An important role of visual systems is to detect nearby predators, prey and potential mates[1], which may be distinguished in part by their motion. When an animal is at rest, an object moving in any direction may easily be detected by motion-sensitive visual circuits[2, 3]. During locomotion, however, this strategy is compromised because the observer must detect a moving object within the pattern of optic flow created by its own motion through the stationary background. However, objects that move so as to create back-to-front (regressive) motion may be unambiguously distinguished from stationary objects because forward locomotion creates only front-to-back (progressive) optic flow. Thus, moving animals ought to exhibit an enhanced sensitivity to regressively moving objects. We explicitly tested this hypothesis by constructing a simple fly-sized robot that was programmed to interact with a real fly. Our measurements indicate that whereas walking female flies freeze in response to a regressively moving object, they ignore a progressively moving one. Regressive motion salience also explains observations of behaviors exhibited by pairs of walking flies. Because the assumptions underlying the regressive motion salience hypothesis are general, we suspect that the behavior we have observed in *Drosophila* may be widespread among eyed, motile organisms.

### Results

The task of identifying moving objects in the environment is relatively easy for a stationary animal, but much more difficult for one that is translating. As an animal moves forward through the world, the image of each stationary feature in the environment will move on the animal's retina in a front-to-back direction with an image velocity that is inversely proportional to its distance from the observer[4]. The net result will be a radiating pattern of progressive image motion with a focus of expansion in the direction of motion. An exafferent stimulus caused by the motion of a small moving entity is thus challenging to detect because it must be distinguished within the large reafferent stimulus generated by

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self-motion. A robust solution to this detection problem is difficult because it requires compensation for self-motion as well as knowledge of the spatial distribution of objects in the environment[5, 6]. Consider, however, an animal on a flat plane that translates forward through the world with no rotational velocity (Fig. 1A). Under these conditions, both moving and stationary objects can create progressive motion on the retina, but only moving objects can create regressive motion (Fig. 1B). Thus, we expect that the visual systems of motile organisms should be particularly sensitive to back-to-front visual motion during locomotion, a hypothesized phenomenon we call ‘regressive motion saliency’. We emphasize that saliency to regressive motion, though a useful ‘rule of thumb’, would not constitute a general solution for the detection of moving objects during locomotion because such a detector would be insensitive to an animal that was moving so as to create progressive optic flow, and the strategy requires straight locomotion without rotation.

We first observed anecdotal evidence for regressive motion saliency while examining the behavior of female fruit flies, *Drosophila melanogaster*, within a large flat arena. These observations and subsequent analysis were derived from previously published data[7]. In particular, we observed two types of peculiar behavioral interactions that occurred when pairs of flies walked near one another on either parallel or intersecting paths. In one type of interaction, which we term ‘T-stops’, two flies walked toward one another on a collision course, but one fly led the other such that it would have reached the intersection point first (Fig. 2B,C). In such cases, we observed that the leading fly continued on its course, whereas the lagging fly stopped, as if to allow the other fly to pass. From accurate camera-based measurements of each fly’s trajectory[7] we estimated the azimuthal motion of each fly on the retina of the other fly (Fig. 2A,B). The patterns show that as the interaction begins, both flies would have seen the approaching animal as a small spot that is relatively stationary on its retina. As the flies draw nearer, however, there is a perceptual bifurcation that depends on whether a fly is leading or lagging. The fly that reached the intersection point first experienced the progressive motion of the other fly’s image, whereas the lagging fly experienced regressive motion. According to the regressive motion saliency hypothesis, the lagging fly stops walking because it is able to detect the presence of a nearby organism, whereas the leading fly continues walking because it does not.

Another type of interaction we observed occurs when two flies walked next to one another on roughly parallel courses, an interaction we term ‘drag races’ (Fig. 2D,E). In these instances, the faster of the two flies continued on its course past the slower fly, while the slower fly stopped. Reconstructing the pattern of image motion for each fly indicates that the slow fly experienced regressive motion whereas the faster fly experienced progressive motion. Again, these behaviors can be explained by regressive motion saliency, assuming that walking female flies reflexively freeze when they detect a nearby moving object.

Although the anecdotal observations described above provide evidence for the saliency of regressive motion they do not provide a rigorous test of the hypothesis nor do they exclude the importance of other sensory cues such as image expansion or fly pheromones. The main factors that interfered with a thorough quantitative analysis of data collected from large groups of flies were the influence of the arena boundary and the fact that, because many flies were moving in the arena at once, it was not possible to isolate the stimulus created by a

single individual. On the other hand, arena experiments performed with small groups of flies do not result in large numbers of analyzable interactions. To circumvent these problems and test the regressive motion hypothesis explicitly, we constructed a simple fly-sized robot that could be programmed to interact with a single real fly. The robot consisted of a small, fly-sized magnet that was actuated by a system of three servomotors controlling the horizontal position and orientation of a larger sub-stage driver magnet (Fig. 3). We developed a machine vision system to track the position and orientation of both the fly and robot, and custom software that controlled the ‘behavior’ of the robot - making it depend on the behavior of the fly. To test the regressive motion saliency model, we programmed the robot to wait until the fly approached it, at which point it would start to move in a rectilinear path so as to create regressive or progressive motion over a range of different angular velocities in the fly’s reference frame (Supplementary Movie 1). For each trial, we calculated the average angular velocity of the robot’s image on the fly’s retina during the 200 ms time window beginning at the onset of robot motion. Preliminary experiments indicated that walking female flies responded to the movement of the robot by freezing, a behavior that is consistent with our observations of fly-fly interactions. In contrast, male flies sometime freeze but often initiate a courtship sequences that included chasing, orientation, and singing. Because the female behavior was easier to analyze, we conducted our analysis of regressive motion saliency in female flies, using freezing behavior as our proxy for whether the flies detected the moving stimulus or not.

To quantify each fly’s response to this stimulus, we analyzed its translational velocity[8] to determine whether it stopped or continued walking during the 850 ms period following the start of robot motion. We also determined each fly’s angular velocity at the start of the trial by differentiating the orientation of its body axis as measured by our machine vision system. Example encounters between a female fly and the robot for both progressive and regressive motion trials are shown in Fig. 4A–D. In Supplementary Movie 2, we provide further examples represented both as an animation in lab coordinates and as a ‘fly’s eye view.’ In the progressive motion cases shown (Fig. 4A,B), the flies continued walking after the onset of robot motion, whereas they quickly stopped after the onset of regressive motion (Fig. 4C,D). Note that as shown in Fig. 4B, forward motion of the robot may still result in progressive motion with respect to the fly’s retina, provided that the robot is moving slower than the fly. This condition is analogous to the drag races plotted in Fig. 1D,E, with the robot playing the role of the slower fly. Because of the automated nature of the experiments, we were able to capture very large data sets. Fig. 3E shows the results of 10,047 fly-robot interactions involving 46 different females. We excluded trials in which the fly stopped walking before the robot started moving (10%). We also excluded trials in which the fly rotated more than 45° within a 1 second time window which began 200 ms before the start of robot motion (14%). This latter criterion excluded cases in which the fly would have experienced large field visual rotation generated by self-motion at the start of the trial, thereby strongly violating the assumption of straight motion required by the regressive motion saliency hypothesis (see also Fig. 4H). Histograms showing the distribution of stimulus angular velocity for all trials as well as the subset of trials that resulted in stops are shown in Fig. 4E. The data in the histograms may be used to calculate a population measure of  $P_{\text{stop}}$  (the probability that a fly stops in response to the robot’s motion) as a function of

the stimulus angular velocity experienced by the fly (Fig. 4F). In addition to constructing the summed probability function by pooling together the trials of all individuals, we also derived probability functions for each fly, and determined a population estimate of the mean and variance of  $P_{\text{stop}}$  in each angular velocity bin (Fig. 4G). The strong similarity between the pooled and average functions indicates that the phenomenon is robust across flies. For progressive motion,  $P_{\text{stop}}$  is roughly constant ( $\sim 0.15$ ) for all angular velocities. The fact that  $P_{\text{stop}}$  is never zero is expected from the intermittent nature of fly locomotion in which the walking bouts of solitary flies are interrupted with stops even in the absence of obvious external stimuli[8]. For regressive motion,  $P_{\text{stop}}$  rises steeply with increasing stimulus angular velocity to a value of about 0.6. Higher values of  $P_{\text{stop}}$  are obtained by imposing even more stringent criteria on the acceptable angular velocity of the fly at the start of the trial. Fig. 4H plots the range of stop probability curves for trials that were parsed according to the flies' absolute angular velocity at the start of the trial. The performance in response to regressive motion is greatest when the flies were walking with low angular velocity at the start of robot motion ( $< 10 \text{ deg sec}^{-1}$ ) and degrades monotonically with increasing angular velocity. An increased difficulty in detecting the moving stimulus when flies are experiencing large field rotatory optic flow is entirely consistent with the regressive motion saliency hypothesis and suggests that the visual circuits responsible are not endowed with a sophisticated mechanism to compensate for the reafferent stimulus created by rotatory self-motion. The upper red curve in Fig. 4H also suggests that flies exhibit some low level ability to detect the robot when it moves progressively, provided they walk with very low angular velocity.

As a control for vibrations and auditory cues generated by the sub-stage motors, we collected 3528 'no robot' trials from 14 flies in which the small magnet was removed from the top of the arena (Fig. 4F,G). The values for  $P_{\text{stop}}$  in these controls show no dependence on the direction of the stimulus angular velocity that would have resulted if the robot had been present (Fig. 4G). The baseline value for  $P_{\text{stop}}$  in these controls is lower than in the experimental case, suggesting that the presence of the robot does somehow influence the flies' behavior even during progressive motion trials, although not in a way that is dependent on the direction of stimulus angular velocity. One possibility is that the mere presence of a nearby physical object might increase stop probability, whether or not the object moves.

One alternative hypothesis to regressive motion saliency is that flies are not more sensitive to back-to-front motion per se, but rather respond more strongly to motion (of any direction) in the rear visual field relative to the front. To test for this, we calculated  $P_{\text{stop}}$  after parsing the data according to the position of the robot at the start of motion. As indicated in Fig. 4I, the shape of the  $P_{\text{stop}}$  curves for data from the front and rear visual fields are quite similar, indicating that differential sensitivity to motion at different azimuthal positions cannot explain the flies' sensitivity to regressive motion. Another cue that the fly might use to detect the approach of the robot is the expansion of its image[9]. However, as seen in the time series plots of Fig. 4A–D, in which the angle subtended by the robot throughout the trial is plotted as width in the bottom row of blue traces, the robot generated little or no expansion during each trial. Indeed, in precisely 50% of all trials resulting in stops, the image of the robot was actually contracting at the start of motion.

The probability curves in Figs. 4F–H were generated from trials in which the fly-robot distance at the onset of motion ranged from 5 to 75 mm. However, the ability to detect a moving object is likely to depend on the size of the object and thus its distance to the observer. In Fig. 4J,  $P_{\text{stop}}$  is plotted for a range of regressive angular velocities ( $-100$  to  $-40$   $^{\circ}/\text{sec}$ ) as a function of the absolute distance between the fly and robot at the start of each trial. The data show that for regressive motion,  $P_{\text{stop}}$  is greatest at short distances and decays monotonically with further distance from the robot. The data suggest that roughly 60 mm is the detection limit for the robot under the lighting conditions we used, which corresponds to an angular threshold of  $1.5^{\circ}$ , or roughly  $1/3$  the acceptance angle of a *Drosophila* ommatidium[10]. Even at a distance of 25 mm, where the flies' performance approaches an asymptotic maximum, the robot subtends only  $3.7^{\circ}$ . The fact that the robot elicited stops when it subtended such small angles further argues against an expansion-based mechanism for detection[11].

## Discussion

Our experiments using a computer-controlled robot indicate that walking female flies respond to a regressively moving fly-sized object with much greater probability than to a progressively moving target. Under the assumption that the freezing behavior of the fly is a proxy for its ability to detect the small target, our results provide strong support for the regressive motion saliency hypothesis and confirm our anecdotal observations of interactions between pairs of flies. Our experiments provide further evidence for the utility of behavioral robotics as a method for analyzing the sensory basis of social interactions [12–14]. Our results might alternatively be taken as evidence for progressive motion blindness, but either way, our experiments suggest that the ability of flies to detect small moving objects during locomotion is strongly constrained by the optic flow patterns created by self-motion and that they can use regressive motion as a simple 'rule of thumb' that does not require sophisticated compensation for self-motion. To our knowledge, this is the first time that this hypothesis has been proposed or tested. However, the phenomenon may be related to the principle of motion camouflage, a mechanism for crypsis that has been proposed for flying insects[15, 16]. To implement motion camouflage, an animal must move in a way so that it appears stationary (to another moving animal) relative to a distant background. Our results would suggest that such camouflage might not require perfect compensation, but might be effective as long as an animal's own motion did not create regressive motion on another's retina.

Our analysis depends critically on the interpretation that walking females reflexively freeze when detecting a nearby moving object. We believe this is justified as many animals freeze upon detecting a nearby animal, a simple behavioral reflex that has several advantages. By stopping an animal's visual performance is no longer compromised by the optic flow created by self-motion, a stationary animal is harder to detect, and once stopped, an animal can better prepare for an action such as an escape. An alternative interpretation of our data is that progressively moving objects are as detectable, but female flies simply 'decide' not to stop. According to this view, the reflex might serve some useful function such as to establish rights of way when animals are on a collision course, similar to rules used by boat captains [17]. However, it is not easy to imagine a selective scenario by which such etiquette would

evolve, and given the distance at which these reflexes operates, we favor the interpretation that the difference in behavioral responses to progressive and regressive motion indicates a limitation of visual processing rather than a behavioral choice. Another interesting question is whether this reflex evolved in flies specifically for mediating interactions between conspecifics, or alternatively, represents a general reaction to nearby organisms.

Sensitivity to regressive motion is not a general feature of visual reflexes in flies. Indeed, studies of object orientation behavior in tethered flying animals indicate that flies are more sensitive to progressively moving objects than to regressively moving ones, and this asymmetry has been proposed to explain the stable fixations of vertical stripes[18–20]. In contrast, studies of object orientation[21] and optomotor equilibrium[22] in walking flies suggests that the sensitivity to regressive and progressive motion is comparable. However, these prior studies focus on a fly's ability to orient toward visual landmarks and walk straight using large-field optomotor cues and may not be relevant to the behavior we describe here, which we interpret as a reflex used to detect the presence of a nearby organism. In particular, the female flies responded to the robot's motion by freezing, not by steering toward the stimulus as would be expected in an object orientation behavior. The neurons responsible for the behavior we observed in *Drosophila* are not known, and our evidence precludes the involvement of looming detector neurons that have recently been described in this species[23, 24]. Large-field neurons might be capable of detecting small targets provided the contrast was sufficient [25]. However, our results indicating that the response to regressive motion may be triggered by targets smaller than an ommatidial acceptance angle implicate the classes of cells in insects termed figure detectors (FDs) [26] and small target movement detectors (STMDs)[27]. The fact that the behavior degrades if the animal is rotating at the onset of stimulus motion suggests that the underlying circuits cannot detect a regressively moving object when superimposed on the reafferent large field rotatory optic flow generated by self-motion [28]. Nevertheless, the detection threshold of roughly 1/3 an ommatidial acceptance angle is impressive for an animal (*Drosophila*) that is not behaviorally specialized for detecting small prey as are dragonflies[29], or detecting mates and territorial interlopers as are hoverflies[30] and houseflies[31]. Further exploration of these hypotheses will require identification of the underlying visual interneurons and recordings of their visual responses during locomotion, an approach that may be possible in *Drosophila* due to recent methodological advances [32, 33].

## Experimental Procedures

### Animals

We used 2–3 day old wild type gravid female *Drosophila* from a laboratory colony originated from 200 field-caught females, maintained on a 16:8 light:dark cycle at 25° C. The general procedure for handling flies has been described previously[7]. Approximately 8–10 hours prior to placement within the arena, we anaesthetized the flies by cooling them to 4°C and clipped off the distal ½ of both wings. The flies were then allowed to recover in vials containing damp tissue (for a source of water), but no food. This starvation regime greatly enhanced the locomotor activity of the flies[8]. At the start of each experiment, individual flies were transferred from vials into the arena using a mouth pipette.

Subsequently, the system collected data continuously for approximately 10 hours. We excluded any data collected within the 1 hour period prior to an animal's last recorded movement.

### Fly-fly interactions

The example traces presented in Fig. 2 were taken from a previously published study which describes all methods for data collection and analysis[7].

### Fly robot

The data presented in Fig. 4 were collected using a custom-built robot apparatus which we have termed 'Flyatar'. A more detailed description of the device is provided at: <http://projects.peterpolidoro.net/caltech/flyatar/flyatar.htm>. The core structure of Flyatar consists of a two-dimensional translation stage (<http://arrickrobotics.com/xy.html>) driven by two servomotors that control the X–Y position of a horizontal plate to which is mounted a third servomotor that controls the azimuthal rotation of a  $3.18 \times 3.18 \times 6.35$  mm horizontally-aligned rectangular neodymium magnet (B664, K&J Magnetics, Inc.). The motor system moves the magnetic sled just beneath the surface of a 230 mm diameter circular arena milled from Delrin. The sub-stage magnet controls the position of a small cylindrical magnet (1.6 mm high, 1.6 mm diameter; D11, K&J Magnetics, Inc.), which sits vertically-aligned on top of the arena. To enhance contrast, the nickel-plated cylindrical magnet was colored black with a Sharpie pen. In these experiments, the magnet would appear identical from all orientations, and thus we did not control the azimuthal orientation of the robot. The circular border of the arena was surrounded by a 3 mm high heat barrier (40° C) to keep flies from escaping[7, 8]. Above the heat barrier, we placed a 230 mm diameter, 230 mm high cylindrical panorama consisting of a random square checkerboard pattern with 50% filling probability[7, 8]. The edge of each  $11 \times 11$  mm square subtended an angle of 5° at the center of the arena. The arena was backlit with an array of 8 rows of white LED festoon bulbs (4210-xH6, <http://superbrightleds.com>). We controlled fly-robot interactions using two layers of software. Low-level firmware onboard an Atmel AVR microcontroller served as an interface between the servomotors and the high-level control software. The high-level software (written in Python) ran on a Linux computer and combined open source functions of the Robot Operating System (ROS; Willow Garage, Menlo Park, CA) with custom routines in order to track the position of both robot and fly and provide movement commands to the robot. The position of both the fly and the robot were imaged at a rate of 25 fps using a firewire camera (A622f; Basler AG, Ahrensburg, Germany) equipped with a 12 mm lens and an IR bandpass filter. Camera calibration was performed using standard functions of ROS to correct for lens distortion and to fix a measurement coordinate system with respect to the arena. In addition to identifying the fly and robot in each time step, the software provided Kalman filtered estimates of their instantaneous position and velocity. This information, combined with the transforms derived during calibration, made it possible to generate movement commands for the robot with a minimal amount of delay in both the arena- and fly-centered frames of reference.

## Experimental Protocol

After placing a fly in the arena, each set of trials was controlled automatically by software that could run iteratively without a human operator in the loop (see examples in Supplementary Movie 1). The default position for the robot was in the center of the arena, where it remained stationary until the fly walked within a predefined circular area. The robot then ‘waited’ until the fly moved past it such that the robot was positioned at a pre-defined location in the fly’s frame of reference (e.g., when the robot was positioned 90° to the fly’s right or left). The robot then moved in a straight line, parallel to the instantaneous orientation of the fly when the trigger condition was met. Because we wanted to examine the flies’ response to motion across a range of velocities, in each trial we programmed the robot to move at a randomly selected target angular velocity in the fly’s frame of reference ranging from  $-120$  to  $+100^{\circ}\text{s}^{-1}$ . The target speed command sent to the motors was based on an estimate of the fly’s velocity in real-time and assumed that the acceleration of the robot would be instantaneous. However, the final determination of the angular velocity in each trial was based on the actual recorded time sequence of fly and robot positions, not the pre-programmed target values. The final distribution of angular velocities in all experiments was skewed slightly towards progressive motion trials because of the flies own forward velocity and the finite acceleration delay required for the robot to reach the target speed. After starting motion, the robot continued to move at a constant speed until it reached the perimeter of the circular area delimited at the beginning of the experimental trial. At the end of each trial, the robot returned to the center of the arena and waited for the fly to move nearby again to initiate another encounter.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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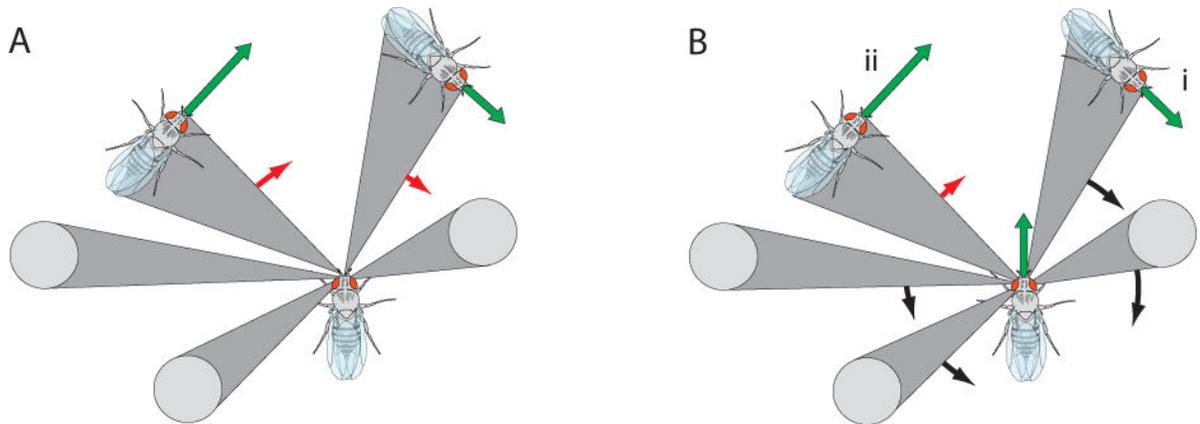
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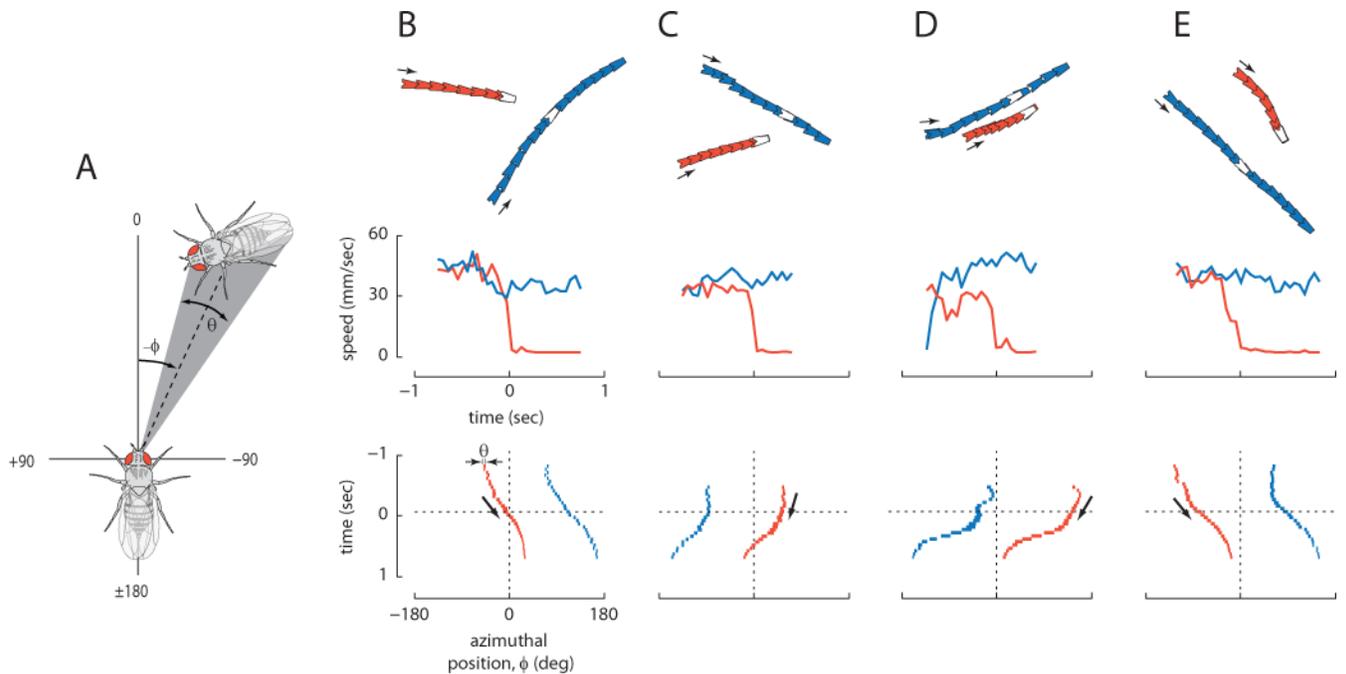
### Highlights

- A programmable fly-sized robot was constructed to study visual interaction between flies.
- Walking flies respond with greater salience to regressively moving objects than progressively moving ones.
- Regressive motion salience functions as a simple visual algorithm for detecting moving objects during locomotion.



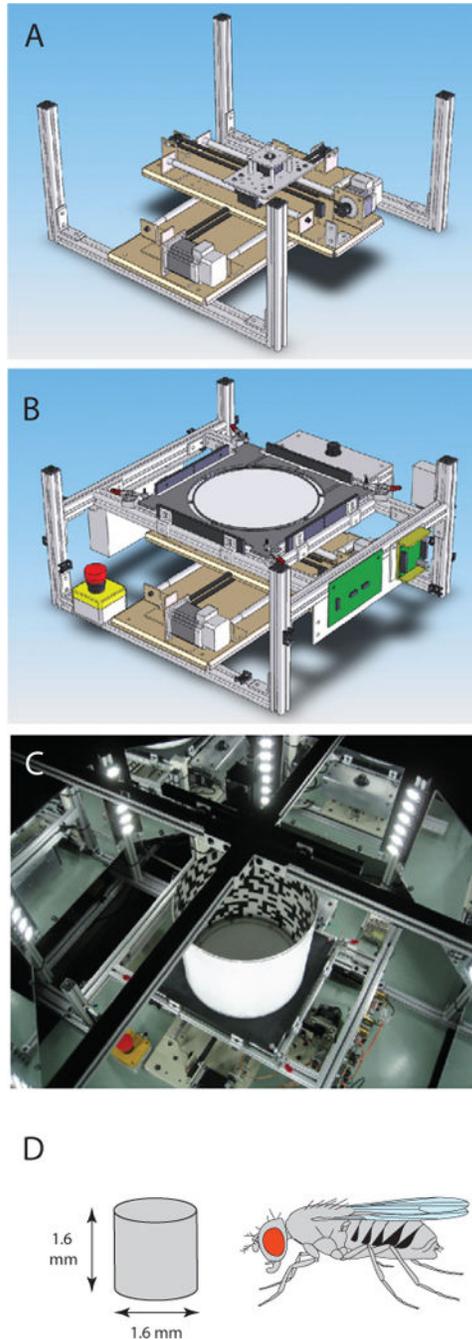
**Figure 1.**

Cartoon illustrating the principle of regressive motion salience. (A) The stationary animal at the center has no difficulty using optic flow to distinguish moving objects (flies) from stationary objects (circles) in the background. Thick green arrows indicate motion of flies and thin red and black arrows indicate the angular velocity of edges subtended by objects on the retina of the fly at center. (B) An animal moving in a straight line without rotation will experience progressive optic flow of all stationary objects in its environment. The magnitude of angular optic flow (indicated by black arrows) that each object creates will depend on its distance to the fly and its orientation relative to the direction of motion. An object that moves in such a way as to create progressive optic flow (i) will be difficult to distinguish from the apparent motion of the stationary background, whereas an object moving so as to create regressive optic flow (ii) will be much easier to detect.



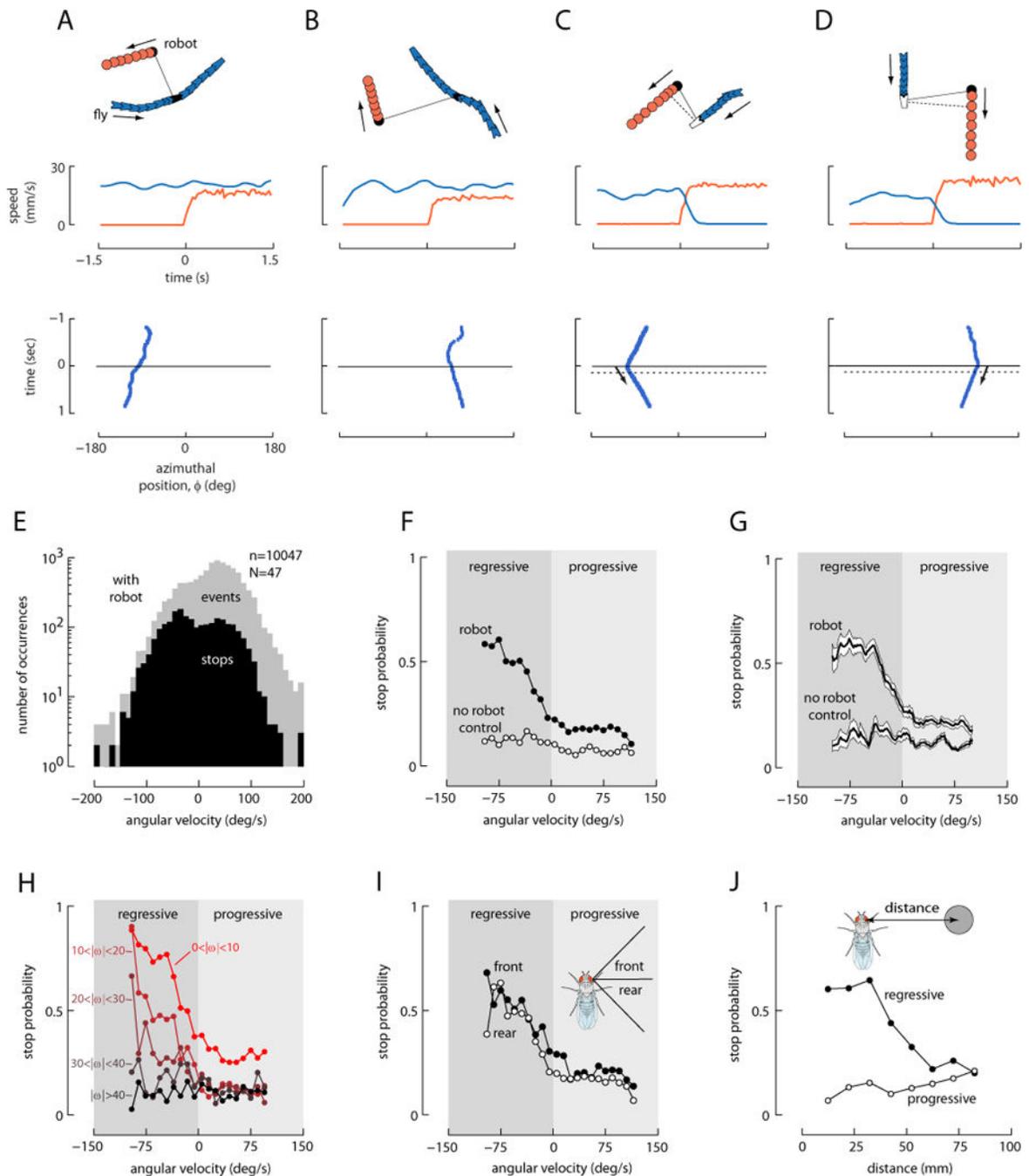
**Figure 2.**

Encounters between walking fruit flies provide support for regressive motion salience. (A) Cartoon illustrating the definitions for  $\phi$ , the azimuthal position of one fly in another's reference frame and  $\theta$ , the angle subtended by the other fly. (B–E) Four example encounters between two flies. Fly-shaped icons in the top panels illustrate the position of the two flies at 100 ms intervals. Initial direction is indicated by small arrows and a white fill color indicates the position of both flies when the red fly stops. The middle panels plot the translational speed of the two flies. The lower panel plots the time course of  $\phi$  and  $\theta$ . In these plots, time runs from top to bottom on the vertical axis and the  $\theta$  is indicated by the width of each point as plotted along the abscissa. Red indicates images experienced by the red fly, blue indicates images experienced by the blue fly. Just prior to stopping, the red flies experience regressive motion, as indicated by the fact that the slope of azimuthal position slants toward the midline (black arrow) (B,C). Examples of encounters in which two flies walk on a collision course ('T-stops'). The fly that would arrive at the intersection point first perceives progressive motion and continues without stopping. The slower fly, which stops, perceives regressive motion. (D,E) Examples of encounters in which two flies walk along parallel courses ('drag races'). In these cases, the faster of the two flies perceives progressive motion while the slower fly, which stops, perceives regressive motion. The examples were selected from a previously published data set[7].



**Figure 3.**

*Flyatar*: a simple fly-sized robot that may be programmed to interact with a real fly. (A,B) CAD drawings of the apparatus illustrating the motors and drives that control the position of a sub-stage magnet that actuates the small robot above the stage. In A, the arena and circular thermal barrier have been removed to show the sub-stage motor system. (C) Photograph of the apparatus showing the checkerboard background around the arena and the lighting system. The mirror array helped provide even lighting conditions. (D) Cartoon showing size and shape of the robot compared to a real fly.



**Figure 4.**

Evidence for regressive saliency in fly-robot interactions. (A–D) Example trajectories in which the robot was programmed to start moving when a fly walked past. Robot (red circle) and fly (blue fly-shaped icons) indicate positions at 200 ms intervals. The frame in which the robot started moving is indicated in black fill and by a solid line. The traces below each sequence indicate the speed of the fly and robot throughout the encounter. (A) Example in which the robot creates progressive motion. (B) Another example of progressive motion. Note that in this case, the robot moves forward in the direction of fly motion, but the speed

differential is such that the image of the robot was still progressive in the fly's reference frame. (C,D) Examples in which the robot creates regressive motion. Note that the flies stop walking (indicated by white fill and dotted line) almost immediately following the onset of robot motion. (E) Histogram of all valid encounters ( $n=10,047$ ) from 46 flies. Values along the ordinate axis are plotted on a log scale to better visualize rare events. Gray area indicates distribution of stimulus angular velocity for all trials and the superimposed black area indicates the distribution of trials in which the flies stopped within 850 ms after the onset of robot motion. (F) Stop probability (calculated as the ratio of the distributions plotted in panel E) as a function of angular velocity when the robot was present (closed circles) and for the 'no robot' controls.  $P_{\text{stop}}$  values for angular velocities above  $+120$  °/sec and below  $-100$  °/sec are not displayed because the small sample size in these ranges render the calculated ratios unreliable. In 'no robot' controls ( $n=3528$  trials, 14 animals), the robot was removed from the arena but the sub-stage actuators and control software operated as in normal trials. (G) Similar plot to that in panel F, but in this case the traces represent a population average and SEM envelopes for the probability functions evaluated for each individual fly ( $N=46$ ). (H) The data in F are replotted after parsing trials in five groups according to the absolute angular velocity of the fly at the start of the trial: ( $0 < |\omega| < 10$ ,  $10 < |\omega| < 20$ ,  $20 < |\omega| < 30$ ,  $30 < |\omega| < 40$ ,  $40 < |\omega|$ ). Each group is plotted as a different tone from red to black. (I) Stop probability as a function of stimulus angular velocity for data parsed according to the initial position of the robot at the start of motion. The probability curves are similar for motion initiated in the front and rear sectors of the visual field. (J) Stop probability plotted as a function of the distance between the fly and robot at the start of robot motion for progressive (open) and regressive (closed) motion. The curves are derived from the range of regressive angular velocities that evoked the peak response ( $-100$  to  $-60$  °/sec), and each point averages trials across a range of angular velocities.