Come Fly with Me

by Michael H. Dickinson

Michael Dickinson (at the head) rides a fruit fly with some of his team—graduate student Seth Budick, postdoc Titus Neumann, and postdoc William Dickson—behind him. Although seeing the world the way a fly does is still a dream, the lab's innovative approach to studying fly flight behavior is bringing them a little closer.

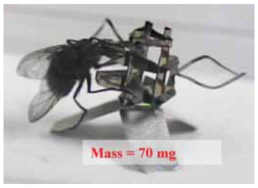
If the goal is to reverse-engineer an insect, and incorporate its design into a miniature flying device, flies are an excellent choice.

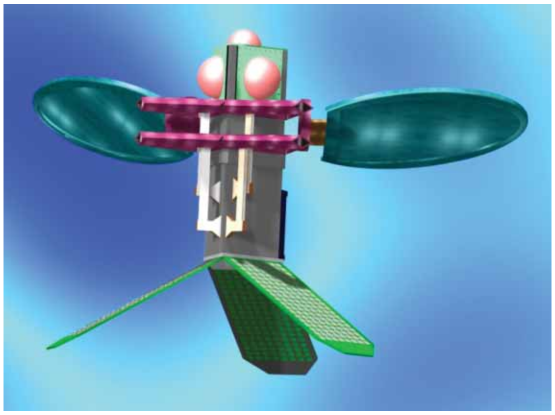
This article is adapted from a talk given to an audience of academics and representatives from a variety of industrial research labs at CNSE Industry Day 2003 in May. Organized by the Center for Neuromorphic Systems Engineering, the theme of the meeting was Machine Awareness and Learning.

The Division of Engineering and Applied Science might seem an odd home for someone with a PhD in zoology who studies flies. Engineers are more likely to view flies as an annoyance than as a topic of study. There are several reasons, however, why one might pause before swatting a fly with a surplus slide rule. In my own research and that of many biologists interested in understanding important problems such as locomotion, engineering approaches are now much more common and powerful than they used to be. Government funding agencies such as NASA, the Defense Advanced Research Projects Agency (DARPA), and the Office of Naval Research (ONR)—not known for their generous support of zoology—have demonstrated a keen interest in insects in recent years, in the hope that a better understanding of aerodynamics and control in these highly successful creatures might provide insights for the design of micro air vehicles (MAVs). These small flying devices would weigh less than a ballpoint pen and fit comfortably in a coffee cup—a description that also fits most of the six million or so species of insects on the planet.

The insect I chose to study is the common fruit fly, *Drosophila melanogaster*, which is famous for its role as a model organism in genetics, developmental biology, and molecular biology. However, it was not its genes that attracted me, it was the sophisticated flying behavior. Flies represent about one out of every 10 species known to science. Distinguished from all other insects in having only two wings and possessing gyroscopic organs called halteres, the fly order Diptera includes mosquitoes, fruit flies, houseflies, gnats, and horseflies. The success of flies is due in part to their many specializations for flight—fast visual systems, powerful muscles, wings capable of generating unsteady aerodynamic forces, and those specialized gyroscopes, the halteres, capable of sensing the rotations of the body during flight. If the goal is to reverse-engineer an insect and incorporate its design into a miniature flying device, flies are an excellent choice.

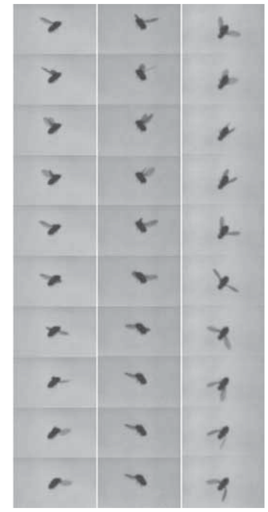
Consider, for example, a routine behavior of the common housefly. Next to mosquitoes, houseflies probably suffer more from the angry swats of rolled newspapers than any other insect. One of the reasons houseflies are so annoying is that the males are territorial and occasionally may claim our bedrooms as suitable cruising grounds. To succeed in mating, males must constantly patrol





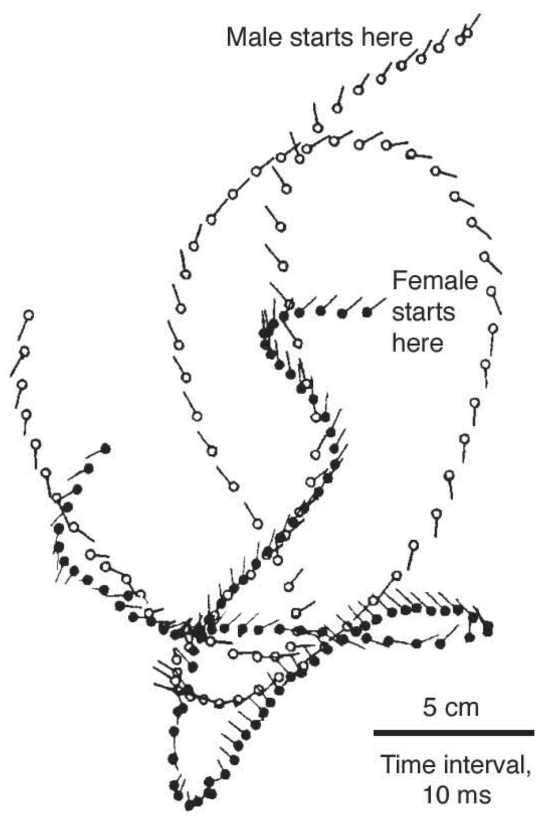
A housefly checks out a prototype micromechanical flying insect (MFI) developed by Ron Fearing's lab at UC Berkeley, above. At right is an early concept drawing of what the MFI would look like. To see what it looks like now, turn to page 19.

their territories looking for both interloping males and potential mates. If an object enters his territory, the male must quickly decide whether it is a predator, another male attempting to usurp the territory, or a receptive female. The animal's behavior depends on his correct classification of the target. If he perceives a predator, he flies away. If it's another male, he must chase and expel the would-be interloper. If it's a female, he must chase, intercept, and catch her to initiate courtship. Just such sequences were first captured, using high-speed film, in the pioneering work of Tom Collett and Michael Land a quarter of a century ago. An example of similar work, a rapid mating chase filmed and analyzed by Hermann Wagner, is shown below. The positions of the male and female every 10 milliseconds are indicated by white and black lollipops, respectively. At the start of the sequence, the male gives chase as the female enters his field of view. Initially, he does a remarkable job of tracking her flight path, but loses her trail when she performs an evasive maneuver. After a long loop, he regains his composure and continues the chase. An analysis of such sequences shows that the male can adjust his flight behavior in less than 30 milliseconds after a change in the trajectory of the female.



Ultra-high-speed video cameras capture stages of a single forward wing movement from three different angles, something extremely difficult to film, as the wings beat up to 250 times a second.

High-speed photography makes it possible to follow a male housefly's attempt to capture a female. This can't be seen with the naked eye because it happens so quickly—the entire chase shown here took just 1 second. The lollipops (white for the male, black for the female) show the flies' head and body angles at 10-millisecond (ms) intervals.



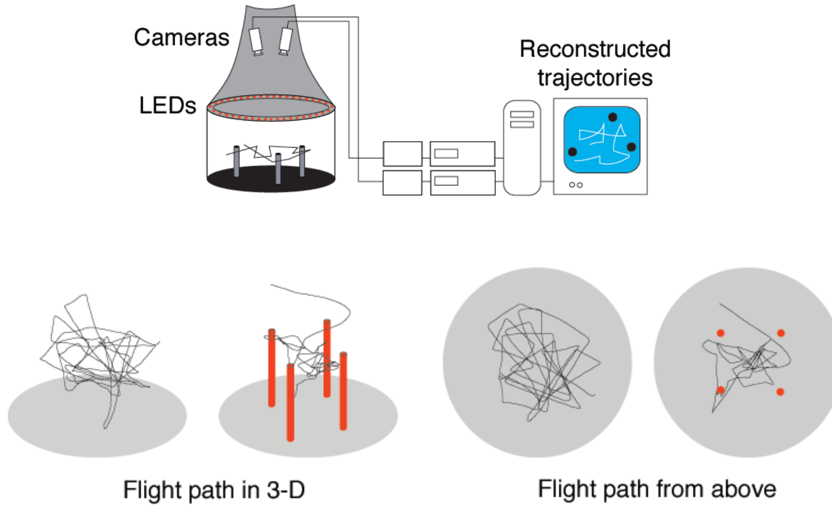
Wagner, H. (1985): Aspects of the Free Flight Behaviour of Houseflies (*Musca domestica*) in *Insect Locomotion*, eds Gewecke, M. & Wendler, G., p. 223. Paul Parey Verlag, Berlin.

This is extraordinarily fast processing, and illustrates why the flight system of flies represents the gold standard for flying machines. Over the short term, flies may teach us about the design of robust control systems, while in the long term, it may eventually be possible to construct a flying robot with a fly's agility.

In order to build a mechanical fly we must first understand how a real fly works. How does one go about characterizing a system that is so complex? Although I was trained in neurobiology and zoology, it became clear when first thinking about fly flight that it would be difficult to understand what the nervous system was doing without understanding the mechanics of the fly's muscles and skeleton—the "physical plant" of the organism. It would also be difficult to reverse-engineer these elements without understanding how the limbs, appendages, and wings interact with the external environment. Further, as the fly moves through space, it receives a stream of sensory information that adjusts the circuits within its tiny brain. So to understand the performance of the system as a whole we have to take a systems-level view that does not isolate the analysis of any one individual component from another.

As flies explore, they move in straight flight segments interspersed with rapid changes in direction called saccades. Each saccade is faster than a human eye blink—the animal changes direction by 90 degrees within about 30 to 50 milliseconds. To study the mechanics of this behavior in greater detail, we track the motion of fruit flies in a large flight arena dubbed Fly-O-Rama by my students. In this arena, we can change the visual landscape surrounding the fly and measure the

In Fly-O-Rama, free-flying flies are filmed with two CCD cameras, and software reconstructs their trajectory as they investigate obstacles in the arena. What looks like a drawing done on an Etch A Sketch is the characteristic fly way of getting around, which is to move forward in a straight line interspersed with rapid changes in direction called saccades.



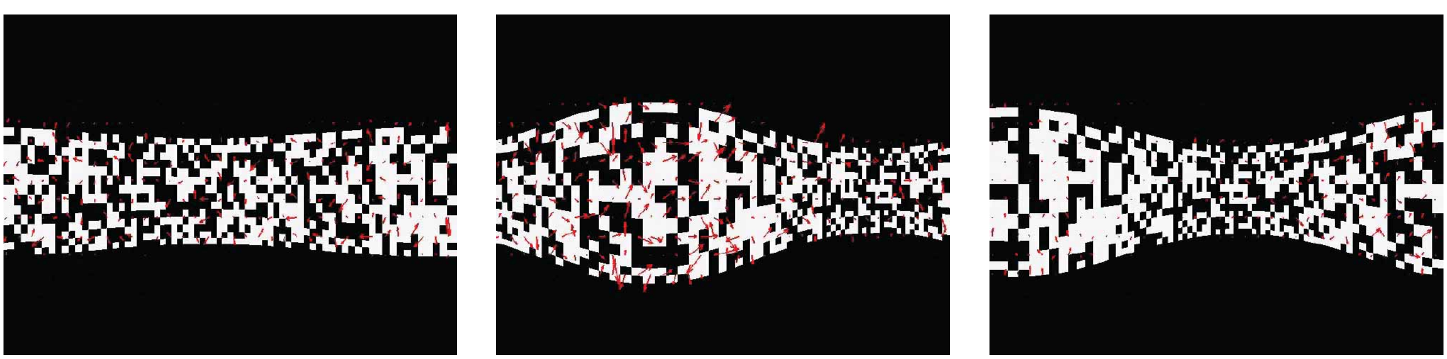
effect on its flight behavior. We've captured saccades on high-speed video shot at 5,000 frames per second in three fields of view, and these images indicate that the fly performs the entire saccade in about eight wing strokes. I'll use our research into this rapid, yet graceful behavior as an example of how we use a systems analysis approach to study fly flight.

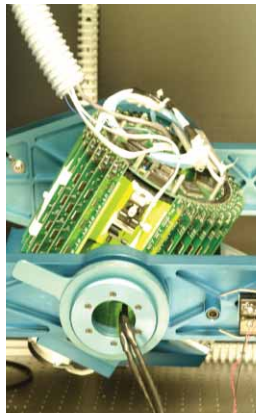
The saccades are so regular that they look as though they're triggered by an internal clock, but this isn't the case. By changing the patterns on the wall of the arena, we have been able to show that the animal's visual system triggers each turn. Insects have quite sophisticated visual systems, and approximately two-thirds of their brain (about 200,000 neurons) is dedicated specifically to processing visual information. Fruit fly's eyes have poor spatial resolution (each eye has a resolution of about 25 × 25 pixels; in comparison, a cheap digital camera has a resolution of 1000 × 1000 pixels), but they have excellent temporal resolution and can resolve flashing lights at frequencies up to 10 times faster than our own eyes can. This means if you take a fly on a date to the movies it will think you brought it to a slide show.

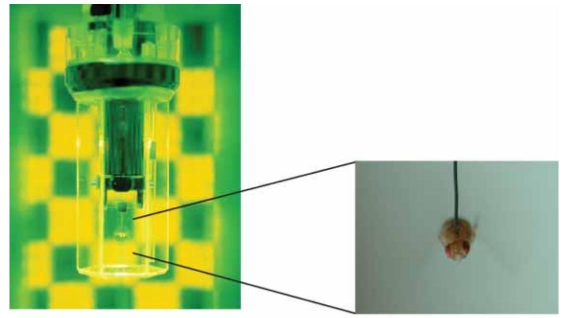
By carefully measuring the animal's flight path in Fly-O-Rama, we can reconstruct the visual world from the fly's perspective—the equivalent of sitting on the back of the fly as it zips around the arena (below). In addition to gaining some sense of what it feels like to be a fly, such reconstruction allows us to ask what goes through the fly's brain just before it turns. After much analysis, the answer has emerged—each saccade is triggered by an expansion of the fly's visual world. The fly travels in a straight line until it perceives an expansion of the visual world, then it veers 90 degrees to the left or the right. These saccades are collision-avoidance reflexes that keep the animal from crashing into objects.

Free-flight studies in Fly-O-Rama are useful because they make it possible to examine the fly's behavior in near-natural conditions, but they don't permit rigorous experimental control. To further

These stills from a movie show what you would see if you were riding on the back of a fly as it heads toward a computer-generated crossword-puzzle landscape on the wall of the arena (left). When the program makes part of the landscape expand (center), the fly immediately saccades to the right, and when you recover your posture, you see you're heading toward the other side of the arena (right).

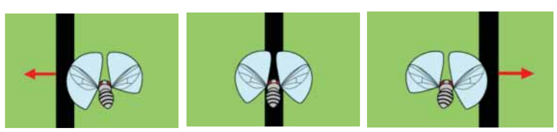






The flight simulator is the green cylinder at far left. Inside, a tethered fly, wings flapping, waits for the virtual reality ride to begin.

refine our analysis of the sensory features that trigger and control saccades, we built a flight simulator that tricks a tethered animal into "thinking" that it is flying. We carefully glue the fly to a fine wire and place it inside a cylindrical arena whose walls are lined with a computer-controlled electronic display. Twelve thousand independently controlled LEDs produce a constantly varying pattern of squares and stripes that give the little fruit fly the feeling of flying in a real landscape. We can measure the fly's intended flight behavior by tracking the motion of its wings with an optical wingbeat analyzer, or by fixing the fly to a sensitive torque meter. The arena can be configured in an open-loop mode, in which we present the animal with a visual stimulus and



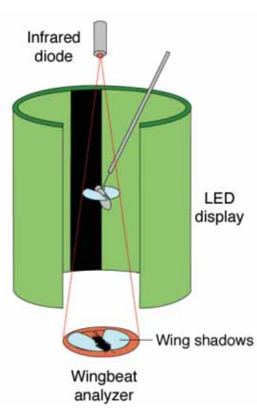


Diagram of the flight simulator showing how the wingbeat analyzer works. The flies try to keep the stripe right in front of their eyes, and adjust their wing strokes to steer it back into place when it moves.

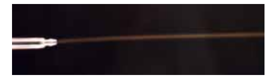
measure its response, or a closed-loop mode, in which the fly itself can control the arena.

For example, in a closed-loop configuration, the fly is allowed to control the angular velocity of a dark stripe on the arena wall by changing the relative amplitude of the left and right wing strokes. It steers toward the stripe—fruit flies are attracted to vertical edges—and whenever the stripe moves away to the left or right, the animal can steer it back into the center of its field of vision by adjusting its wing strokes. It's like a child playing a video game: The flies seem to enjoy this "fixation" paradigm, and they'll happily fly toward the stripe (like a dimwitted horse following a carrot suspended in front of it) for about an hour until they run out of energy.

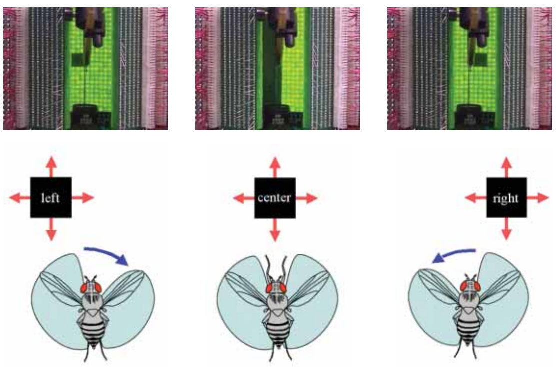
When we place the fly in the arena at the start of an experiment, we give it a little piece of paper to cling to. When we're ready to start, we blow the paper away. Tiny touch sensors on the legs detect the loss of terra firma, and the fly begins to fly. We can stop each experiment by carefully replacing the piece of paper. The fly's legs sense the contact and trigger the wings to stop. If we place sugar water on the paper, taste cells on the feet activate a feeding reflex, and the fly extends its proboscis and refuels for the next flight.

One informative experiment that is possible in the flight simulator is the fly-swatter paradigm. Under closed-loop control, we let the tethered fly fixate on a little black square that is programmed to expand at random times. Each time the square expands, it triggers a saccade. Because we know precisely where the square was when it began expanding, we can construct a precise spatial map of the collision-avoidance behavior (facing page). The results indicate that the fly is clever, but not too clever. It doesn't carefully calculate the size of the turn depending on the direction or speed of the impending impact. Rather, an expansion to the left of it triggers a 90-degree turn to the right, and an expansion on the right-hand side triggers a turn to the left. If the fly sees an expansion directly in front, it saccades either

Clinging to a scrap of sugar-watered paper, this fly is taking a refueling stop before starting the next sortie.



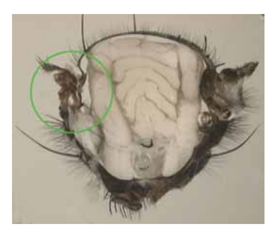
Graduate student Seth Budick uses a wind tunnel to study how fruit flies search for food, and what they do when they find it. A thin plume of smoke with the delicious odor of rotting fruit is released from a nozzle (top right) into a 0.4-meters-per-second wind. A free-flying animal enters the tunnel and makes its way upwind to the odor source, while cameras keep track of the fly's progress.



In the fly-swatter experiment, a black square expanding on the left of the fly prompts it to make a saccade to the right. If the square expands on the right, there's a saccade to the left. And if the expanding square is straight ahead, the fly saccades either left or right, and also stretches out its legs in preparation for landing.

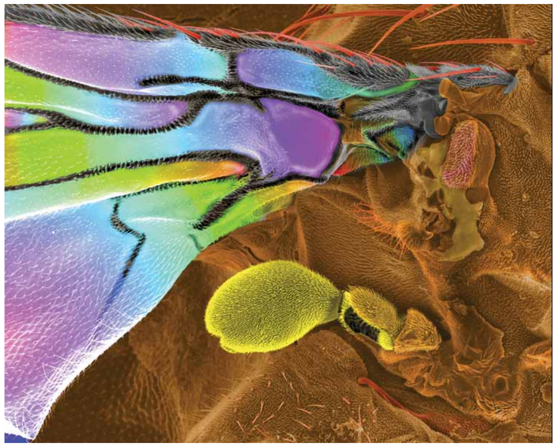
to left or right with equal probability. Central expansion also triggers an additional behavioral response—the fly reflexively sticks out its legs and prepares for landing. Such results suggest that the search algorithm of this tiny organism consists of stereotyped "all-or-nothing" reflexes. Although simple, this algorithm works elegantly, and when modulated by a sense of smell, enables the fly to search and locate small targets such as rotting bananas in a fruit bowl.

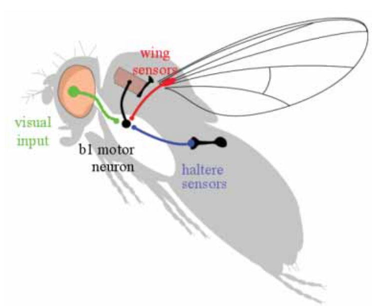
Keeping with the spirit of the systems-level analysis, we would also like to understand how the fly mechanically alters its wingbeats to perform these different visually elicited behaviors. Here things get rather humbling, because it's the mechanical component of this biological system that we, as engineers, are the furthest away from being able to replicate. Flies don't have an internal skeleton consisting of individual bones or cartilage. Instead, they're surrounded by an external skeleton, the cuticle—a single, topologically continuous sheet composed of proteins, lipids, and the polysaccharide chitin. During development, complex interactions of genes and signaling molecules spatially regulate the composition, density, and orientation of protein and chitin molecules. Temporal regulation of protein synthesis and deposition allows the construction of elaborate, layered cuticles with the toughness of composite materials. The result of such precise spatial and temporal regulation is a complex, continuous exoskeleton separated into functional zones. For instance, limbs consist of tough, rigid tubes of "molecular plywood" connected by complex joints made of hard junctures separated by rubbery membranes. Perhaps the most elaborate example of an arthropod joint, indeed one of the most complex skeletal structures known, is the wing hinge of insects—the morphological centerpiece of flight behavior. The hinge consists of an interconnected tangle of tiny, hard elements embedded in a thinner, more elastic cuticle of a rubberlike material called resilin, and bordered by the thick side walls of the thorax. In flies, the muscles that actually power the wings are *not* attached to the hinge. Instead, flight muscles cause small strains within the walls of the thorax, and the hinge amplifies these into large sweeping motions of the wing. Small control muscles attached directly to the hinge enable the insect to alter wing motion during



The wing hinge is the part circled in green in this cross-section of a fly thorax. The white tissue is the flight muscle.

The hindwings of flies have evolved into halteres, small knobs that beat antiphase to the wings and act like gyroscopes to help maintain balance in flight. In the colorized close-up of a fly's thorax (courtesy of MicroAngela) at right, the haltere is the green drumstick below the wing. How the sensory organs, eyes, and brain are wired to the wings and halteres is shown below.





steering maneuvers. Although the material properties of the elements within the hinge are indeed remarkable (resilin is one of the most resilient substances known), it is as much the structural complexity as the material properties that endows the origami-like wing hinge with its astonishing properties.

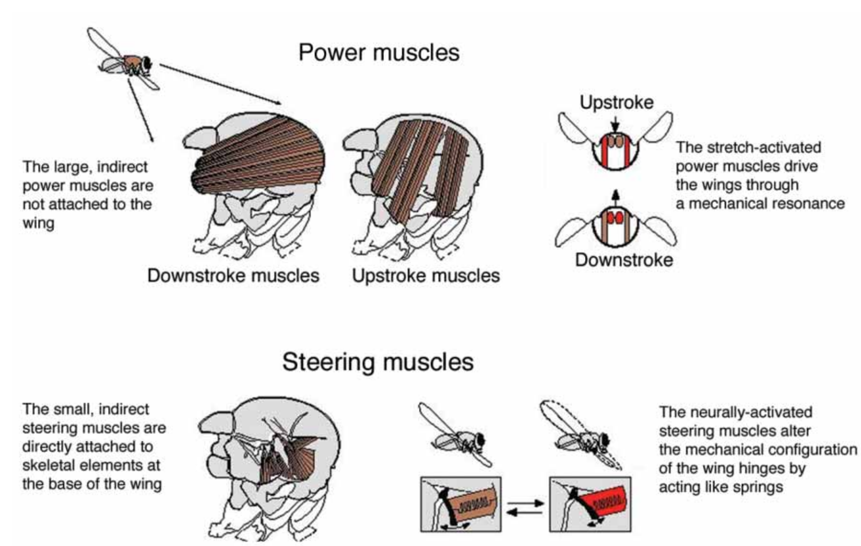
By controlling the mechanics of the wing hinge, the steering muscles act as a tiny transmission system that can make the wing beat differently from one stroke to the next. Electrophysiological studies indicate that this is a phase-control system. Most of the fly's steering muscles are activated once per wingbeat, but the phase at which they're activated is carefully regulated by the nervous system. This is important, because the stiffness of these muscles changes depending on the phase in which they are activated within the stroke. Even when the steering muscles are not actively contracting under the control of a motor neuron, they're still being stretched back and forth by other muscles around them. If a muscle is activated by its own motor neuron while it is lengthening, it becomes stiff; if activated while shortening, it's relatively compliant. The fly uses the steering muscles as phase-controlled springs to alter the way the large strains produced by the power muscles are transformed into wing motion.

If all the sophisticated flight behavior that flies exhibit boils down to subtle changes in the activity of tiny steering muscles, what controls the steering muscles? The nervous system must activate each muscle at the appropriate phase in each cycle and modulate that phase during steering maneuvers. The regular firing pattern of the steering muscles would suggest that they are controlled by an internal clock (such circuits are common in locomotor behaviors), but it turns out that the fly's steering muscles fire in phase with the wing stroke because they're activated by sensory reflexes. During each wingbeat, sensory cells on the wings and halteres send timing signals into the brain that are used to tune the firing of the muscles.

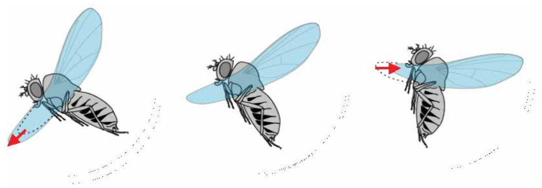
The information coming from the haltere, a hindwing modified by evolution and resembling a very small chicken drumstick, is particularly important because it is essential in stabilizing reflexes. Beating antiphase to the wings, the halteres function as gyroscopes during flight. When the fly rotates, each haltere is deflected from its beating plane by Coriolis forces, which are pseudoforces present when an object has a velocity in a rotating frame of reference. Sensors at the base of the haltere detect Coriolis-force deflections and activate appropriate compensatory reflexes.

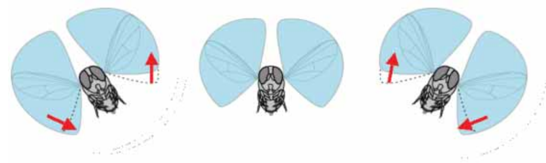
We study haltere-mediated reflexes by placing one of our flight simulators inside a large three-degree-of-freedom rotational gimbal, called the

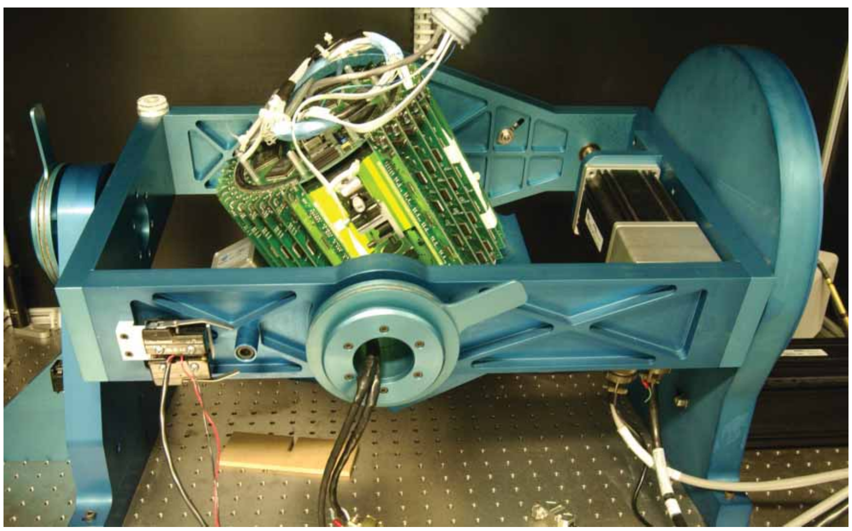
The fly thorax is packed with two sets of antagonistic power muscles that move the wings up and down, but are not attached to the wing hinge. The much smaller steering muscles are attached to tiny elements at the base of the wing and work as springs that can vary in stiffness.



voluntarily? What if it's a male fly and it really *wants* to turn left toward a female? Or a female who wants to steer away from a male? Although we don't know the full answer to this complicated question, one possibility is that the fly can actively steer by fooling its own gyroscope. In addition to having control over the steering muscles of the wing, the visual system and higher brain centers can control tiny steering muscles of the halteres. By actively manipulating the motion of the







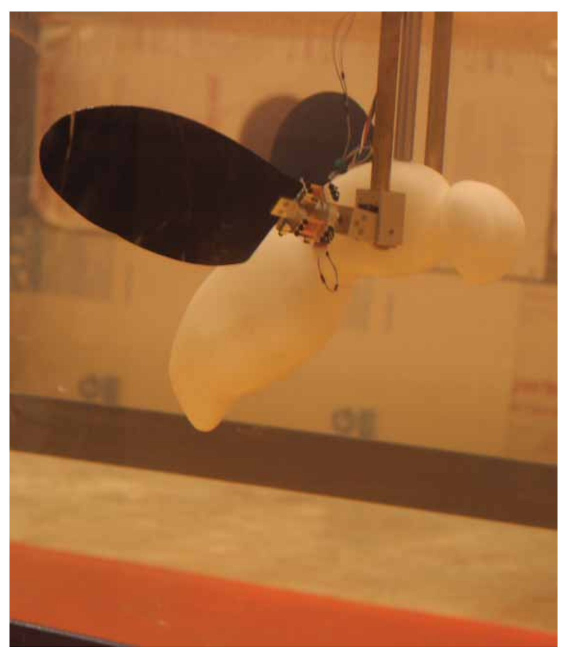
haltere, the fly's brain might initiate compensatory reflexes in the haltere that make the insect change its flight path.

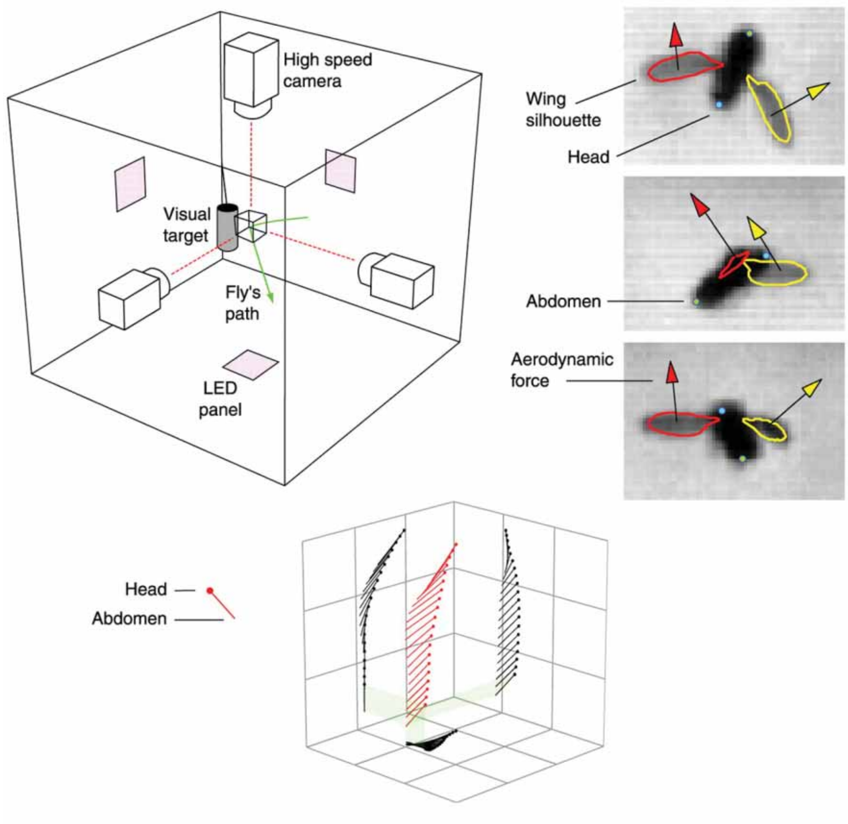
Because of the complexity of fly aerodynamics, understanding wing motion does not necessarily translate into an understanding of flight forces. It is a common myth that an engineer once proved a bumblebee couldn't fly, and while the true story is really much kinder to the engineer, it underscores the difficulties of studying fly aerodynamics. At present, even brute-force mathematical computations on supercomputers cannot accurately predict the forces created by a flapping wing. For this reason, my lab has constructed Robofly, a dynamically scaled insect with a wingspan of half a meter, on which it is possible to directly measure aerodynamic forces and flows. Most aeronautic engineers take large airplanes and model them as

A Rock-n-Roll Arena is used to analyze how a fly keeps its balance during flight. The flight simulator is attached to a rotational gimbal that pitches, yaws, and rolls the animal around as it steers toward a stripe. The diagrams above show how the fly changes wing stroke to stabilize itself when pitched forward or backward, or rolled sideways. The blue areas show the wingbeat envelopes. Robofly, right.

Rock-n-Roll Arena. As the animal steers toward the stripe, we can rotate the apparatus at up to 2,000 degrees per second about the yaw, pitch, or roll axes of the fly. The animal detects these rotations with its halteres and responds with compensatory changes in wing stroke. These reflexes are extraordinarily robust—if the fly pitches forward, the haltere detects it, and the stroke amplitude of both the left and right wings increases. If the fly pitches backwards, the stroke amplitude decreases. Similar reflexes act if the fly yaws (a sideways turn about the vertical axis) or pitches. The changes in wing motion occur because the haltere sensors shift the activation phase of the steering muscles—and thereby their stiffness—which in turn changes the way the wing beats, altering the production of aerodynamic forces. The halteres are essential elements of the fly's control system. Cut them off, and a fly rapidly corkscrews to the ground.

But if the fly possesses such a robust autonomous control system, how does it ever do anything





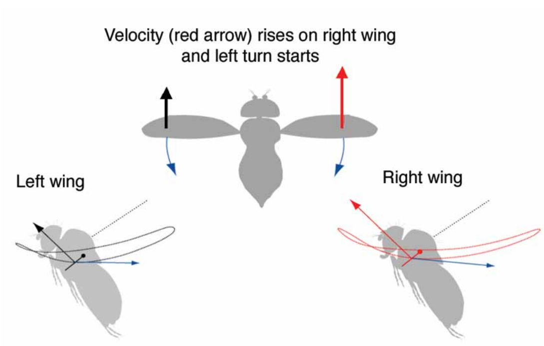
Fruit flies were imaged with high-speed cameras at 5,000 frames per second as they flew freely around an enclosed chamber (diagram, left). Their 3-D body and wing positions were extracted from each frame and fed into Robofly to calculate wing forces, which were then superimposed on the wings as vectored arrows. The next diagram, below, shows one of the sequences analyzed, in which a fly climbs vertically and performs a saccade at the top. The red lollipops correspond to the body orientation every 5 ms; black lollipops, the corresponding orthogonal projections.

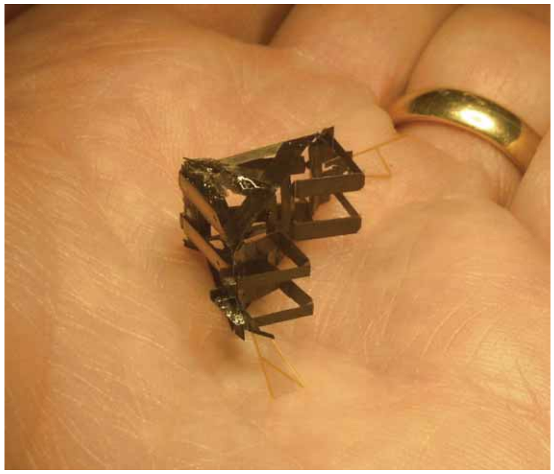
small things in a wind tunnel. We take a tiny fly and model it as a giant thing in 200 metric tons of mineral oil. Although a bit messy, Robofly has proven to be a scientifically very productive instrument.

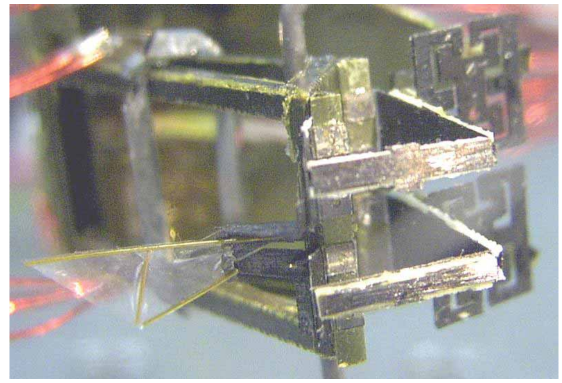
One application is to use high-speed video to take the patterns of wing motion measured in freely flying fruit flies, and play them out directly on Robofly to study how the fly alters flight forces during a maneuver such as a rapid saccade. Once we measure the forces generated by Robofly and scale them down appropriately, we can superimpose the aerodynamic force vectors onto the original video sequences.

In one such example, shown above, we found that the animal ascended with almost zero horizontal velocity, rotated its body by precisely 90 degrees, and then accelerated forward. We were surprised to find that it accomplished this rapid maneuver with very minute and barely detectable changes in wing motion—which explains in part why the fly needs such a well-tuned control system. Another surprise was that the body dynamics of these tiny flies is not dominated by the viscosity of the air (which, to

Above: Robofly in action. Bubbles have been injected into the mineral oil to visualize the fluid flow created by the wingbeats. Right: To make a turn to the left, the fly creates a torque by increasing stroke amplitude on the right wing, and by tilting the stroke plane backward.







MFI, the micromechanical flying insect being developed by Ron Fearing's lab at UC Berkeley is about the size and weight of a large housefly. It has two functioning wings and a carbon-fiber thorax. The close-up above right shows the ingenious wing hinge and flapper.

PICTURE CREDITS:
10, 14-16 – Bob Paz;
10 – Doug Cummings;
11, 19 – Ron Fearing, UC Berkeley; 11 – Joseph Yan, UC Berkeley; 15 – Wai Pang Chan, UC Berkeley; 19 – Srinath Avadhanula & Rob Wood, UC Berkeley

a fly, has the consistency of mineral oil), as was previously thought, but rather by inertia—the need to stop the body from continuing to spin. This means that during each saccade they must first generate torque to start the turn, but after only four wingbeats they must quickly generate countertorque so that they can stop turning. The fly's brain must regulate the timing between turn and counterturn to generate the precise 90-degree rotations. Recent evidence suggests that while a visual signal triggers the start of the saccade, it's the haltere that detects the initial rotation and triggers the counterturn.

So what can we do with this emerging blueprint of a fly? Do we know enough to build a robotic insect? In a collaboration with Ron Fearing at UC Berkeley, we're working on a five-year project jointly sponsored by ONR and DARPA, to build a micromechanical flying insect (MFI). The aerodynamics of this device, which is the size and shape of a housefly, are all based on what we've learned about these little insects. Ron and his students have designed an ingenious flexure joint that can replicate the flapping and rotating motion of the wing and, so far, they have a two-winged fly that can generate about 70 percent of the force required for flight. With a few improvements they should soon have a configuration capable of supporting its own weight. The next challenge will be to design a control system that enables the device to hover stably.

In the end, it's just a fly. Is such an insignificant little organism really worth all this effort? The natural world is filled with complex things, like immune cells, the human brain, and ecosystems. Although we've made great progress in deconstructing life into its constituent parts such as genes and proteins, we have a ways to go before we have a deeper understanding of how elemental components function collectively to create rich behavior. The integrative approach that we are using to study fly flight is an attempt to move beyond reductionism and gain a formal understanding of the workings of a complex entity. The fly seems a reasonable place to start, and if successful, I hope such work will stimulate similar attempts throughout biology. The lessons learned along the way may provide useful insight for engineers and biologists alike. Even if you don't buy such grand visions, I hope you will at least think before you swat.□

A zoologist with a fine grasp of engineering, Michael Dickinson, the Zarem Professor of Bioengineering, has equipped his lab to study fly flight in a multidisciplinary way. Trained as a zoologist (ScB in neural sciences from Brown University in 1984; PhD in zoology from the University of Washington in 1989), he began his transition toward engineering while a postdoc at the Max Planck Institute for Biological Cybernetics in Tübingen, Germany, studying insect flight aerodynamics. In 1991, he started his own lab as an assistant professor at the University of Chicago. He moved to UC Berkeley in 1996, and was named the Williams Professor of Integrative Biology. Dickinson joined the Caltech faculty in Engineering and Applied Science and Biology in 2002. He was a recipient of a prestigious MacArthur Fellowship in 2001, and was awarded the George Bartholomew Award of the American Society of Zoologists in 1995, and the Larry Sandler Award of the Genetics Society of America in 1990. The lecture on which this article is based can be viewed on Caltech's Streaming Theater Web site, http://today.caltech.edu/theater/list?subset=science.