Insect and insect-inspired aerodynamics: unsteadiness, structural mechanics and flight control

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Abstract

Flying insects impress by their versatility and have been a recurrent source of inspiration for engineering devices. A large body of literature has focused on various aspects of insect flight, with an essential part dedicated to the dynamics of flapping wings and their intrinsically unsteady aerodynamic mechanisms. Insect wings flex during flight and a better understanding of structural mechanics and aeroelasticity is emerging. Most recently, insights from solid and fluid mechanics have been integrated with physiological measurements from visual and mechanosensors in the context of flight control in steady airs and through turbulent conditions. We review the key recent advances concerning flight in unsteady environments and how the multi-body mechanics of the insect structure—wings and body—are at the core of the flight control question. The issues herein should be considered when applying bio-informed design principles to robotic flapping wings.

Flapping wing aerodynamics

Aerodynamic forces are determined by the manner in which flow moves around an object. The issue is well known in aeronautics, where a rotating propeller pushes air backwards, or a fixed wing ensures the production of lift as a result of its motion respective to the surrounding fluid. The main design criterion of aerodynamic performance decides the geometry of the wing when considering, for example, the lift-to-drag ratio. Early efforts used the tools of classical aerodynamics to understand flight performance in animals – see e.g. [1] for a review. But flapping wings bring two main elements that increase complexity: on one hand, flapping wings must contribute lift and thrust production; on the other hand, the problem is intrinsically unsteady, because of the periodicity of the flapping motion [2-6]. Unsteadiness certainly brings complexity, but is also intimately linked to the outstanding maneuverability that can be achieved [7,8]. This is not only true for flying insects, but also for flying vertebrates, where convergent evolution has modified the forelimbs to make wings. From the fluid-dynamical perspective, one of the most fascinating points is that aerodynamic force production using such periodic flapping motion is typically governed by the physics of separated flows and vortex dynamics. Details of the kinematics and body-wing geometry are thus of crucial importance and determine several distinct mechanisms. These include the prevention of stall through an attached leading-edge vortex (LEV) or lift enhancement through the interaction of wings—the well-known clap-and-fling. These mechanisms, and others, are reviewed in [2] and [9]. A detailed breakdown of observed LEV topologies can be found in [4].

In the case of insects, although the aerodynamics of merely a few archetypal species have been thoroughly scrutinized (recent examples for: mosquitoes [10]; bees [11]; dragonflies [12]; hawkmoths [13-15]; fruit flies [16]; hover flies [17,18]; blow flies [19]; desert locusts [20,21]), it is reasonable to say that the key aerodynamic mechanisms have been now identified, including, in addition to the aforementioned LEV and clap-and-fling dynamics, other subtle mechanisms related to added-mass, rotational circulation or wake capture [2,6,10]. To understand the role of each of these mechanisms in any specific case, one must recall that flow separation and vortex dynamics are ruled by the relative importance of inertial versus viscous forces: a balance determined, in the language of fluid mechanics, by

the Reynolds number ($Re = \rho UL/\mu$, where ρ and μ are the air density and viscosity, respectively, and U and L represent characteristic velocity and length scales). Except for a few unusual applications, such as the feasibility of designing flapping wing robots that could fly in rarefied atmospheres [22], the Reynolds number for flapping flyers in an earthly atmosphere is thus solely determined by wing kinematics and size. For insects, Re ranges between ~10^1 and 10^4 [9], in which the vortex dynamics driven by flapping motion evolve rapidly. Caution is therefore required because the same type of structure or mechanism can behave in a substantially different fashion for insects of different sizes and wingbeat frequencies. A clear example is the LEV; despite being always originated by flow separation at the leading edge during each stroke, its structure and associated flow topology—presence of span-wise flow, connections between neighbouring vortices—present substantial differences between different species [4]. Wing flexibility can also substantially change the aerodynamic force coefficients across this size range [23].

Turbulent environments

A question that has engaged considerable attention recently concerns the dynamics of insect flight in turbulent environments, i.e. in realistic conditions [11,24-29]. Experimentally, it is challenging to study insect flight subjected to wind gusts, or to turbulence in the wake of landscape features like vegetation or other animals. However, recent efforts have begun to shed light on turbulence-mitigation strategies used by biological fliers [30], such as the mechanisms used by bumblebees to increase stability. One example found that bumblebees respond to turbulence with changes in wing kinematics that are both static (as in altered mean values) and dynamic (stroke by stroke) [31].

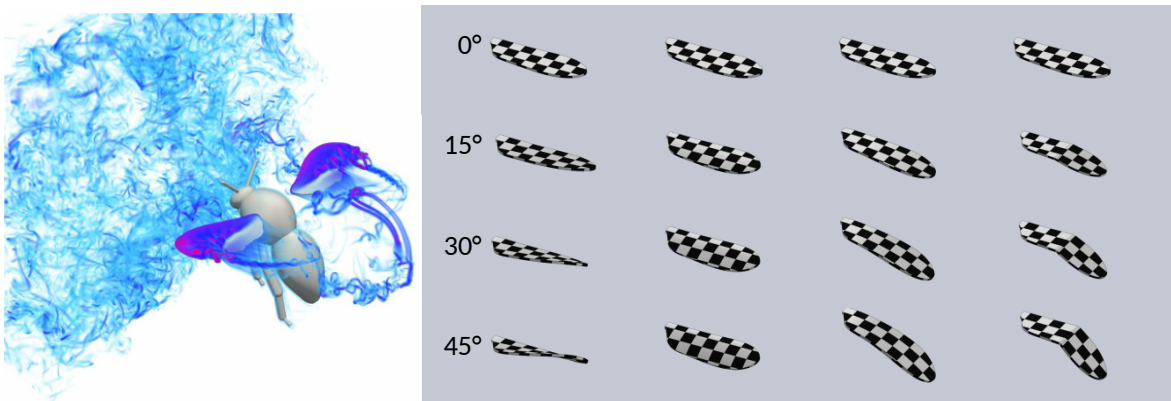

Figure 1. Left: Numerical simulation of a bumblebee model with rigid wings and imposed kinematics, subjected to an incoming turbulent flow. Image provided by T. Engels [29]. A leading-edge vortex is visualized on both wings (pink-purple). Right: Four deformation modes at four different amplitudes (indicated in degrees) for a flapping insect-inspired wing. Columns from left to right: twist, chord-wise bending (camber), span-wise bending and localized folding.

Recent works have found a remarkable resilience of the LEV in turbulent environments. Engels and colleagues [11] used a numerical simulation for bumblebees subjected to incoming homogeneous isotropic turbulence (Fig. 1) to show the LEV persisted even at a turbulence intensity of 100%. Experimentally, the recent study by Matthews *et al.* for

hawkmoth flight in a flower wake showed that the LEV not only persists in the unsteady wake, but also maintains the same qualitative structure seen in steady air [28]. In most cases, the persistence of a consistent aerodynamic structure over the wing is likely to be because the intrinsically-transient vortex dynamics are governed by the timescales of the flapping frequencies and associated wing tip speeds, which are typically much faster than fluctuations in the incoming flow velocity.

Flexible wings

The effect of wing flexibility has been studied extensively (see, for example [32,33] or [34] for a review), extrapolating observations from biological systems to robotic applications. Since the wing contains no musculature outboard of the thoracic hinge, much of the observed deformation is passive aeroelasticity, driven by inertia and aerodynamic loads. Of these, the inertial loads greatly exceed the aerodynamic loads [35-37], at least in larger insects [38]. However, non-trivial mechanisms have been shown to govern the performance of flexible wings in terms of their aerodynamics. In particular, drag induces a phase lag between the leading and trailing edges of the wing that brings a beneficial effect in terms of aerodynamic force production [39,40].

Faux *et al* [41] recently studied the use of two resonant modes in a flexible wing to reproduce typical insect-wing kinematics with a simplified actuation. The geometry and elastic characteristics of artificial wings are such that the span-wise and chord-wise bending modes respond with a quadrature phase shift, resulting in a larger flapping amplitude. We can expect to see such mechanisms in future robotic implementations. With the advent of insect-sized robotic flyers [42], there has been a pressing drive to combine optimal kinematics with optimal geometry to produce optimal aerodynamic output. Bio-inspiration can be a dominant influence on robotic wing design. Simulations (Fig. 1) and empirical studies (Fig. 2) of the fluid and solid mechanics will be crucial for understanding the fluid-structure interactions of the wings and their surrounding fluid.

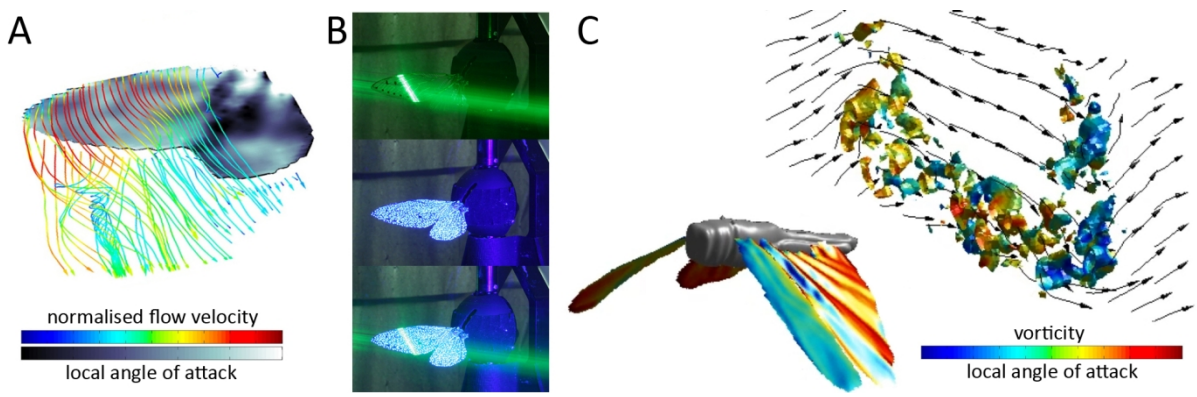

Figure 2. (A) Simultaneous three-dimensional surface and pseudo-volumetric flow measurements of a cicada wing on a unique three-axis flapping device [43]. A conical separation bubble enclosing a leading-edge vortex appears as fast red streamlines; the flow slows (yellow) as it reattaches to the wing surface. (B) For cicada measurements we required a green laser for stereo particle image velocimetry (stereo-PIV: upper), the UV fluorescent speckle pattern for surface digital image

correlation (DIC: middle), and both together (lower). (C) shows a similar DIC measurement from a live, flapping, tethered desert locust and also the wake, measured using volumetric tomo-PIV in a thick transverse plane. Corrugations of the hind wing and the vortex wake are clearly visible. Images originally published in [44].

Wing deformation and how to sense flexibility

The nature and degree of deformation exhibited by insect wings in flight is determined by the wing architecture. The membrane provides stiffness under planar tensile loads but compliance under compressive loads. Wing veins have a diverse pattern of longitudinal and cross-veins, typically tapering from root to tip and from leading to trailing edge, causing an exponential decline in stiffness in each axis [45]. The veins often have cross-sections that are elongated in the axis aligned with the load, with expected consequences for anisotropic stiffness within the plane normal to the vein central axis [46]. Geometric features of the fluid-filled tubular cross section and layered microstructure of veins prescribe larger scale wing deformation patterns and damping characteristics [46,47] that can be regulated further by the presence of a pterostigma [48]. Joints between veins are also critical for macroscale wing deformations *via* features such as resilin joints or spikes that confer dorso-ventral anisotropy and non-linearity in flexural stiffness [49-51]. The combination of these features and corrugations defined by the longitudinal veins lead to a general principle (drawn across six insect orders) that spanwise flexural stiffness is 1-2 orders of magnitude greater than chord-wise flexural stiffness [52]. Wing size is the strongest determinant of flexural stiffness, irrespective of venation pattern [52].

Insect wings bend, twist and fold on each wing stroke (e.g. [53,54]) and these deformations can have a substantial effect on flight efficiency and the aerodynamic forces they produce [55]. Thus, for controlled flight insects must precisely regulate wing shape, which requires a feedback loop incorporating kinematic actuation and a mechanosensory state observation. While there is some limited neural evidence that longer trichoid sensilla on the wing can provide aerodynamic information [56], and similarly limited evidence that chordotonal organs in some insects could provide load-dependent proprioceptive information at the wing hinge [57], the majority of aeroelasticity sensing is done by a relatively small collection of campaniform sensilla. Fields of campaniform sensilla close to the wing base and isolated sensilla toward the margin are well-placed to maximise observability of rotations [58]. With the majority of the sensilla placed proximally, they are also more protected from degraded observability owing to wing damage (e.g. [59]) although the more distal sensilla at the trailing edge are informative for fine-scale control of aerodynamic loads at that location [10,60].

Processing aeroelastic and inertial information from the campaniform sensilla

Campaniform sensilla detect strain in the cuticle. The sensilla most pertinent to flight control are located on insect wing veins and also the halteres of the Diptera and Strepsiptera. Their dome structure is integral to the transduction process; it attenuates higher frequencies and can act as a gain multiplier for chord-wise wing deformations [61].

Their frequency response appears broadly tuned to wing beat frequency, and the output of each sensillum is rectified such that they only fire at a precise phase of the wingbeat cycle and can therefore assess larger scale deformations when processed as a sensor array [62]. Thus, the physical properties of the sensilla and their location can provide sensory pre-filtering [63], simplifying the subsequent encoding and processing necessary for flight control.

Artificial stimulation of campaniform sensilla has long been known to affect behaviour by, for example, effecting a response in the flight motor neurons [64] or postural changes in the abdomen [65]. Stimulation of fly haltere [66] and moth wing [65] sensilla have revealed similarities in spike timing and precision, which is perhaps to be expected given their shared evolutionary history.

Natural mechanical cues for campaniform sensilla on flexible wings are provided in a number of ways: the periodic strains expected from each flapping cycle in steady flight; the unexpected aerodynamic loads incurred when flying in turbulent airs; and the torsion induced in flexible wings by voluntary or involuntary body rotations [67]. Pratt and colleagues showed recently that the neural architecture that underlies haltere function, is also present in hawkmoths, supporting the idea that the wings are simultaneously acting as aerodynamic actuators and gyroscopic sensors [68].

Flight control from wing strain sensing

While we can be confident that distal, isolated campaniform sensilla in concert with proximal fields close to the wing hinge detect wing loads, far less is known about how that information is encoded and interpreted by the flight controller [69]. An important task for the controller is to determine whether signal magnitude and timing are those to be expected from periodic steady-state flapping, whether they correspond to a voluntary manoeuvre, or if they are the result of external perturbation. Thus, information from wing-mounted mechanosensors parallels that originating from the array of chordotonal sensilla comprising the Johnston's organs at the base of the antennae, or indeed the horizontal and vertical system descending neurons of the compound eyes' visual system that monitor self-motion via optic flow [70]. How the neural architecture directly links such sensory input to motor output remains poorly understood. Recently, three pairs of descending interneurons in flies were discovered to integrate wide field information from visual interneurons and subsequently project to motor centres that activate steering control [71]. We might expect similar discoveries to be made that elucidate the processing of mechanosensory information in due course.

When discussing several ways in which the feedback loop comprising the Johnston's organ flight speed controller might track forward commands instead of opposing them during voluntary manoeuvres, Taylor and Krapp [56] suggested that opposition might be avoided by the use of an efferent copy of the command to cancel feedback from the antennae. However, they concluded that the most parsimonious mechanism was to rely instead on the temporal difference between sustained voluntary changes in air speed as opposed to transient perturbations. The principal objection of the forward model hypothesis was the

lack of evidence in support of an efferent copy. With respect to the case of wing strain sensing, the same is true, and efferent copy is less likely to be required if the output of the campaniform sensilla is once per cycle [62,69]. However, recent work by Kim and colleagues suggest that efference copies from mechanosensors might exist [72]. They discovered that visual neurons in fruit flies receive motor related inputs during turns with signs and latencies that suppress the targeted cells visual response during manoeuvres. Kim *et al* consider these signals to be representative of a predictive internal model, used to suppress the expected visual response. This important finding is set in the wider context of biological image stabilisation during flight in Hardcastle and Krapp's recent comprehensive review [73]. Studies linking motion vision to flight putative controller models are becoming more widespread. For example, a model implementing closed-loop control of pitch using visual cues associated with free fall in hover flies has shown good agreement with experimental measurements [74]. In any case, it is clear that flight control is typically multimodal with mechanosensation working in tandem with vision and various methods are available that can disentangle the cues (e.g. [75,76]). A comprehensive recent study [77] has shown that generation of steering motor commands that are known to be the result of visual perception, is modulated (in opposing ways) by mechanosensory information from the wings and halteres. A review of experiments concerning the fruit fly autopilot concludes that halteres provide the derivative input for a proportional-derivative controller model that accurately predicts response behaviour when flies are subjected to in-flight perturbations around each axis [78]. There is typically a three wing beat delay prior to observable kinematic adjustments that modulate wing pitch by shifting the resting point of a torsional spring at the wing hinge [78]. Using a reverse engineering approach and extensive simulations, Hedrick and Daniel [79] could control sustained hovering flight in a virtual moth with three degrees of freedom using variable wing stroke kinematics and a simple aerodynamic model. Rapid sensory information was required for pitch control, postulated to be sourced from mechanosensation of wing strain. For a review of how insect experimentation can use the framework of control theory to make predictions of behaviour in novel contexts, the reader is referred to Roth *et al* [80]. For a summary of our current understanding of logical computation in the neural circuitry controlling wing kinematics during manoeuvres and stabilisation in *Drosophila* flight, we refer the reader to Muijres and Dickinson [81].

Concluding remarks

There is cause for optimism that our knowledge of aerodynamics, structural mechanics and mechanosensory state observation can be transferred successfully to micro technology on aerial systems. For example, Suryakumar and colleagues have suppressed gust-loads using information from a hot-film sensor array that monitors the stagnation point at the leading edge [82]. Thapa Magar *et al* have used artificial hairs based on trichoid sensilla in a feedforward network to predict aerodynamic characteristics on wings in unsteady conditions [83]. Armanious and Lind have proposed a control architecture for mechanosensory-based systems [84]. The benefits of so-called fly-by-feel systems are that they are fast, lightweight, robust and computationally inexpensive. Insects are an ideal model for bio-informed approaches, offering capabilities that are highly desirable for a new generation of aerial vehicles. This new suite of designs that we predict will emerge over the

next decade or so, will be capable of sustained hovering flight. Hovering is both energetically intensive and also more challenging to control, in part due to the time scales at which the controller must operate. Hovering is a capability far more characteristic of insects than of birds (with the notable exception of hummingbirds) where robotic likenesses are already reasonably widespread.

Of course, these questions that link aerodynamics, structural mechanics and flight control are only part of the full flapping flyer problem. Other exciting issues where insect-inspired solutions can be expected include take-off manoeuvres, where the interplay between jumping and the first flapping strokes determine a non-trivial multi-body problem [85]; or the collective dynamics of multiple flapping wings, where stable configurations understood with simple models [86] could bring ideas in realistic applications for swarms of flapping-wing robotic flyers.

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