Insects in flight: direct visualization and flow measurements

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Abstract
The study of insect flight has been advanced in recent years by the advent and application of
new quantitative flow diagnostic techniques, not least digital particle image velocimetry. More
classical qualitative methods such as smoke flow visualization have also been applied with
new goals for the rigorous description of flows around insects. The combination of techniques
has led to the development of ideas which may be of some consequence to the designers of
micro-air vehicles wishing to follow a biomimetic principle. Specifically, kinematic
parameters such as wingbeat frequency and amplitude are discussed, along with some
discussion of the investigation of morphological parameters such as wing design.

1. Introduction

Many issues pertaining to the aerodynamics and kinematics of insect flight remain something of a mystery, not least because investigation is problematic due to difficulties regarding scale and frequency. Following the first attempts to apply aerodynamic theory to the subject, it soon became evident that at least some insects have wings which are too small to support their bodyweight using conventional aerodynamics. This conclusion is based on a 'quasi-steady' approach. The quasi-steady approach assumes that at any moment during the wingbeat, the wings generate aerodynamic forces identical to those that would be measured if the wings were isolated, and fixed at the same speed and angle of attack, in a steady flow. Once integrated over the whole wingbeat cycle, if the forces do not sum to produce a mean vertical component of the force that equals the body weight of the animal (using coefficients of lift calculated or measured from steady-state experiments), the quasi-steady approach must be rejected. If the quasi-steady approach fails, there must be further underlying aerodynamic mechanisms making up the lift deficit. The difficulty comes in determining what those novel aerodynamic mechanisms might be.

In this paper, I provide a brief history of the recent major findings in insect flight research and the methodologies which made the discoveries possible. Beginning with postulated flow topologies around the wing, head and thorax for a variety of species, I then move on to the more distant wake structure and

what determines it, before assessing what has been learnt from the various studies. Finally I discuss this body of research's utility to those working in the field of biomimetics, specifically focusing on what can be gleaned for the design of micro-air vehicles from an aerodynamics point of view.

2. Flow features around the wing

In 1973 Weis-Fogh (1973) and Lighthill (1973) presented the first high-lift mechanism for the explanation of insect flight: Weis-Fogh's model animal was the Chalcid wasp (*Encarsia formosa*). He proposed that after the wings closed together at the top of the upstroke, their rapid separation at the beginning of the downstroke could induce a fast flow around the leading edges into the opening gap, thus generating high circulation around the wings even before they translated through the downstroke. He called this inviscid mechanism the Clap-and-Fling, and postulated that it reduced the effect of a phenomenon known as the Wagner effect, which limits build-up of circulation for an impulsively started wing (Wagner 1925). Circulation does not reach its peak in a steady flow until the wing has translated seven chord lengths from its starting point. Until then growth of circulation around the wing is inhibited by the negative influence of its own starting vortex—a vortex left behind in the fluid, rotating with equal strength but opposite direction from that of the circulation around the wing. The negative effect is due to the wing operating in

the unfavourable downwards moving portion of air driven by the starting vortex directly behind the trailing edge. Thus, any mechanism negating, or reducing, the Wagner effect will benefit the animal by increasing circulation around its lifting surface, particularly in the early stages of each half-stroke.

Not all insects perform clap and fling kinematics, for example it is exceedingly rare that dragonflies close their wings to such an extent. Recent work with dragonflies by Thomas *et al* (2004) has cast a doubt as to whether the Wagner effect plays a significant role in their flight, as they reported no evidence for starting vortices in the wake of dragonflies after a detailed qualitative analysis of their aerodynamics. Starting vortices are present behind impulsively started wings under certain flow conditions, and it may be that the dragonfly does not accelerate its wings fast enough to be considered impulsive. Other factors could be kinematic adjustment at stroke reversal which minimizes angle of attack, or simply a result of a relatively high advance ratio, although the latter is unlikely since starting vortices were not present even in hovering flight. Furthermore, the authors saw that at the beginning of the downstroke (the time at which the Wagner effect should be at its most destructive to bound circulation) the forewing was operating in the beneficial upwash generated by the flow structure shed from the previous stroke. Since many insects do not clap their wings together at the top of the upstroke in the same way that Chalcid wasps or butterflies do, high-lift mechanisms associated with rotation at stroke reversal remains a subject of debate. It has been shown through force measurements on models, and also computationally, that wing rotation can not only augment lift production, but also provide a basis for turning manoeuvres if the timing of rotation is modified (e.g. Dickinson *et al* (1999), Liu *et al* (1998)).

Soon after Weis-Fogh's initial proposal came further mathematical (Lighthill 1973) and experimental (Maxworthy 1979) studies of his mechanism. Maxworthy utilized a hand-operated mechanical device to replicate the motion of an insect wing pair during the downstroke. He confirmed Lighthill's earlier hypothesis that leading-edge separation could increase the magnitude of circulation calculated for the unseparated case (Lighthill 1973). Indeed, Maxworthy found that the flow over his model separated at the leading edge of the wings, rolling up into a conical leading-edge vortex stabilized by a strong axial flow '. . . set up along the span of the wing by pressure gradients required to balance centrifugal forces' (Maxworthy 1981). This vortex remained over the wings for the duration of the downstroke, augmenting the lift by greatly increasing the circulation. The conical leading-edge vortex on each wing ran parallel to the leading edges until they inflected at the wingtips, draining vorticity into the circular wingtip vortices. There was a connection between each of the contralateral wingtip vortices, and each of the contralateral wingroot vortices to make a single, large, contorted but complete vortex ring (figure 1(*A*)). Subsequently, mean and instantaneous lift coefficients were shown to be significantly enhanced during the clap and fling by Spedding and Maxworthy (1986) who provided direct force measurements and calculations from simultaneous quantitative flow field measurements.

The Chalcid wasp is a tiny (<1 mm) animal, rendering direct visualization of the flow around a freely flying subject a considerable technical challenge, although by no means impossible. However, flow visualization has been successfully attempted on other, larger, flying animals. In 1979, Kokshaysky (1979) identified flows that resembled vortex rings behind birds in slow forward flight, and Spedding produced a series of papers on the wakes of kestrels, jackdaws and pigeons (Spedding 1986, 1987a, 1987b, Spedding *et al* 1984). Spedding also pioneered the use of a manual cross-correlation technique to measuring the flow velocities in order to quantify the fluid motion for the first time, and thus gain estimates of the momentum transferred to the wake. Simultaneously, more qualitative data for insects were being measured using particle visualization techniques by the Luttges group (including dragonflies and hawkmoths (Luttges 1989, Saharon and Luttges 1987, 1988, 1989, Somps and Luttges 1985)), and by the Russian groups of, Brodsky (peacock butterflies (Brodsky 1991)) and Grodnitsky (functionally two-winged insects (Grodnitsky and Morozov 1993)).

Following the work in the late 1990s of Ellington's group on the hawkmoth, *Manduca sexta*, the leading-edge vortex emerged as the main contender in the race to find the high-lift mechanisms of insects (Ellington *et al* 1996, Van den Berg and Ellington 1997a, Van den Berg and Ellington 1997b, Willmott *et al* 1997). Utilizing smokewire visualizations, they found evidence of flow separation over the wings of live tethered hawkmoths. To see greater detail of the vortex, they used another large mechanical flapping model. Ellington's 'flapper' was dynamically scaled to precisely replicate the wingbeat kinematics whilst preserving the fluid phenomena via control of the Reynolds number. The leading-edge vortex topology was described in 1996, and was comparable with that described by Maxworthy in that the flapper revealed a conical, spiral shaped core, with a strong axial, or spanwise, component to the flow velocity from root to tip—a structure bearing strong resemblance to that found over Concorde and other swept or delta-wing aircraft. This structure implies attached flow over the thorax, and therefore necessitates a focal point at the base of the wing, from which the leading-edge vortex structure emanates (figure 1(*C*)). (The focus is, in fact, a singularity in the flow; one type of critical point which will be elaborated on later.) Once again, the spanwise flow could act as a sink for vorticity (which would otherwise accumulate during the downstroke), draining it into the wingtip vortices. The vortex would thus be prevented from growing too large during the downstroke (to the extent that it can no longer remain bound, shedding from the wing) because of the continuous removal of vorticity. Further qualitative results from hawkmoths, obtained as preliminary data for a quantitative paper by Bomphrey *et al* (2005a, 2005b), showed similar flow structures to those seen by Ellington at the midwing position. However, late in the downstroke, approaching stroke reversal, the flow also separated over the thorax (a position not investigated by Ellington *et al*) creating an attached cylindrical vortex extending from wingtip to wingtip. Thus it appears that flow topologies can change throughout the stroke and have
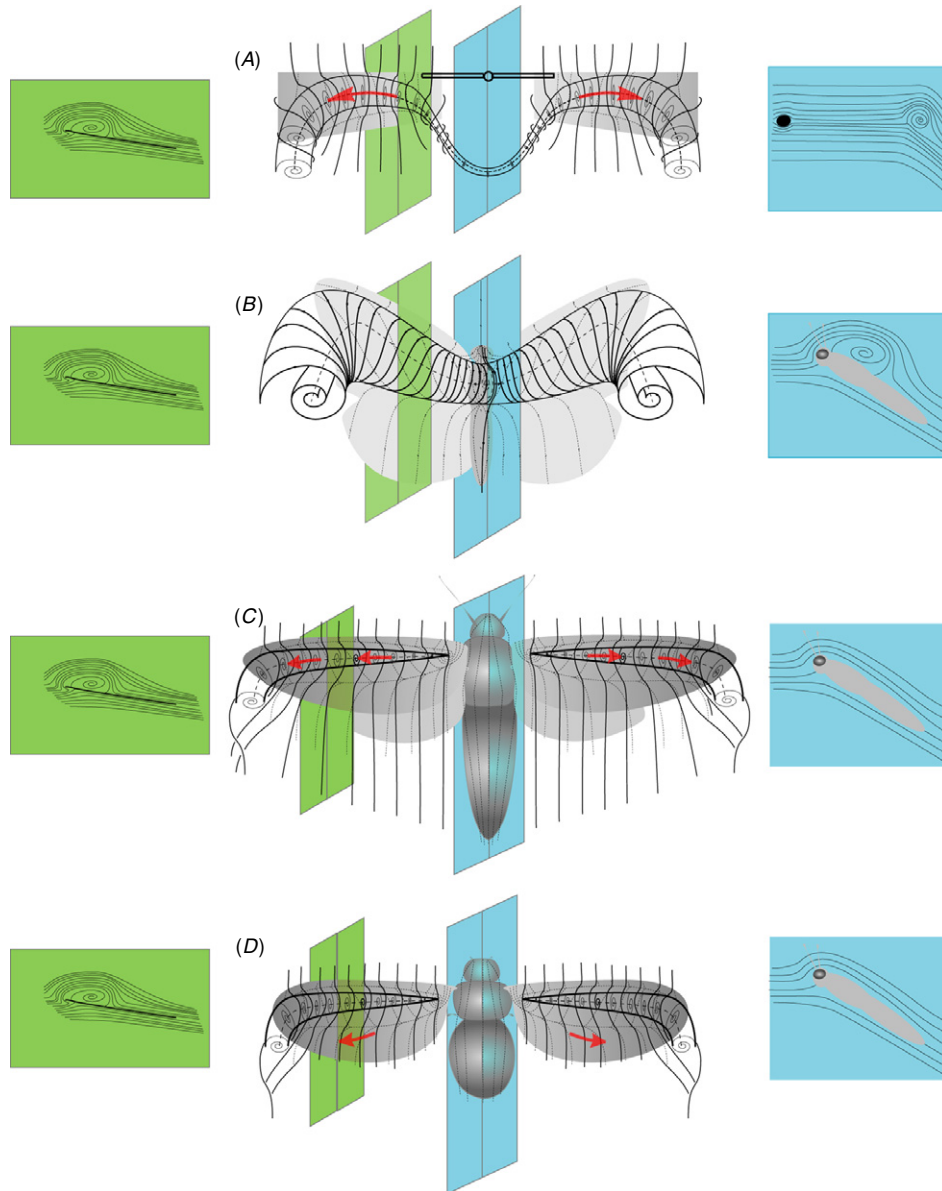
Figure 1. Topologies of the leading-edge vortex (LEV). Four postulated LEV flow topologies for flying insects. Green inserts show cross section of flow at the midwing position; blue inserts show cross section of the flow at the centreline of the animal. (*A*) The first class of LEV shows the hand operated flapper of Maxworthy (1979). (*B*) The second class of LEV was first described by Luttges (1989) but shown here as described by Srygley and Thomas (2002) for Red Admiral butterflies. (*C*) The third class of LEV as described by Ellington *et al* (1996) for hawkmoths. Hawkmoths were later shown to have the second class LEV shown in (*B*) late in the downstroke by Bomphrey *et al* (2005a). (*D*) A second form of the third class of LEV described by Birch and Dickinson (2001) for fruitflies (*Drosophila*). (*C*) and (*D*) differ by virtue of their spanwise flows, shown in orange if present. Reproduced from Bomphrey *et al* (2005a).

temporary or intermediate stages, with differences even after separation has occurred, most likely in response to changes in angle of attack (Thomas *et al* 2003).

Other recent qualitative data (from smokewire flow visualization) for insect leading-edge vortices have been collected from butterflies (*Vanessa*; Srygley and Thomas 2002), and dragonflies (*Sympetrum*, *Aeschna*; Thomas *et al* 2004) in which the topology was found to be different once again. For butterflies, a functionally 2-winged insect, a leading-edge vortex was seen to extend from wingtip to

wingtip across the thorax (Srygley and Thomas 2002). The vortex consisted in a single cylindrically shaped core, rather than a pair of conical vortices (figure 1(*B*)) much like the latter stages of the hawkmoth downstroke described above, but the duration and timing remain uncertain. A topologically similar structure was observed on the forewing of both free flying and tethered dragonflies, which are capable of modifying the phase relationship of fore- and hindwings. The most common topology seen in dragonflies is an out of phase flight mode, with a large leading-edge vortex extending from wingtip to

wingtip over the wings and thorax adjacent to the forewings, and attached flow over the hindwings. The vortex formed as soon as the downstroke began, and persisted into the upstroke. This pattern was seen in 75% of the informative images, while the others consisted of other topologies such as attached flow over both wings, and in-phase flapping with a large leading-edge vortex beginning at the leading-edge of the forewing, but reattaching near the trailing-edge of the hindwing, such that the wings acted as a continuous surface. Spanwise flows were not seen in the tethered insects, and seen only infrequently in the free flying subjects. When present, spanwise velocity components were revealed as flowing from root to tip or from tip to root, correlated with any side slipping manoeuvre the animal was performing in the wind tunnel.

The above topologies can be differentiated by the flow at the centreline of the animal in question, and are summarized using this method in figure 1, taken from Bomphrey *et al* (2005a). Thus the leading-edge vortex does indeed appear to be a common feature of insect flight, but at this stage measurements were difficult to perform on live insects, especially those in free flight. Fortunately, the recent rapid developments of digital cameras, in terms of both frame rate and resolution, have helped the researcher enormously, allowing closer, clearer images of the growth, development, and shedding of vortical structures which typically take place over time intervals between ~1/20 (e.g. hawkmoths, *Manduca*) and ~1/200 of a second (e.g. bees, *Bombus*; and flies, *Drosophila*).

3. Using critical points to describe the flow

Description of flows can be conducted in a variety of ways, however one which has become more common in recent times is that first proposed in the insect flight literature by Srygley and Thomas (2002), later greatly developed by Thomas *et al* (2004), and also utilized by Bomphrey *et al* (2005a) for the analysis of instantaneous streamlines. They used 'critical point' theory, a method developed from the mathematician Poincaré's work on differential equations, to describe singularities in the flow. A critical point is a location in space where the flow's velocity is indeterminate. There are groups of such points, and in much the same way that there is a mathematical relationship between the number of edges, faces and vertices on a solid body, so there is between nodes of attachment and separation, foci and saddles within the flow. Critical points within the flow can be unambiguously identified using careful smoke flow visualization, or more quantitative techniques which reveal instantaneous streamlines, the latter being more rigorous, yet suffering from issues relating to frames of reference. Using the well-defined rules, the simplest description of the flow topology can be characterized by simply following the rules and 'joining the dots'. There is no need therefore to evaluate how fast the flows are or the relative sizes of different elements of the same structure (yet the streamline maps generated using the techniques are a method of distinguishing between known analytical local solutions to the Navier–Stokes equations—for more explanation see Thomas *et al* (2004)). Thus the topological approach greatly simplifies the issue, and avoids the problems of geometry, where streamline lengths, enclosed region sizes, and particle speeds along streamlines would have to be classified also. A more rigorous discussion of the application of critical point theory to insect flight can be found in Bomphrey *et al* (2005a). Figure 2 shows some examples of critical points (nodes, saddles and foci) identified using smokewire flow visualization.

4. Use of DPIV

Parallel with these qualitative discoveries, a new technique was being applied to the study of complex flows. Particle image velocimetry (PIV) involves the cross correlation of image pairs to measure fluid motion using marker, or seeding particles (Adrian 1991, Gharib and Dabiri 2000). The technique was quickly applied to mapping flows around aquatic organisms (copepods, tube-living shrimps, fish—e.g. Drucker and Lauder (2000), Liao *et al* (2001), Muller *et al* (1997), Nauen and Lauder (2001), Stamhuis and Videler (1995), Stamhuis *et al* (2002)), but very few attempts were made initially to measure the flow velocities around flying animals using PIV. The first use of digital particle image velocimetry (DPIV—an automated progression from PIV which shifts the burden of laborious manual tracking of particles to a relatively fast computational technique) to investigate flight was by Dickinson's group (Birch and Dickinson 2001, Dickinson *et al* 1999). He used a scaled model of a fruit fly wing to measure fluid velocities, and determine the contribution of the leading-edge vortex to overall force production. Dickinson also showed the effects of the previous half stroke's wake on the aerodynamics of the current half stroke, highlighting and quantifying the important role of 'wake capture'. Wake capture can have a variety of meanings, but here it is defined as any time the wing passes back through its own wake with aerodynamically beneficial effects for the animal.

It was not until Spedding and Hedenström that the first measurements were taken from flows behind freely flying animals in a wind tunnel (Spedding *et al* 2003a, 2003b). They studied the far wake of thrush nightingales. With this first application to live animals, two profound conclusions were reached. The first was that there was a continuum of intermediate wake patterns between the classical vortex ring model for low speed or hovering flight, and the constant circulation model for bird flight at higher speeds. This refuted the long standing argument for gaits in animal flight, whereby animals were thought to employ a small, discrete and discontinuous selection of more aerodynamically efficient wake topologies, switching between them at certain flight speeds or advance ratios (in the same way a horse might choose to either walk, trot, canter or gallop, yet he will not walk at a fast speed, nor canter at walking pace). The second conclusion was significant because they showed that it was indeed possible to fully audit the momentum in the wake of a flying animal. Previous attempts had shown a so-called momentum deficit. This result is intrinsically linked to the first revelation because the remaining momentum was contained within smaller, previously undetectable and
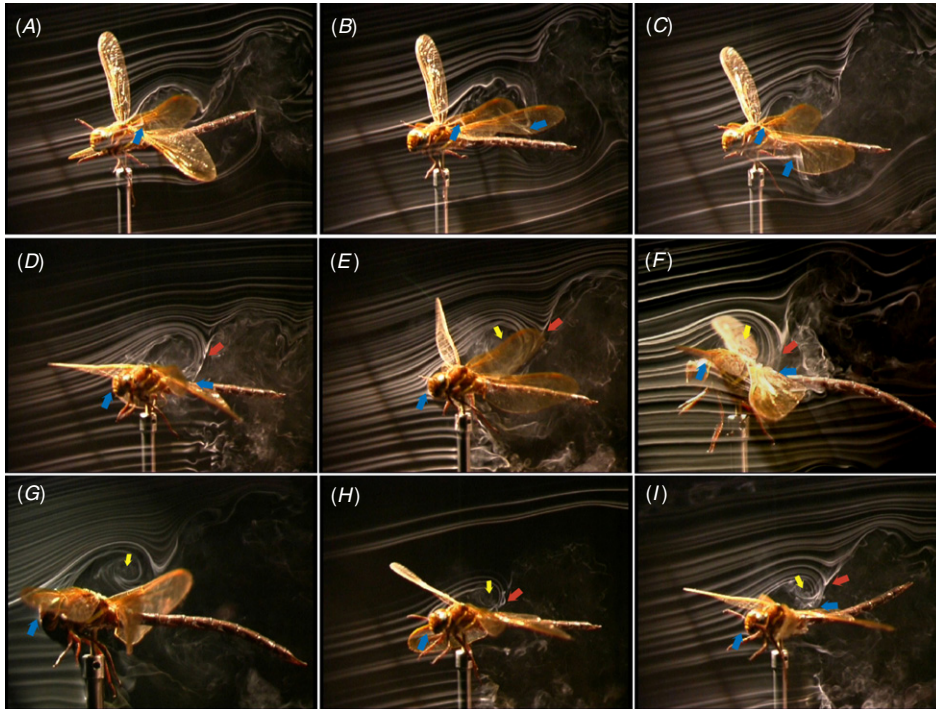
Figure 2. Critical points identified by smoke flow visualization. The critical points shown in (*A*) to (*I*) are nodes of attachment, or reattachment (blue arrows), foci (yellow) and saddles (red). The subject in this case is a tethered dragonfly flying at 2.5 m s^{-1} (*Aeschna grandis*). Reproduced from Thomas *et al* (2004). The images were recorded using a conventional digital video camera (Canon XL-1) capturing at 25 Hz. This frequency is approximately the same as the wingbeat frequency.

therefore unaccounted for, turbulent structures in the wake. DPIV allowed quantification and summation of these more disparate vortices, and thus the momentum was found not to be entirely contained within the coarsely defined vortex wake.

In a similar fashion, Bomphrey *et al* (2005a, 2005b) measured the flow behind tethered hawkmoths at two speeds (1.2 m s^{-1} and 3.5 m s^{-1}). Once again, intermediate wake formations were observed, and they bore striking similarity with those seen behind thrush nightingales (figure 3). This suggests some universality despite the vertebrate and invertebrate sharing very little in terms of wingbeat kinematics. That they are both constrained by root flapping and equalize to the same Strouhal number (explained in more detail below) are two of the few features common to both. The leading-edge vortex was observed over the midspan (figure 4) and also the centreline. With the quantitative method of DPIV, two things could be seen which would not have been possible with smoke visualization. Firstly, it was shown that spanwise flow had an upper boundary less than had been previously postulated by Ellington *et al*. Secondly, determination of flow velocities at the separatrix and within the leading-edge vortex which appears over the thorax late in the downstroke, showed that the structure was not merely shedding from a bluff body (the head), but was an actively driven process, perhaps initiated by the onset of supinatory rotation at stroke reversal.

Given the very different kinematics of hawkmoths (with their wing shapes controlled solely by the combination of muscles at the wing bases, and the aero-elastic and inertial forces acting on the wing) and thrush nightingales

(with muscular and infinitely controllable folding and flexing wings), why should the wakes be so similar? In 2003, Taylor and colleagues applied work by Triantafyllou *et al* on pitching and plunging (or 'heaving') aerofoils and their propulsive efficiencies to basic animal wingbeat parameters (Taylor *et al* 2003, Triantafyllou *et al* 1991, 1993—see also Nudds *et al* (2004)). Triantafyllou noted that for maximum propulsive efficiency, the Strouhal number ratio (*St*) of plunge frequency (*f*) multiplied by plunge double amplitude (*a*) to forward speed (*U*) should fall into the range $St = (fa/U) = 0.2$–0.4. Taylor *et al* examined data from many authors across a huge range of swimming and flying animals, and performed a meta-analysis (taking wingtip excursion as the measure of plunge double amplitude) which revealed that all cruising animals for which there are data configure their Strouhal numbers to this range. At first this is a striking result, but the underlying aerodynamics show that it is an inevitable consequence for plunging wings. If the product of amplitude and frequency are too high for a given forward speed, a high thrust wake is formed and the wing will accelerate, thus decreasing *St*. Conversely, if the numerator is too low for a given speed, the drag will decelerate the wing, increasing *St* (see Vandenberghe *et al* (2004, 2006)). Note that the Strouhal number has an inverse relationship with the vortex formation number described in Milano and Gharib's study into rectangular flat plates flapping with two degrees of freedom. Formation number has the advantage that it can also be applied to the hovering flight modes if insect flight which Strouhal number cannot (Milano and Gharib 2005).
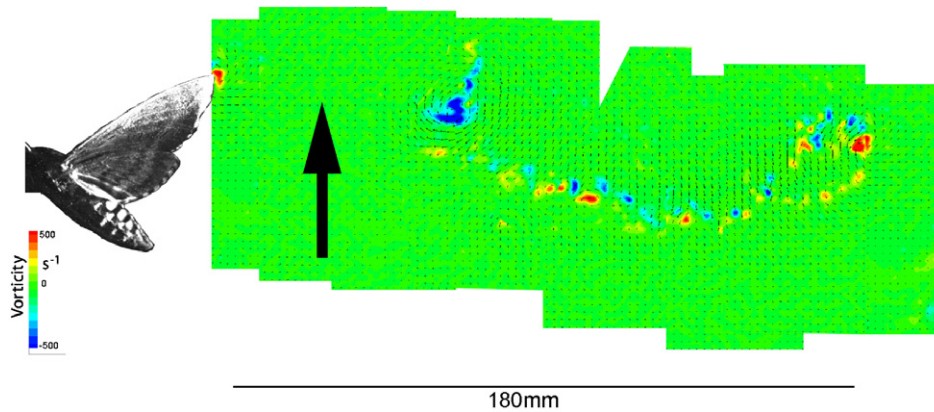
Figure 3. The composite wake of a tethered hawkmoth (*Manduca sexta*) flying at 3.5 m s^{-1}. The light sheet is located at the midwing position with flood colour indicating vorticity. The black arrow indicates a moment when the wings are close together at the top of the upstroke and are not penetrating the para-sagittal light sheet.
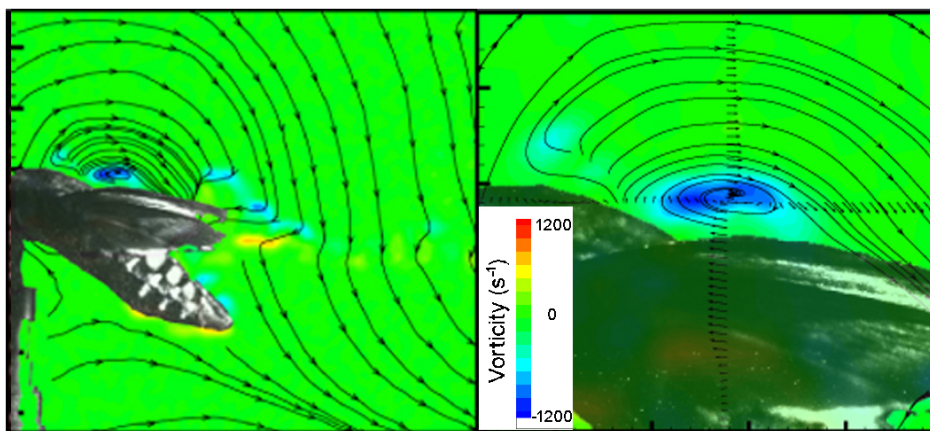

Figure 4. Instantaneous streamlines revealed using DPIV with a hawkmoth (*Manduca sexta*) flying tethered at 1.2 m s^{-1}. The global pattern at the midwing position after a freestream vector has been subtracted is shown on the left, with a close up of the leading-edge vortex on the right. The streamlines separate and reattach, and within the separation bubble, they spiral into a critical point forming what is known as a focus. The fields of view (length of the *x*-axis) are 92 mm and 35 mm respectively.

This result has been beautifully demonstrated by flow visualization on a novel, rotating, mechanical plunger by Vandenberghe *et al* (2004). Here the authors made a model whereby plunge amplitude and frequency could be set, but the plate was free to rotate about a central axle, and thus set its own forward speed. Once again the same Strouhal number range emerged, but the most striking result was that the wing eventually rotated and settled on a particular forward velocity with symmetrical pure plunge starting conditions. Simple plunging inevitably leads to symmetry breaking, which in turn leads to asymmetric thrust, and therefore forward propulsion. More recently, the result has been examined numerically using computational simulations by Alben and Shelley (2005). It is postulated that this mechanism could have been the beginnings of insect flight. Furthermore, the leading-edge vortex was a prominent feature of the flow topologies observed, and it might therefore be an evolutionarily basal flow topology, rather than an adaptation for higher lift and accelerations. It may even be the more derived insects which have evolved into a situation

whereby they can maintain the attached flows which might be important for long distance, or migratory, flights.

5. Comparing insect wing designs

A significant benefit of directly measured quantitative data from real animals is its compatibility and comparability with computational simulations. Dickinson has used this to great effect, particularly when combined with the work of Wang (Wang 2000, Wang *et al* 2004). Wang has performed numerous simulations of insect like flapping motions at transitional Reynolds number flow regimes, which determine when lift-based mechanisms are important, and when drag-based mechanisms take the lead role in weight support. This is especially relevant to insects which hover with inclined stroke planes—e.g. dragonflies (Wakeling and Ellington 1997). A second benefit is that the quantitative data can be readily integrated into theoretical predictions. This second route was pursued by Bomphrey *et al* (2006) with work on desert locusts
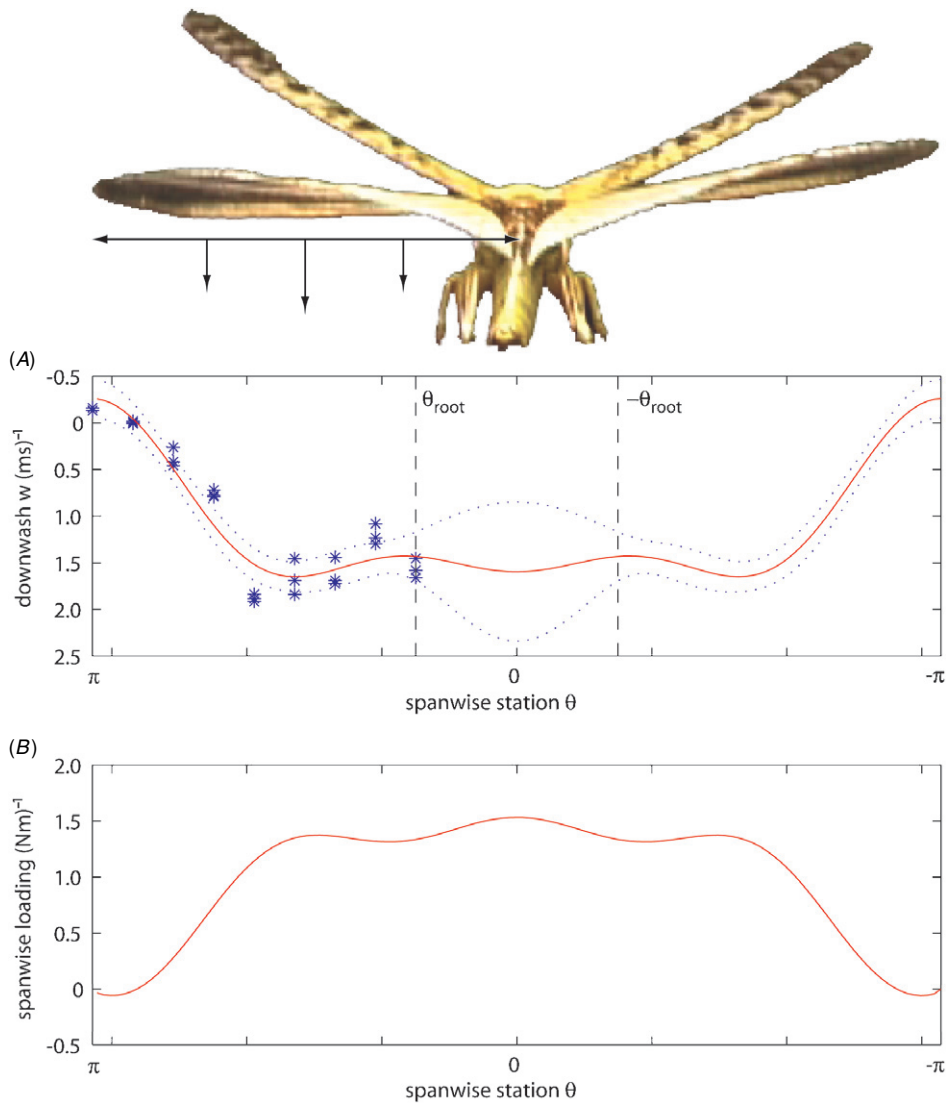
Figure 5. The downwash distribution behind a desert locust (S*chistocerca gregaria*). DPIV measurements at several locations out along the span of a locust (from 0 = centreline to $\pm\pi$ = wingtips) with curve fitted showed the downwash to differ from an ideal (even) downwash such that the induced power correction factor, $k = 1.12$. (*A*) shows the downwash velocity profile; (*B*) shows the associated spanwise loading. Reproduced from Bomphrey *et al* (2006). For this locust hindwing length (π) = 49 mm.

(*Schistocera gregaria*) in an attempt to formally lay down a method by which to measure the aerodynamic efficiencies of various insect wing designs.

Bomphrey and colleagues used DPIV data from immediately behind the trailing edge as a measure of downwash. A model which has proven to be very useful in understanding insect flight has been that of the actuator disc, a theory borrowed from helicopter theory whereby the stroke plane (or rotor plane) can be assumed to be a disc which imparts momentum to the air below it by exerting a constant pressure across its diameter. The actuator disc has been described as 'pulsed' for insects due to the periodic nature of force production. (For the first applications of actuator disc theory to insect flight see Ellington (1978, 1984a, 1984b) and Rayner (1979)). Only ideal (i.e. theoretical) rotors or sweeping wings can apply an even pressure to the fluid,

because there are always inefficiencies caused by wingtip vortices, and potentially other factors such as, for example, wingroot vortices, or changes in wing twist or planform along the length. Aerodynamic inefficiencies mean that the actual power required for the disc to generate a given thrust increases over the ideal power requirement, and thus a correction factor, k, was introduced and defined as the ratio of the actual induced power to ideal induced power for a given thrust. Until DPIV became available k had been either selected to fit the above ratio, or deduced from indirect measurements of muscle masses, muscle efficiencies or metabolic rates (e.g. Dudley and Ellington (1990)). However, as it is based on downwash, k is an aerodynamic parameter which can be directly measured. Bomphrey *et al* (2006) measured downwash and found a value of $k = 1.12$ for the desert locust at mid downstroke, which

corresponds reasonably well with previous estimations (see figure 5).

6. Conclusions

Once the qualitative topology of the flow is well described, and has been quantified also, much can be understood about the way animals fly. The topologies can be determined using qualitative smoke visualizations or DPIV, although the latter is vitally important for flow velocity measurements around the wings, in wake structures, and for other specific measurements such as downwash velocity profiles. The results are of great importance to those engineers working in the field of micro-air vehicles (e.g. Shyy *et al* (1999), Zbikowski (2002)), as these data can be used to confirm numerical simulations, and generalizations to assist with design parameter starting points. Biologists interested in understanding, for example, why wingbeat kinematics are configured the way they are, and whether or not they are constrained by factors such as maximum muscle contraction rates (Hedenström 1997, Norberg 1976, Pennycuick 1996, Rayner 1995, Srygley and Ellington 1999, Taylor *et al* 2003) will also benefit greatly from aerodynamic experiments of this nature. If we can assume that the wings of each flying animal have at least a locally optimal design in terms of aerodynamics, then a comparative DPIV approach measuring, for example, high-lift mechanisms, and other wing–fluid interactions, would allow the determination of similarities in design, leading to groupings of aerodynamic solutions, which are conserved despite compromises enforced by other evolutionary selective pressures. Noting that all insects are not the same in terms of wing design and aerodynamics, and understanding why those differences arise, will be of value to MAV designers because, as for insects, their flight apparatus and requirements might be mission specific. Following the biomimetic principle, insects have solved problems relating to any number of problems including load carrying, hovering, high speed flight and aerobatics. These performance measures are achieved using light-weight materials and smart architectural construction, simultaneously gust tolerant and impact resistant due to their deformability. Behavioural features include predator avoidance, target tracking and interception, but these are just a few aspects of insect flight currently occupying the MAV designers' thoughts. A firm understanding of the aerodynamics involved (alongside the neurological control of the aerodynamic surfaces) is the cornerstone for answering these questions. This can be achieved through parametric studies across the class of insects to discover which wing shapes are used for different tasks, and which flow features are conserved.

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