

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

Richard J Bomphrey<sup>a\*</sup> and Ramiro Godoy-Diana<sup>b</sup>

<sup>a</sup> Structure and Motion Laboratory, Royal Veterinary College, London, United Kingdom

<sup>b</sup> Physique et Mécanique des Milieux Hétérogènes laboratory (PMMH), CNRS, ESPCI Paris – PSL Research University, Sorbonne Université, Université Paris Diderot, Paris, France

\*author for correspondence: [rbomphrey@rvc.ac.uk](mailto:rbomphrey@rvc.ac.uk)

Declarations of interest: none.

## *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 air 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*

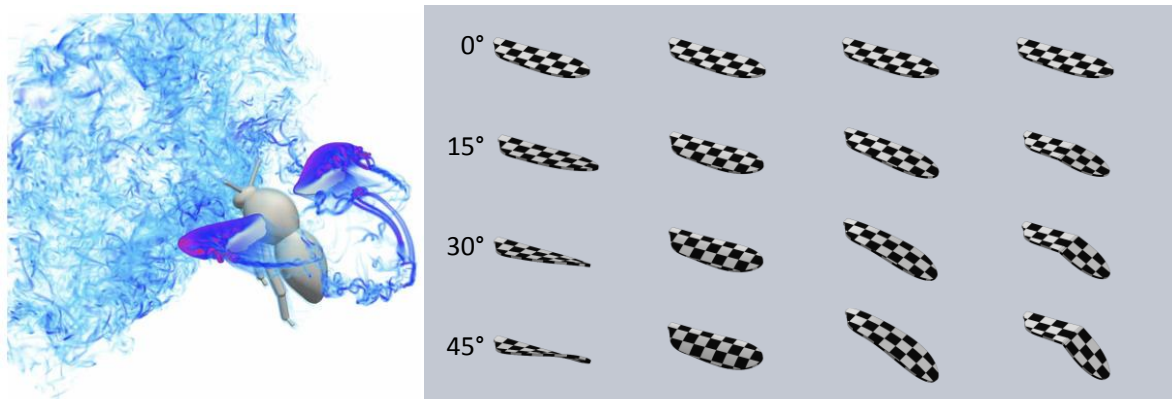
Aerodynamic forces are determined by the manner in which flow moves around an object. The issue is well known in aeronautics, where a rotating propeller pushes air backwards, or a fixed wing ensures the production of lift as a result of its motion relative to the surrounding fluid. The main design criterion 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  $\rho$  and  $\mu$  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  $\sim 10^1$  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. A volume reconstruction of vorticity magnitude is shown. 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.

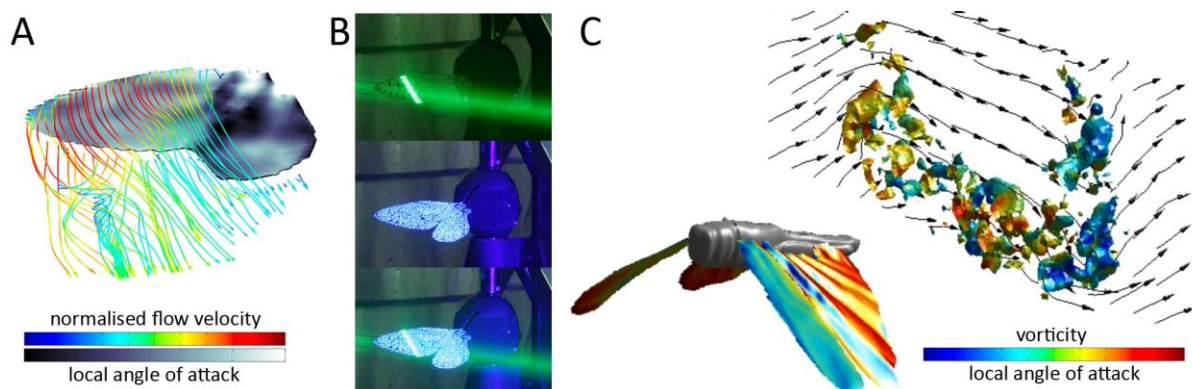


Figure 2. (A) Simultaneous three-dimensional surface and pseudo-volumetric flow measurements of a cicada wing on a unique three-axis flapping device [43]. A conical separation bubble enclosing a leading-edge vortex appears as fast red streamlines; the flow slows (yellow) as it reattaches to the wing 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 aeroelasticity*

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 air; 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.

### *Acknowledgements*

The authors are grateful to Thomas Engels for kindly providing Figure 1a, and to Jérôme Casas and Barbara De Salvo for the invitation. This work was supported by the Biotechnology and Biological Sciences Research Council (BB/R002657/1) to RJB.

### *References*

1. Spedding GR: **The aerodynamics of flight**. In *Mechanics of animal locomotion*. Edited by Alexander RM: Springer-Verlag; 1992:51-111.
2. Sane SP: **The aerodynamics of insect flight**. *Journal of Experimental Biology* 2003, **206**:4191-4208.
3. Bomphrey RJ: **Advances in Animal Flight Aerodynamics Through Flow Measurement**. *Evolutionary Biology* 2011, **38**:1-11.
4. Bomphrey RJ: **Insects in flight: direct visualization and flow measurements**. *Bioinspiration & Biomimetics* 2006, **1**:S1-S9.
5. Nabawy MRA, Crowther WJ: **The role of the leading edge vortex in lift augmentation of steadily revolving wings: a change in perspective**. *J R Soc Interface* 2017, **14**.
6. Chin DD, Lentink D: **Flapping wing aerodynamics: from insects to vertebrates**. *Journal of Experimental Biology* 2016, **219**:920-932.
7. Dudley R: **Mechanisms and implications of animal flight maneuverability**. *Integrative and Comparative Biology* 2002, **42**:135-140.
8. Liu H, Ravi S, Kolomenskiy D, Tanaka H: **Biomechanics and biomimetics in insect-inspired flight systems**. *Philosophical Transactions of the Royal Society B: Biological Sciences* 2016, **371**.
9. Wang ZJ: **Dissecting insect flight**. *Annual Review of Fluid Mechanics* 2005, **37**:183-210.
10. Bomphrey RJ, Nakata T, Phillips N, Walker SM: **Smart wing rotation and trailing-edge vortices enable high frequency mosquito flight**. *Nature* 2017, **544**:92-95.
11. Engels T, Kolomenskiy D, Schneider K, Lehmann FO, Sesterhenn J: **Bumblebee Flight in Heavy Turbulence**. *Physical Review Letters* 2016, **116**:028103.



12. Bomphrey RJ, Nakata T, Henningsson P, Lin H-T: **Flight of the dragonflies and damselflies.** *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 2016, **371**.
  13. Greeter JSM, Hedrick TL: **Direct lateral maneuvers in hawkmoths.** *Biology Open* 2016.
  14. Henningsson P, Bomphrey RJ: **Span efficiency in hawkmoths.** *Journal of the Royal Society Interface* 2013, **10**:20130099.
  15. Nakata T, Liu H: **Aerodynamic performance of a hovering hawkmoth with flexible wings: a computational approach.** *Proceedings of the Royal Society B: Biological Sciences* 2012, **279**:722-731.
  16. Muijres FT, Elzinga MJ, Melis JM, Dickinson MH: **Flies Evade Looming Targets by Executing Rapid Visually Directed Banked Turns.** *Science* 2014, **344**:172-177.
  17. Walker SM, Thomas ALR, Taylor GK: **Operation of the alula as an indicator of gear change in hoverflies.** *Journal of The Royal Society Interface* 2012, **9**.
  18. Du G, Sun M: **Effects of wing deformation on aerodynamic forces in hovering hoverflies.** *The Journal of Experimental Biology* 2010, **213**:2273-2283.
  19. Balint CN, Dickinson MH: **Neuromuscular control of aerodynamic forces and moments in the blowfly, *Calliphora vicina*.** *Journal of Experimental Biology* 2004, **207**:3813-3838.
  20. Bomphrey RJ, Henningsson P, Michaelis D, Hollis D: **Tomographic particle image velocimetry of desert locust wakes: instantaneous volumes combine to reveal hidden vortex elements and rapid wake deformation.** *Journal of The Royal Society Interface* 2012.
  21. Henningsson P, Michaelis D, Nakata T, Schanz D, Geisler R, Schröder A, Bomphrey RJ: **The complex aerodynamic footprint of desert locusts revealed by large-volume tomographic particle image velocimetry.** *Journal of The Royal Society Interface* 2015, **12**.
  22. Bluman J, E. , Pohly J, Sridhar M, Kang CK, Landrum DB, Fahimi F, Aono H: **Achieving bioinspired flapping wing hovering flight solutions on Mars via wing scaling.** *Bioinspiration & Biomimetics* 2018.
  23. Miller LA, Peskin CS: **Flexible clap and fling in tiny insect flight.** *J Exp Biol* 2009, **212**:3076-3090.
  24. Combes SA, Dudley R: **Turbulence-driven instabilities limit insect flight performance.** *Proceedings of the National Academy of Sciences* 2009, **106**:9105-9108.
  25. Ravi S, Crall JD, Fisher A, Combes SA: **Rolling with the flow: bumblebees flying in unsteady wakes.** *The Journal of Experimental Biology* 2013, **216**:4299-4309.
  26. Ortega-Jimenez VM, Greeter JSM, Mittal R, Hedrick TL: **Hawkmoth flight stability in turbulent vortex streets.** *The Journal of Experimental Biology* 2013, **216**:4567-4579.
  27. Ravi S, Kolomenskiy D, Engels T, Schneider K, Wang C, Sesterhenn J, Liu H: **Bumblebees minimize control challenges by combining active and passive modes in unsteady winds.** *Scientific Reports* 2016, **6**:35043.
  28. Matthews M, Sponberg S: **Hawkmoth flight in the unsteady wakes of flowers.** *bioRxiv* 2018.
  29. Engels T, Kolomenskiy D, Schneider K, Farge M, Lehmann FO, Sesterhenn J: **The impact of turbulence on flying insects in tethered and free flight: high-resolution numerical experiments.** (under review).
- \*\*High resolution numerical simulations of a bumblebee interacting with fully developed turbulent inflow. Both tethered and free flight are considered. The authors investigate how the scale-dependent turbulent energy distribution is relevant for body orientation control in flying insects.
30. Vance JT, Faruque I, Humbert JS: **Kinematic strategies for mitigating gust perturbations in insects.** *Bioinspiration & Biomimetics* 2013, **8**:016004.
  31. Crall JD, Chang JJ, Oppenheimer RL, Combes SA: **Foraging in an unsteady world: bumblebee flight performance in field-realistic turbulence.** *Interface Focus* 2017, **7**.
  32. Shyy W, Aono H, Chimakurthi SK, Trizila P, Kang CK, Cesnik CES, Liu H: **Recent progress in flapping wing aerodynamics and aeroelasticity.** *Progress in Aerospace Sciences* 2010, **46**:284-327.

33. Gursul I, Cleaver DJ, Wang Z: **Control of low Reynolds number flows by means of fluid–structure interactions.** *Progress in Aerospace Sciences* 2014, **64**:17-55.
  34. Shyy W, Aono H, Kang C-k, Liu H: *An Introduction to Flapping Wing Aerodynamics.* Cambridge: Cambridge University Press; 2013.
  35. Combes SA, Daniel TL: **Into thin air: contributions of aerodynamic and inertial-elastic forces to wing bending in the hawkmoth *Manduca sexta*.** *Journal of Experimental Biology* 2003, **206**:2999-3006.
  36. Thiria B, Godoy-Diana R: **How wing compliance drives the efficiency of self-propelled flapping flyers.** *Physical Review E* 2010, **82**:015303.
  37. Mountcastle A, Daniel T: **Aerodynamic and functional consequences of wing compliance.** *Experiments in Fluids* 2009.
  38. Jankauski M, Daniel TL, Shen IY: **Asymmetries in wing inertial and aerodynamic torques contribute to steering in flying insects.** *Bioinspiration & Biomimetics* 2017, **12**:046001.
  39. Ramanarivo S, Godoy-Diana R, Thiria B: **Rather than resonance, flapping wing flyers may play on aerodynamics to improve performance.** *Proceedings of the National Academy of Sciences* 2011, **108**:5964-5969.
  40. Godoy-Diana R, Thiria B: **On the diverse roles of fluid dynamic drag in animal swimming and flying.** *Journal of The Royal Society Interface* 2018, **15**.
  41. Faux D, Thomas O, Cattan E, Grondel S: **Two modes resonant combined motion for insect wings kinematics reproduction and lift generation.** *EPL (Europhysics Letters)* 2018, **121**:66001.
- \*The authors demonstrate experimentally the production of insect-like kinematics from a combination of flapping and twisting modes of artificial wings. Large amplitudes are obtained from two quadrature actuation frequencies close to the flapping and twisting resonances.
42. Ma KY, Chirarattananon P, Fuller SB, Wood RJ: **Controlled Flight of a Biologically Inspired, Insect-Scale Robot.** *Science* 2013, **340**:603-607.
  43. Phillips N, Knowles K, Bomphrey RJ: **The effect of aspect ratio on the leading-edge vortex over an insect-like flapping wing.** *Bioinspiration & Biomimetics* 2015, **10**:056020.
  44. Nila A, Phillips N, Bomphrey RJ, Bleischwitz R, de Kat R, Ganapathisubramani B: **Optical measurements of fluid-structure interactions for the description of nature-inspired wing dynamics.** In *2016 RAeS Applied Aerodynamics Conference.* Edited by. Bristol, UK: Royal Aeronautical Society; 2016.
  45. Combes SA, Daniel TL: **Flexural stiffness in insect wings II. Spatial distribution and dynamic wing bending.** *Journal of Experimental Biology* 2003, **206**:2989-2997.
  46. Rajabi H, Shafiei A, Darvizeh A, Dirks J-H, Appel E, Gorb SN: **Effect of microstructure on the mechanical and damping behaviour of dragonfly wing veins.** *Royal Society Open Science* 2016, **3**.
- \*High-resolution imaging techniques inform a mechanical model, providing crucial information for future computational models that incorporate detailed geometries and fluid-structure interactions.
47. Wootton RJ, Herbert RC, Young PG, Evans KE: **Approaches to the structural modelling of insect wings.** *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 2003, **358**:1577-1587.
  48. Norberg RÅ: **The pterostigma of insect wings as an inertial regulator of wing pitch.** *J. Comp. Physiol.* 1972, **81**:9-22.
  49. Rajabi H, Ghoroubi N, Darvizeh A, Dirks JH, Appel E, Gorb SN: **A comparative study of the effects of vein-joints on the mechanical behaviour of insect wings: I. Single joints.** *Bioinspiration & Biomimetics* 2015, **10**:056003.
  50. Mountcastle AM, Combes SA: **Wing flexibility enhances load-lifting capacity in bumblebees.** *Proceedings of the Royal Society B: Biological Sciences* 2013, **280**.

51. Hou D, Zhong Z, Yin Y, Pan Y, Zhao H: **The Role of Soft Vein Joints in Dragonfly Flight.** *Journal of Bionic Engineering* 2017, **14**:738-745.
52. Combes SA, Daniel TL: **Flexural stiffness in insect wings I. Scaling and the influence of wing venation.** *Journal of Experimental Biology* 2003, **206**:2979-2987.
53. Dalton S: *Borne on the wind: the extraordinary world of insects in flight.* New York: Reader's Digest Press; 1975.
54. Wootton RJ: **Support and deformability in insect wings.** *J. Zool.; Lond.* 1981, **193**:447-468.
55. Young J, Walker SM, Bomphrey RJ, Taylor GK, Thomas ALR: **Details of insect wing design and deformation enhance aerodynamic function and flight efficiency.** *Science* 2009, **325**:1549-1552.
56. Taylor GK, Krapp HG: **Sensory systems and flight stability: What do insects measure and why?** In *Advances in Insect Physiology: Insect Mechanics and Control.* Edited by; 2008:231-316. *Advances in Insect Physiology*, vol 34.]
57. Field LH, Matheson T: **Chordotonal Organs of Insects.** In *Advances in Insect Physiology.* Edited by Evans PD: Academic Press; 1998:1-228. vol 27.]
58. Hinson BT, Morgansen KA: **Gyroscopic sensing in the wings of the hawkmoth *Manduca sexta* : the role of sensor location and directional sensitivity.** *Bioinspiration & Biomimetics* 2015, **10**:056013.
59. Fernández MJ, Driver ME, Hedrick TL: **Asymmetry costs: effects of wing damage on hovering flight performance in the hawkmoth *Manduca sexta*.** *The Journal of Experimental Biology* 2017, **220**:3649-3656.
60. Hinson BT, Morgansen KA: **Observability-Based Optimal Sensor Placement for Flapping Airfoil Wake Estimation.** *Journal of Guidance, Control, and Dynamics* 2014, **37**:1477-1486.
61. Dickinson MH: **Directional Sensitivity and Mechanical Coupling Dynamics of Campaniform Sensilla During Chordwise Deformations of the Fly Wing.** *Journal of Experimental Biology* 1992, **169**:221-233.
62. Dickinson MH: **Comparison of Encoding Properties of Campaniform Sensilla on the Fly Wing.** *Journal of Experimental Biology* 1990, **151**:245-261.
63. Sane SP, McHenry MJ: **The biomechanics of sensory organs.** *Integrative and Comparative Biology* 2009, **49**:i8-i23.
64. Elson RC: **Flight motor neurone reflexes driven by strain-sensitive wing mechanoreceptors in the locust.** *Journal of Comparative Physiology A* 1987, **161**:747-760.
65. Dickerson BH, Aldworth ZN, Daniel TL: **Control of moth flight posture is mediated by wing mechanosensory feedback.** *Journal of Experimental Biology* 2014, **217**:2301-2308.
66. Dickinson MH, Palka J: **Physiological properties, time of development, and central projection are correlated in the wing mechanoreceptors of *Drosophila*.** *J Neurosci* 1987, **7**:4201-4208.
67. Eberle AL, Dickerson BH, Reinhall PG, Daniel TL: **A new twist on gyroscopic sensing: body rotations lead to torsion in flapping, flexing insect wings.** *Journal of The Royal Society Interface* 2015, **12**.
68. Pratt B, Deora T, Mohren T, Daniel T: **Neural evidence supports a dual sensory-motor role for insect wings.** *Proc Biol Sci* 2017, **284**.
- \*\*Innovative neurophysiology methods confirm the ability of hawkmoths to detect body rotations via deformations of the wings under Coriolis forces.
69. Fayyazuddin A, Dickinson MH: **Haltere afferents provide direct, electrotonic input to a steering motor neuron in the blowfly, *Calliphora*.** *J Neurosci* 1996, **16**:5225-5232.
70. Krapp HG, Hengstenberg R: **Estimation of self-motion by optic flow processing in single visual interneurons.** *Nature* 1996, **384**:463.
71. Suver MP, Huda A, Iwasaki N, Safarik S, Dickinson MH: **An Array of Descending Visual Interneurons Encoding Self-Motion in *Drosophila*.** *J Neurosci* 2016, **36**:11768-11780.
- \*\*Using a comprehensive array of genetics and biomechanics techniques, the authors identify descending interneurons that integrate information from wide-field visual interneurons.

They show how these project onto flight motor centres controlling steering, and confirm the result using a virtual reality behavioural assay and wing kinematics analyses.

72. Kim AJ, Fitzgerald JK, Maimon G: **Cellular evidence for efference copy in *Drosophila* visuomotor processing.** *Nature Neuroscience* 2015, **18**:1247.
73. Hardcastle Ben J, Krapp Holger G: **Evolution of biological image stabilization.** *Current Biology* 2016, **26**:R1010-R1021.
74. Goulard R, Vercher J-L, Viollet S: **Modeling visual-based pitch, lift and speed control strategies in hoverflies.** *PLOS Computational Biology* 2018, **14**:e1005894.
75. Roth E, Hall RW, Daniel TL, Sponberg S: **Integration of parallel mechanosensory and visual pathways resolved through sensory conflict.** *Proceedings of the National Academy of Sciences* 2016.
- \*The authors disentangle the relative roles of visual information and proprioception from the hawkmoth proboscis by exposing individuals to conflicting cues.
76. Taylor GK, Bacic M, Bomphrey RJ, Carruthers AC, Gillies J, Walker SM, Thomas ALR: **New experimental approaches to the biology of flight control systems.** *Journal of Experimental Biology* 2008, **211**:258-266.
77. Bartussek J, Lehmann F-O: **Proprioceptive feedback determines visuomotor gain in *Drosophila*.** *Royal Society Open Science* 2016, **3**.
78. Ristroph L, Bergou AJ, Berman GJ, Guckenheimer J, Wang ZJ, Cohen I: **Dynamics, Control, and Stabilization of Turning Flight in Fruit Flies.** In *Natural Locomotion in Fluids and on Surfaces 2012//; New York, NY*, Edited by Childress S, Hosoi A, Schultz WW, Wang J: Springer New York: 2012:83-99.
79. Hedrick TL, Daniel TL: **Flight control in the hawkmoth *Manduca sexta*: the inverse problem of hovering.** *The Journal of Experimental Biology* 2006, **209**:3114-3130.
80. Roth E, Sponberg S, Cowan NJ: **A comparative approach to closed-loop computation.** *Current Opinion in Neurobiology* 2014, **25**:54-62.
81. Dickinson MH, Muijres FT: **The aerodynamics and control of free flight manoeuvres in *Drosophila*.** *Philosophical Transactions of the Royal Society B: Biological Sciences* 2016, **371**:20150388.
82. Suryakumar VS, Babbar Y, Strganac TW, Mangalam AS: **Unsteady Aerodynamic Model Based on the Leading-Edge Stagnation Point.** *Journal of Aircraft* 2016, **53**:1626-1637.
83. Thapa Magar K, Reich GW, Rickey MR, Smyers BM, Beblo RV: **Aerodynamic characteristics prediction via artificial hair sensor and feedforward neural network.** In *ASME 2015 Conference on Smart Materials, Adaptive Structures and Intelligent Systems; Colorado Springs, Colorado, USA*: 2015:V002T006A004.
84. Armanious G, Lind R: **Fly-by-Feel Control of an Aeroelastic Aircraft Using Distributed Multirate Kalman Filtering.** *Journal of Guidance, Control, and Dynamics* 2017, **40**:2323-2329.
85. Bimbard G, Kolomenskiy D, Bouteleux O, Casas J, Godoy-Diana R: **Force balance in the take-off of a pierid butterfly: relative importance and timing of leg impulsion and aerodynamic forces.** *The Journal of Experimental Biology* 2013, **216**:3551-3563.
86. Ramanarivo S, Fang F, Oza A, Zhang J, Ristroph L: **Flow interactions lead to orderly formations of flapping wings in forward flight.** *Physical Review Fluids* 2016, **1**:071201.