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Centre for Genetics and Genomics, School of Biology, University of Nottingham, University Park, Nottingham NG7 2RD, UK.
E-mail: John.Brookfield@nottingham.ac.uk

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Animal Behavior: Fly Flight Moves Forward

A new study has resolved the paradox of how flies maintain reflexive aversion to your approaching swatter, whilst tolerating similar visual signals during normal forward flight.

Jessica L. Fox and Mark Frye

Animal nervous systems come equipped with many built-in rapid reflexes. These simple behaviors maintain an animal's physical stability without requiring much neural overhead, and they permit animals to respond rapidly in situations where taking the time to make complex calculations within the central nervous system would jeopardize survival. During rapid locomotion, reflexes are crucial to keeping the body in its correct posture and responding to external perturbations, such as an obstacle in the path of a runner or a gust of wind knocking a bird off of its flight path. Low-level sensory-motor reflexes enable the nervous system to efficiently maintain control while walking, swimming, or flying through varied and often unpredictable environments. Managing these reflexes, however, can be complicated: the nervous system must have means by which the reflexes can be deployed in the right circumstances, and suppressed in the wrong ones. A new study by Reiser and Dickinson [1] has revealed how the visual systems of flies in flight use a surprisingly simple algorithm to decide when a reflex should be employed, and when it should be overridden.

In insects, a reflex known as the looming avoidance response keeps the animals from colliding with objects, or becoming snatched by oncoming predators. The image of an object on the retina increases in size as the object gets closer, and the rate of change in image size will speed up as the object and the observer close in on one another. Insect nervous systems are able to use this rate of change in perceived size to calculate the time to collision, and standing insects will jump to avoid the oncoming object [2,3], whereas flies in flight similarly turn away from looming objects [4]. An approaching object generates optic flow across the eye that forms a 'vanishing point': the optic flow pattern expands outward along the direction of motion from the focus of expansion and disappears in a point behind the observer (the focus of contraction). Expanding optic flow on its own triggers collision-avoidance turning reflexes in flies [4], suggesting that the looming avoidance response is not selective for objects in particular, but is a more generalized reflex for avoiding any image expansion. Focus-of-expansion avoidance is obviously a useful response for preventing impact or dodging a swatter, but it presents the fly with a paradox: if it turns away from all looming signals, how can it ever fly forward?

Over the past five years, three papers from the Dickinson lab have found common scenarios in which the fly overrides its escape reflex to fly towards a focus of expansion instead of turning away from it. First, Budick *et al.* [5] found that flies will more readily orient towards a focus of expansion if they can fly against a gentle headwind, which would be induced by normal forward flight in still air. Also, noting that a fly will readily approach a vertically-oriented object representing a landing perch or a gap in the foliage, Reiser and Dickinson [6] found that placing such an object within the focus of expansion switched their behavior from expansion avoidance to object tracking, and thus permitted them to fly forward into the focus of expansion. Now, Reiser and Dickinson [1] have further demonstrated that the focus-of-expansion avoidance response is dependent on the strength or velocity of the expanding optic flow emanating from it, and that if the expansion velocity is sufficiently low, then flies will fly towards rather than away from the focus of expansion, even without oncoming wind or any other attractive feature.

Reiser and Dickinson [1] used an electronic flight simulator to present visual stimuli to tethered fruit flies in flight. In this arena, the flies can flap their wings, but cannot move their bodies. A photodiode measures the amplitude of the wing strokes, and the fly's attempts to turn in one direction or another are proportional to the difference between the two wingbeat amplitudes. The authors first confirmed that flies readily steer away from a focus of expansion, but then they go on to show that flies will steer towards the focus of expansion if the velocity of expanding motion is sufficiently low. Both of these stimuli were presented passively to the fly, but what happens when the fly is allowed to choose the stimulus in front of her? To test this, they turned the flight arena from a passive 'movie screen' into an active 'video game' by coupling the steering signal from the fly's wings to the position of the focus of expansion on the screen, effectively letting the fly decide whether it wanted to either fly towards the focus of expansion by keeping it in front, or avoid that signal and instead fly towards the focus of contraction. In this scenario, flies do indeed fixate the focus of expansion if the velocity of continuous expansion is low, as would be encountered by flying through a distant landscape; however, they rapidly switch from focus of expansion fixation to focus of expansion avoidance if the effective expansion velocity is suddenly increased, as would be encountered by a nearby looming wall.

How does the fly's brain determine whether to fly towards or away from the focus of expansion? Does this behavioral switch require some high-level brain function of the variety seen in primates [7], or can a simpler calculation explain the behavior? Reiser and Dickinson present some computer simulations revealing that a classical model of motion detection, proposed decades ago by Hassenstein and Reichardt [8] and known as the elementary motion detector, is adequate to explain the fly's behavior in tethered and free flight. The proposed control circuit is impressive in its simplicity. The elementary motion detector model is truly 'elementary' in that it computes visual motion by using only two light sensors, delaying the signal of one, then multiplying the two signals. The model thus provides the strongest output when light moves from the delayed to the undelayed sensor. A downstream collating cell would pool the inputs from the many elementary motion detector modules and report the direction of movement over a large visual field. The velocity range that the unit can detect is determined by highpass and lowpass filters, neural computations that are performed on the output of the two sensors.

What is powerful about Reiser and Dickinson's [1] results is that the response of the elementary motion detector model, combined with a simple threshold above which the attraction response switches to an avoidance response, can predict the behavior of flies in free flight without requiring the fly brain to calculate parameters such as the distance to the wall, the time to collision, or even the velocity of the visual expansion. Freely-behaving flies generally avoid flying close to the walls of an arena [9], and an elementary motion detector model with an appropriate lowpass filter and a simple threshold will result in the same behavior, in which the fly turns to avoid the visual expansion once the output of the elementary motion detector model exceeds a particular threshold. The mechanism by which this threshold is set, how and where it is implemented by the brain, and whether or not it is innately fixed or plastic are important open questions.

This new paper [1] completes a triptych of research projects in which three conditions that would very reasonably be encountered during normal forward flight — a gentle headwind, a salient object in the frontal field of view, or relatively slow expansion velocity — are each found to be sufficient to override the powerful expansion avoidance reflex, and instead stabilize flight into an expanding flow field. Reiser and Dickinson [1] show that the simplest known motion detection model, requiring very few processing steps and minimal computational resources, can be used to balance the fly's behavior so that it can progress safely through the world, while at the same time dodging your swatter.

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Howard Hughes Medical Institute, Department of Integrative Biology and Physiology, University of California Los Angeles, Los Angeles, CA 90095, USA.
E-mail: frye@ucla.edu

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Mitochondrial Fission: Rings around the Organelle

Mitochondria form a dynamic network in which organelles fuse or divide in response to metabolic changes or cellular stress. New work shows that mitochondria do not divide in isolation from other cellular structures. Rather, they carry out this process in partnership with the endoplasmic reticulum and actin filaments.

Liza A. Pon

Mitochondrial division (or fission) is mediated by the dynamin-related protein Drp1 and its yeast homologue Dnm1p. Drp1/Dnm1p is a GTPase that is recruited to mitochondria by mitochondrial