Fluid dynamics and control of insect flight

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Insects have mastered flight to a degree that scientists are only now starting to comprehend. Itai Cohen and colleagues discuss some of the outstanding challenges and opportunities for studying this fascinating and beautiful behaviour.

The manoeuvres of flying insects are impressive feats of acrobatics. Whether watching a dragonfly hunting above a pond or just trying to swat an annoying mosquito, observation makes it clear that after millions of years of evolution, these insects have mastered flight to a degree that is only just starting to be comprehended. The flows generated by insect wings (FIG. 1) can be described using the Navier–Stokes equations and, on this bicentennial of George Stokes' birth year, we take a moment to reflect upon some of the advances made in understanding these flows as well as the many outstanding questions that remain unanswered about insect flight.

Insects such as mosquitoes beat their wings at rates of up to 800 Hz. The flows they generate are characterized by intermediate Reynolds numbers of about 100, a regime in which standard fluid dynamics approximations do not hold. In particular, neither Stokes flow (the viscosity-dominated limit) nor potential flow (the inertia-dominated limit) applies. Even in the simple case of a plate moving through a fluid in this regime, no analytical solution for the resulting flow is known. In insect flight, this problem is compounded by vortices that are generated, trapped and shed, the interaction of the wing with its own flow field, and by fluid–structure interactions that arise from wing and hinge elasticity. Additionally, it has been shown that flapping flight is mechanically unstable owing to coupling between the body and wing motions. Because the wings are offset relative to the body's centre of mass — and, therefore, so is the point at which the sum of the surrounding pressure field acts — a flying insect experiences instabilities akin to an inverted pendulum such as a ruler balanced upright on one's open palm. Smaller pendula require faster reaction times to stabilize, and, similarly, to stay aloft small flying insects must make constant adjustments to their wing motion at a timescale of only a few milliseconds, pushing the limits of both biomechanics and neural response. Thus, determining how insects implement various control strategies is also integral to understanding flapping flight.

Despite these formidable challenges, advances in areas such as mechanical modelling, hydrodynamic computations and data acquisition and analysis have enabled pioneering studies that have made great inroads into understanding basic elements of flapping flight. For example, flow visualization and mechanical modelling studies have established that a leading-edge vortex — a circulating fluid structure that forms above the flapping wing — is a major mechanism for augmenting the aerodynamic lift via a substantial pressure drop above the wing[1]. Additional studies and simulations showed that this complex unsteady flow could be modelled using a quasi-steady approximation that is quadratic in the wing velocity with effective lift and drag coefficients[2]. Such approximations can account for upwards of 90% of the lift and drag forces for insects such as hawk-moths. Subsequently, methods for extracting free-flight wing and body kinematics have enabled researchers to use these flow approximations to determine how insects generate aerodynamic forces to manoeuvre[3]. For example, it has been shown that insects such as fruit flies can use drag forces to generate forward and sideways thrust, as well as yaw turns (that is, changes in heading). These drag-based manoeuvres are achieved using very slight manipulations about the typical 45° angle-of-attack, the angle of the wing relative to its velocity. This strategy takes advantage of the fact that around 45°, the lift force is maximum, whereas the drag force linearly depends on the angle-of-attack.

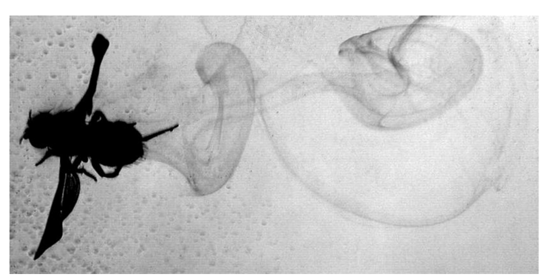

Fig. 1 | **Aerodynamic vortex pattern shed by a flying fruit fly.** The flow is made visible by dispersing glycerol vapour in the air surrounding the fly and using schlieren imaging with a fast camera. Image courtesy of Irmgard Bischofberger, MIT, USA.

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Thus, such slight manipulations of the angle-of-attack alter the drag force while keeping lift nearly constant.

Impressively, insects can achieve such manipulation of the angle-of-attack on a sub-millisecond timescale, which is shorter than the timescale for neural activity. Studies suggest that some insects modulate the elastic components of their wing hinge, which, in conjunction with the aerodynamic lift and drag forces, passively determine the complicated time course of the wing's rotation. Despite the complexity of the wing hinge — one of the most complicated joints found in the animal kingdom — modelling it as a simple torsional spring accurately captures this passive wing stroke manipulation. It appears, therefore, that insects take advantage of this fascinating fluid–structure interaction to simplify the modulation of their wing kinematics.

One of the lessons learned from these studies is that very small forces, comparable to a few per cent of the total lift, are sufficient to elicit manoeuvres. Thus, despite the high accuracy of current quasi-steady models, even more accurate modelling of the aerodynamic flows may be required for understanding the full range of manoeuvres these insects are capable of performing. This lesson is especially true for insects such as mosquitoes, whose wing modulations are particularly subtle and for which quasi-steady analysis captures only ~50% of the aerodynamic force[4]. In such cases, full-blown computational fluid dynamics simulations, although computationally intensive, may be needed to understand flight manoeuvres. Yet, despite these difficulties, progress over the past decades in understanding mechanisms such as leading-edge and trailing-edge vortices (in which vortices attached to different parts of a wing augment lift), wake capture (in which a wing intercepts a previously shed aerodynamic flow) and clap-and-fling (in which new vortices are created and transported by touching the wings together and pushing them apart) leaves us optimistic that such higher-precision studies will not be solely descriptive, but rather continue to uncover general strategies and principles.

In parallel with these advances in modelling, advances in techniques used to perturb free flight — ranging from virtual reality video displays to flow perturbations and even neural circuit perturbations that trigger muscle contractions — have made it possible to glean general insights into how insects control their flight[5]. For example, by attaching a tiny magnet to a fruit fly and imposing an external magnetic field, researchers have been able to induce mid-air stumbles and investigate the response[6]. Impressively, the response latency periods are about 5 ms, ranking these reflexes among the fastest in the animal kingdom. These response times are too rapid to be driven by the visual system and are instead thought to be informed by specialized gyroscope-like organs called halteres. Measurement of the flight kinematics during the subsequent correction manoeuvres of the flies established that they are effectively implementing reflexive proportional–integral (PI) controllers to stabilize their flight along yaw, pitch and roll. Specifically, it appears that flies use measurements of the body angular velocity (the proportional term in the PI controller) and angular displacement (the integral term in the PI controller) in linear combination to reflexively determine the appropriate wing stroke parameters for controlling each rotational degree of freedom. When coupled with targeted neural manipulations, such perturbation experiments open the door to determining, with exquisite precision, how flight control is implemented at the neuromuscular level, namely, which neurons and muscles are responsible for implementing different aspects of the controller and wing motion.

Perhaps most impressively, despite lingering questions regarding aerodynamics, flight manoeuvres and the implementation of control at the neuromuscular level, insect flight is now understood well enough to create flapping wing drones[7,8]. Whether such flapping drones will become useful for practical applications or remain at the level of an important tool for studies in flapping flight, remains an open question. Its answer may depend on how much researchers continue to learn about the graceful and efficient manner in which insects achieve this beautiful behaviour of flight.

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Competing interests
The authors declare no competing interests.