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Invited Articles

Flight of the fruit fly

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There comes a time in each of our lives where we grab a thick section of the morning paper, roll it up and set off to do battle with one of nature's most accomplished aviators—the fly. If, however, instead of swatting we could magnify our view and experience the world in slow motion we would be privy to a world-class ballet full of graceful figure-eight wing strokes, effortless pirouettes, and astonishing acrobatics. After watching such a magnificent display, who among us could destroy this virtuoso? How do flies produce acrobatic maneuvers with such precision? What control mechanisms do they need to maneuver? More abstractly, what problem are they solving as they fly? In this article and the associated video presentation of my invited lecture from the 71st Annual Meeting of the American Physical Society's Division of Fluid Dynamics, I describe the challenges associated with answering these questions, our attempts to investigate them, and, through various demonstrations depicted in the video, qualitatively illustrate the mechanisms used by these insects to achieve these astonishing behaviors.

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I. INTRODUCTION–THE CHALLENGE

The challenge of determining how insects fly with such precision is formidable. A fruit fly, for example, has wings that are on the order of a millimeter in length and flap back and forth at ~220 Hz, or 30 times in the blink of an eye. The aerodynamic flows achieved by these motions are characterized by intermediate Reynolds numbers of about 100 so that neither Stokes flow nor potential flow is appropriate. Moreover, the leading-edge vortices generated by the wings are sometimes held attached to generate larger lift forces and at other times shed to generate rapid maneuvers. Understanding how flies manipulate these flows requires tracking their wing and body kinematics with exquisite precision while they are in free flight. Thus, even if we consider the wings and body to be rigid, 18 kinematic parameters (three center-of-mass and three angular coordinates each for the body and two wings) must be tracked over at least 40 moments in time throughout the wing stroke with an angular precision of just a few degrees. Even if this kinematic tracking were achieved, it is impossible to know whether an insect executed a given maneuver because it wanted to (volition) or because some gust of air destabilized it or due to some mechanical reflex. It is therefore remarkable that as a community we have, nevertheless, been able to make great progress in studying the flight of these amazing creatures.

At the time when we threw our hat into this field, the research groups of Ellington at Cambridge and Dickinson at Caltech used dynamically scaled robotic wings to make major breakthroughs in understanding how insects produce their large lift forces [1,2]. The key insight gained from these studies and those that followed is that insects flap their wings at a sufficiently high angle of attack that they generate a leading-edge vortex that lowers the pressure over the wing and generates extra lift. In fixed-wing aircraft such vortices are often shed and the vehicle eventually stalls. By pivoting their stroke around their wing hinge, fruit flies are able to keep these vortices attached [3]. This discovery led to a series of seminal papers by the Dickinson group and others, including my colleague Jane Wang at Cornell, in which quasisteady approximations where the fluid forces were averaged over an entire wing stroke could be used to estimate effective lift and drag coefficients that account for about 90% of the aerodynamic forces acting on the wings of animals like fruit flies. Of course, 90% is not 100%, and so many scientists were and still are focused on determining where the missing 10% is coming from.

II. DISCUSSION–OUR APPROACH

Our group took a decidedly different approach. To a physicist 90% is a problem that has been solved, at least to first order. If you take this attitude, what the field was missing is the kinematic data to tell us how these forces were being used to generate maneuvers. So, as a young faculty member, I blew a substantial part of my startup funds on three fast cameras and we started taking fast videos of these insects in free flight. Collecting the data is trivial. Simple triggering circuits can be used to collect hundreds of movies a night. The major issue with tracking the three-dimensional (3D) kinematics of insects is that the three images collected by the cameras cannot be used to uniquely identify the object producing them. For example, imagine that each camera sees a disklike shadow. It might seem obvious that the object creating these disks is a sphere, since the two-dimensional (2D) projection of a sphere looks like a disk from any angle. A little thought, however, might bring you to the conclusion that this 3D object could just as easily have been comprised of three intersecting disks, or, alternatively, a Steinmetz solid—the volume formed by the intersection of three cylinders. Thus, there is no unique shape that can be determined from the images on the cameras. Instead, we had to rely on extra geometric information that we already knew about the fly. For example, we know that there are only two wings and that they are nearly flat. With this added intuition we were able to construct a computational analysis scheme that would enable extraction of the wing and body kinematics at a much faster rate and, more importantly, with much greater precision than was previously possible [4].

This achievement opened the door to a number of interesting studies. Once access became available to the kinematic data, we were able to understand how insects are able to take advantage of drag forces to achieve sideways flight [4], forward flight [5], and yaw turns [6–8]. Using an ingenious apparatus developed by my student (now Professor Ristroph at NYU), where in-flight perturbations could be induced using magnetic fields that torqued tiny magnets we glued onto the backs of flies, we were able to show that such wing manipulations are also crucial for stabilizing flapping flight [9]. In fact, flapping-wing insect flight is inherently unstable and is only made possible by near-constant, often-subtle corrective actions [10]. Without these corrective actions, insects would start rocking back and forth and eventually topple in a manner similar to the way humans would if they did not constantly correct their posture to stay vertical. For fruit flies, such corrective responses need not only be robust but also fast: the Drosophila flight control reflex has a response latency time of $\sim$5 ms, ranking it among the fastest reflexes in the animal kingdom [11].

We have gone on to show that such reflexes can be modeled using a proportional integral (PI) control scheme common to many engineered systems. Here, the fly seems to be measuring the body's angular velocity and its integral, the total angular displacement, to determine the appropriate change in the wing-stroke parameters (Fig. 1) [9,11,12]. Remarkably, flies accomplish this feat of stabilization using a relatively sparse motor system, with only 12 steering muscles to modulate the kinematics of each wing. Through a collaboration with the groups of Card, Stern, and Korff at the Howard Hughes Medical Institute and Dickinson at Caltech, we are using optogenetic manipulation of the Drosophila motor neurons to activate/inactivate individual muscles to try to tease apart what muscles are responsible for different terms in the PI controllers stabilizing each degree of freedom.

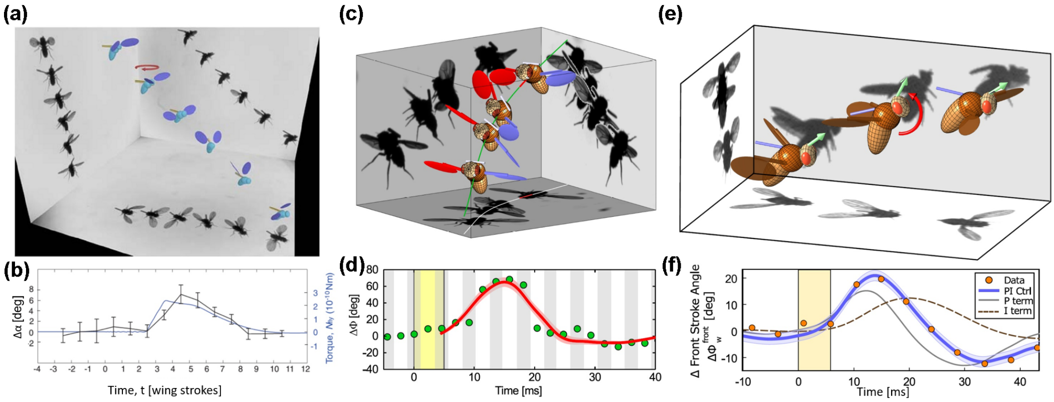
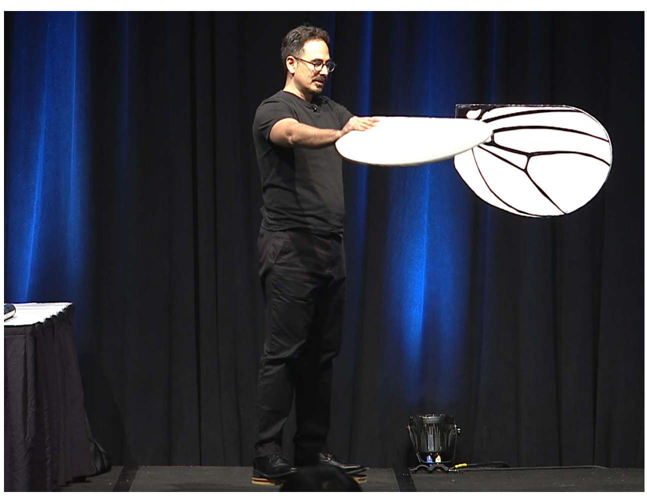


FIG. 1. We successfully modeled Drosophila's flight stabilization reflex as a PI controller. PI controller models describe Drosophila flight stabilization along yaw (a), (b), roll (c), (d), and pitch (e), (f) body angles. (a), (c), (e) Representative perturbation and correction maneuvers, with image data and corresponding 3D reconstructions. (b), (d), (f) Controlled wing kinematic quantity vs time (data points), with curve fits corresponding to predictions of a PI controller model. In each case, the body angular velocity and total angular displacement about a particular degree of freedom (yaw, roll, or pitch) is summed with appropriate coefficients to determine the PI controller prediction for the relevant wing-stroke parameter: difference in angle of attack for the left and right wing for yaw; difference in wing-stroke amplitude for roll; difference in the front stroke angle for pitch. In F, we plot the body pitch velocity representing the proportional term (P term: solid gray line), the total angular displacement representing the integral term (I term: dashed black line), and their appropriately weighted sum that corresponds to the PI controller prediction (PI Ctrl: solid blue line). Adapted from Refs. [9,11,12].

III. VIDEO PRESENTATION

In the attached video presentation of my talk (see Video 1), delivered at the 71st Annual Meeting of the American Physical Society's Division of Fluid Dynamics (APS/DVD), I highlight these results using the beautiful images and movies that we have collected over the past decade of studying these magnificent creatures. In addition, I attempt to illustrate the intuition for the various



Video. 1. *Flight of the Fruit Fly*. Full lecture delivered at the 71st Annual Meeting of the APS DFD.

mechanisms we have discovered using a variety of demonstrations. One of the most gratifying aspects of giving this talk is watching the journey that the audience takes and the change in their attitude as they consider an insect which is often categorized as a pest. Building an appreciation for flies and other insects is especially important, since we as a civilization have reached a point where our effect on the environment has caused these animals to experience a significant decline in numbers, with over 40% of insect species threatened with extinction [13]. I hope that through the attached video I am able to change some minds and perhaps drive some action towards preserving these fellow inhabitants that have been so vital to generating and sustaining the ecology of our planet.

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