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DRAGONFLY AERODYNAMICS AND UNSTEADY MECHANISMS: A REVIEW

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Quasi-steady assumptions can be used to model animal aerodynamics. It has been known for over two decades that this approach fails to explain all the lift generated during dragonfly flight. Hovering is a specific area of dragonfly flight which is least applicable to the steady state analysis. Proposed unsteady effects which start to explain novel lift generating mechanisms are outlined.

INTRODUCTION

Steady state aerodynamic theory, developed for fixed wing aircraft, can explain how lift is generated over aircraft wings which move through air with a constant velocity. Dragonflies beat their wings in an unsteady manner, however, with their wings repeatedly accelerating and changing direction. It has been known for the last two decades that steady state aerodynamic theory is unable to account for the forces involved during dragonfly hovering, but this in itself does not mean that we cannot explain how dragonflies hover. Recent work has suggested a variety of unsteady mechanisms which may explain the unusually high forces involved.

This article will outline the areas of dragonfly aerodynamics which can be explained using steady state aerodynamic theory, and for areas which can not be explained it introduces the unsteady mechanisms that may be involved. Due to limitations of space only the aerodynamic mechanisms that may apply to dragonflies are considered. No attempt has been made to address either insect aerodynamics in general or non-aerodynamic topics such as the power and energy requirements for flight. I have tried to keep the number of equations to an absolute minimum, but for the more mathematically minded there are references cited that treat the models involved with exacting detail.

An excellent, recent review of animal aerodynamics in general can be found in SPEDDING (1992). For a more detailed treatment of hovering flight in insects then the clear set of papers by ELLINGTON (1984 a-f) is to be highly recommended.

DRAGONFLY STEADY STATE AERODYNAMICS VERSUS UNSTEADY MECHANISMS

Dragonflies are without doubt outstanding fliers. They can fly quickly forwards, hover, fly backwards, and change between any of these in several wingbeats. Being predators of many small insect fliers, they are able to outmanoeuvre many other insects when in the air. This ability is surprising given their ancient body form, and it is brought about purely by the motion of their wings.

Dragonflies have a vast repertoire of flight patterns, so to simplify the understanding of their complex aerodynamics it is usual to consider two cases - fast forward flight, and hovering. As I will outline in this section, fast forward flight involves mainly conventional steady state aerodynamic mechanisms. Hovering flight, however, may involve unsteady flows that produce lift forces greater than can be accounted for by these steady state theories.

FAST FORWARD FLIGHT

In fast forward flight the dragonfly covers a large distance with each wingbeat; the forward velocity of the animal is much faster than the flapping velocity of the wings. Gliding can be considered an extreme example of this, where the dragonfly has a forward velocity but no flapping velocity of the wings.

The steady flow of air over the wings during gliding, with the wings neither accelerating, decelerating, nor rotating, creates a steady lift force on the wings normal to the relative airflow. This lift is given by

$$L = 1/2\ \rho\ S\ U^2\ C_L \tag{1}$$

where ρ is the air density, S the wing area, U the flapping velocity of the wing, and C_L the lift coefficient. The lift coefficient can be calculated from the force measurements on a wing in a steady air flow in a wind tunnel.

Steady state theory can be used for all flight where the steady state flows predominate over unsteady ones. An indication to the steadiness of the flight is to calculate the ratio of the flapping velocity of the wings to the forward velocity of the dragonfly. Two dimensionless parameters which describe this ratio are

$$k = 2\ n\ \phi\ r\ /\ V \tag{2}$$

(WALKER, 1925, 1927), where n is the wingbeat frequency, ϕ the amplitude of the wingbeat, r the wing semi-span and V the flight velocity of the dragonfly, and

$$N = n\ L\ /\ V \tag{3}$$

(HOLST & KUCHEMANN, 1941, 1942), where L is a characteristic wing length (semi-span or chord). These parameters equal zero during gliding, and tend to infinity for hovering; a value of less than 1.0 can justify a steady state approach to analysis of the insect's aerodynamics.

It is to be expected that for fast forward flight these parameters have values between 0.1 and 1.0, thus justifying a steady state approach to the aerodynamics of the animal. This is indeed the case for dragonflies; data from RÜPPELL (1989) show that for eleven species of Odonata, both Zygoptera and Anisoptera, when they fly at their maximum forward velocity, N takes values between 0.16 and 0.46 (using L as the wing length). Steady state aerodynamic theory is thus sufficient to explain the lift forces generated during the fast forward flight of dragonflies.

It should be noted at this point that sufficiency of a theory to explain the flight for dragonflies is not proof of the validity of that theory (ELLINGTON, 1984a).

HOVERING FLIGHT

In hovering flight the dragonfly is stationary in the air. Its wings beat to generate the lift needed to support its weight. The wings are repeatedly accelerated, decelerated and rotated as they beat up and down, and there is no steady forward velocity component to the wing motion. Steady state theory may, however, still be sufficient to account for all the lift generated during hovering in a quasi-steady analysis.

The quasi-steady analysis fits steady state aerodynamic theory to the complex motion of flapping wings. It assumes that, at every instant, the forces acting on a wing are the same as if the wing were moving at a constant velocity at that instant. The mean forces acting over a complete cycle are balanced; for hovering the net horizontal force must be zero and the net vertical force must equal the animal's weight. The mean lift coefficient, $\overline{C_L}$, that is necessary to generate enought lift to support the animal's weight over the whole wingbeat cycle can then be calculated. If this $\overline{C_L}$ does not exceed the maximum steady state lift coefficient possible from the animal's wing, as measured on an isolated wing in a steady flow, then the quasi-steady analysis with all its assumptions is sufficient to account for the lift generated during hovering.

The hovering flight for a large number of insects was analysed by WEIS-FOGH (1972, 1973), and he concluded that 'most insects perform normal hovering on the basis of the steady-state flow'. One of the assumptions used in this analysis was that the insects beat their wings in a horizontal stroke plane, thus having an equal lift generating capacity on the morphological up and downstroke. Dragonflies provide an exception to this assumption. They fly and hover with their body aligned horizontally and their wings beating in an inclined stroke plane; thus they can only generate weight supporting lift on the downstroke. Nevertheless the Weis-Fogh analysis on *Aeshna juncea* (based on SOTAVALTA,

1947) and *A. grandis* (WEIS-FOGH, 1967) predicted a minimum C_L of 2.3 for each of the four wings. The value of maximum lift coefficient, C_{Lmax}, is commonly about 1 for insect wings, and is certainly less than the value of 2.3 for $\overline{C_L}$, yet the actual value of $\overline{C_L}$ should be greater still to account for all the weight supporting lift being produced only on the downstroke.

NORBERG (1975) filmed *Aeshna juncea* during free hovering flight in the field. After modifying the analysis for an inclined stroke plane, and using several alternative assumptions, the $\overline{C_L}$ values obtained were between 3.5 and 6.1. Again these values are far higher than could be explained by the dragonfly wings only experiencing steady state lift. During hovering flight the unsteady motion of the wings generates unsteady lift forces that are larger than their quasi-steady equivalents, and these are necessary to support the weight of the dragonfly.

OTHER FLIGHT MANOEUVRES

Extensive recordings of dragonfly flight in the field (RUPPELL, 1989) show that some of their flight behaviours other than hovering may also involve unsteady mechanisms. These data show a reduced frequency parameter (equation 2) greater than 1.0 for the following activities: *Calopteryx splendens* undergoing short forward and backwards flights and also a short forward courting flight, *Lestes viridis* undergoing both a fast forward and climbing flight, *Megaloprepus coerulatus* in both a tandem fast forward and a climbing copulatory flight, and finally *Anax imperator* during slow forward flight. The aerodynamic forces generated during these particular flights would have been due to predominantly unsteady mechanisms. Rüppell noted that whenever great demands were made on flight performance the wingbeat frequency, n, was increased (in contrast to it decreasing for descending flight); also the stroke angle, ϕ, increased for accelerating flight. An increase in both these parameters will tend to increase the unsteady component during flight. Measurements on *Anax parthenope* show that, as its flight velocity decreases to slow forward flight at 70 cm/s, its reduced frequency parameter increases (data from AZUMA & WATANABE, 1988). The reduced frequency parameter for the two slowest forward velocities suggests a predominance of unsteady mechanisms.

A further consideration in dragonfly aerodynamics must be the phasing of their wings. Dragonflies, unlike most other insects, have two pairs of wings which they beat independently. Counter stroking of the wings is common (CHADWICK, 1940; NEVILLE, 1960; ALEXANDER, 1984) and produces a very smooth flight. Due to the inclined stroke plane, the wings on the downstroke produce weight supporting lift whilst those on the upstroke produce a forward thrust. By having each pair of wings in a different stage in the cycle, the dragonfly can continuously generate both lift and thrust. A transition to parallel stroking of the wings occurs for forceful manoeuvres such as sudden vertical take-offs

(RÜPPELL, 1989), or reversing the direction of flight (ALEXANDER, 1984). It seems as though parallel stroking can generate an even greater aerodynamic force than counter stroking, and this is probably due to altered airflow interactions between the fore and hind wings.

Unsteady mechanisms should not only be considered significant during hovering flight in dragonflies, as they also predominate in many moving flight manoeuvres.

AERODYNAMIC ASPECTS OF WING MORPHOLOGY

During fast forward flight and gliding, dragonfly wings are characterised by predominantly steady state flows and mechanisms. Under these conditions it can be seen that many features of the dragonfly wing are particularly suited for efficient lift generation. Slow flight and hovering commonly involve unsteady flows and the wings can be flown at angles of attack greater than the stalling angle. It is not known which features of wing morphology may be beneficial under these unsteady conditions.

DRAG CRISIS AND FLOW SEPARATION

The Reynolds number gives an indication as to the drag forces that an animal must overcome. Forward flying dragonflies typically fly at Reynolds numbers in the order of 10^4 (Re = cU/v, where U is wing velocity, c the characteristic length (wing chord) and v the kinematic viscosity (a measure of the fluidity of the air)). At lower Re the drag on a body is dominated by viscous forces and laminar flow, whereas at higher Re the drag is dominated by pressure forces and turbulent flow. The transition between the predominant drag forces occurs in a critical range which, for a characteristic insect wing profile, is in the range Re = 3×10^4 - 8×10^4. By postponing this 'drag crisis' to a higher Re, and thus velocity, the dragonfly can fly with less drag at any given fast forward speed.

HERTEL (1966) described a T-shaped leading edge (costa) with three rows of serrations for the dragonfly wing. These features act as turbulators to trip the laminar flow around the leading edge of the wing and give it a little turbulence; this controlled amount of turbulence allows the flow to reattach near the rear of the wing. Were these turbulators not there, then at higher Re the flow could separate from the wing completely in a turbulent wake, giving higher pressure drag costs. These features were tested by using a pair of model gliders with dragonfly-type wing sections (NEWMAN et al., 1977). The larger glider, designed to fly at Re $\approx 4\times10^4$, showed that there was indeed an abrupt performance drop at the critical Re; also when leading edge turbulators were added to the wing the drag increased slightly but the lift increased considerably. Turbulators were not added to the smaller model, designed for Re $\approx 1\times10^4$, despite which it showed a performance at Re = 1.2×10^4 that could only be matched by a well tuned aircraft aerofoil, with turbulator, at Re = 2.5×10^4.

The dragonfly wing profile can thus be seen as a very efficient aerofoil. Structures on the leading edge can act as turbulators that delay drag crisis over the wing, and so promote an efficient fast forward flight.

CAMBER

Insect wings comprise a thin membrane suspended between supporting veins. The membrane gives the wing a very thin, flat plate structure. Within the range of Reynolds numbers at which insects typically fly (Re < 4×10^4) a cambered profile can generate more lift than a flat profile (HERTEL, 1966; VOGEL, 1967; ELLINGTON, 1984d). Dragonflies have two mechanisms to ensure their wings have a cambered profile.

HERTEL (1966) described the dragonfly as having a framework of longitudinal pleats in the anterior half of each wing. At low angles of attack, separation bubbles form within these pleats (Fig. 1) giving the wing an effective thickness and a smooth profile as for a bird or aircraft wing (NEWMAN et al., 1977). As the angle of attack increases the lower bubble size decreases while the upper bubble increases in size, both effects increasing the effective camber of the wing. The effective wing profile changes with angle of attack, thus giving rise to a greater lift production than would otherwise be predicted.

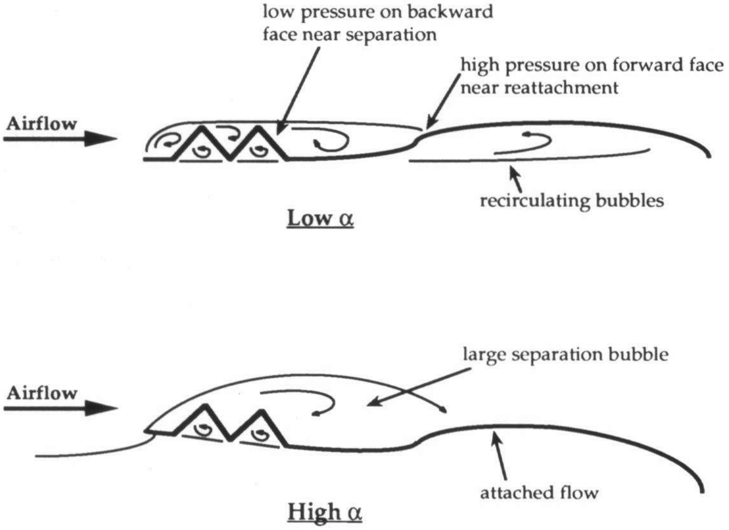

Fig. 1. Increasing the angle of attack (α) alters the distribution of separation bubbles, and so increases the effective camber of the wing (from NEWMAN et al., 1977).

Dragonfly wings have a well supported leading edge but a flexible trailing edge. A series of posterodistal veins curve back towards the trailing edge from a straight leading edge spar (WOOTTON, 1992). A wing undergoing lift in an airflow tends to be twisted by the aerodynamic forces unless the centre of pressure lies on the torsional axis (WOOTTON, 1981). The aerodynamic centre of pressure occurs behind the centre of torsion for most insects (WOOTTON, 1992), and this twisting is converted to automatic camber generation by the curved posterodistal veins (ENNOS, 1988a). As the rear portion of the wing is flexible, aerodynamic loading will cause camber to form in the correct direction, that is with the convex surface uppermost, for both the up and downstrokes.

NEW MECHANISMS IMPLICATED FOR DRAGONFLY FLIGHT

Since it was first suggested, twenty years ago, that classical aerodynamic theories may be inadequate to explain some aspects of dragonfly flight, the study of their aerodynamics has been prominent in the field of animal mechanics. An understanding of the novel lift generating processes that may be involved has repercussions beyond that of animal locomotion. Flapping insect wings have many features in common with helicopter rotors; novel animal lift generating mechanisms may have uses in aeronautics to produce greater fuel efficiency in aircraft, or to achieve slower flight speeds.

In this section I will outline the novel lift generating mechanisms that have been proposed for dragonfly flight and which may produce more lift than would otherwise be expected. First, however, I will introduce the local circulation method, adapted specifically for the dragonfly, which predicts that dragonflies can 'perform low speed flight with ordinary aerofoil characteristics' (AZUMA et al., 1985).

LOCAL CIRCULATION METHOD

The local circulation method (AZUMA et al., 1985; AZUMA & WATANABE, 1988) is based on the blade element theory (a form of the quasi-steady analysis) but corrections are made on each wing for the effect of the trailing vortex wake. These two papers involve slightly different methods for the calculations. In the first, *Sympetrum frequens* was studied during a slow climbing flight. After lengthy calculations, two predictions were made for the phase difference for the wings, based on a requirement for no net pitching moment. The two stable phase differences were with the hind wing leading by 80° for slow forward flight and 150° for fast forward flight. All other phase differences were predicted to have unstable pitching moments including 240° at which the maximum lift and thrust could be generated, and also for parallel (0°) stroking where behavioural observations suggest that very high accelerations are possible.

In the second paper *Anax parthenope* was studied at four forward flight velocities, and from these the power requirements were predicted for flight. The conclusion that all the aerodynamic forces can be explained without unsteady mechanisms contradict those of WEIS-FOGH (1973), NORBERG (1975), ELLINGTON (1984a), and SOMPS & LUTTGES (1985). The predicted power curve shows a deep minimum; this contradicts recent power measurements showing the power expenditure for hovering in bees is not much more than for intermediate speeds (DUDLEY & ELLINGTON, 1990; ELLINGTON et al., 1990). A good account of the areas in which the local circulation method differs from the established view, along with the necessary adjustments to the Azuma power curve for muscle power output, can be found in MAY (1991).

The adjusted power curve for *A. parthenope* shows that the power output necessary for hovering matches the maximum power available by the thoracic flight muscles (MAY, 1991), yet dragonflies can lift 2.5 times their body weight during take off (MARDEN, 1987) and during tethered hovering (SOMPS & LUTTGES, 1985). This discrepancy may be evened out by invoking unsteady mechanisms; as the forward velocity for *A. parthenope* decreased to 70 cm/s, the reduced frequency parameter (equation 2) increased to a mean value of 4.0 for each wing and thus unsteady mechanisms are probably involved. This could explain how a lower power output can result in the necessary lift for flight and hovering.

The proof by contradiction argument (ELLINGTON, 1984a) should again be remembered. The ability of a theory to explain all the lift required for flight proves neither that the theory is correct, nor that other mechanisms cannot be involved as well.

The local circulation method assumes that the wings leave behind them a sheet of undulating vortex wake. Other studies, however, show that shed vortices and unsteady flow interactions are produced by dragonfly wing motions (SOMPS & LUTTGES, 1985). Similar shed vortex structures have been observed with flow visualisation on an oscillating flat plate (KLISS et al., 1989), and the generation of vortices has been correlated with an increase in measured lift force, suggesting that vortex structures do indeed play a crucial role in augmenting the aerodynamic forces necessary for hovering flight. Computer simulation has recently modelled vortex shedding for an oscillating flat plate following a 'normal hovering' path, that is with a horizontal stroke plane (GUSTAFSON & LEBEN, 1991). Similar simulations are underway for hovering with an inclined stroke plane, as for dragonflies, and it will be interesting to see if they too result in distinct shed vortices.

WAGNER EFFECT AND WAKE VORTICITY

An aerofoil moving steadily through a fluid, with a non-zero angle of incidence, has a circulation of fluid around it. The value of this circulation, Γ, is given by the Kutta condition for linear motion.

$$\Gamma = \pi\, c\, U \sin \alpha' \tag{4}$$

where c is the wing chord, U the flapping velocity of the wing, and α' the angle of incidence of the wing.

The lift per unit span due to the circulation around an aerofoil in steady motion is given by the Kutta-Joukowski theorem.

$$L = \rho\, U\, \Gamma \tag{5}$$

were ρ is the air density.

When the aerofoil is at rest U=0, and so there is no net circulation around it. Kelvin's circulation theorem states that circulation is neither created nor destroyed, hence when the aerofoil is brought into motion it must leave behind an equal and opposite vortex to the one around the aerofoil. This vortex is known as the starting vortex, and takes a value $-\Gamma$.

The starting vortex effectively provides a large downwash which deflects the relative airflow past the aerofoil downwards; this in turn reduces the effective angle of incidence, α_r' (Fig. 2). The lift coefficient, and hence lift (equation 1), of an aerofoil increases approximately linearly from a zero angle of incidence to the angle at which the aerofoil stalls. A reduction of the effective angle of incidence by the starting vortex thus results in a reduction of the lift generated by the aerofoil. The strength of the starting vortex decays with the distance from its centre ($\omega = \Gamma/2\pi r$, where r is the radius from the centre), and so its effect on the aerofoil also decreases with distance. This phenomenon is known as the Wagner effect (WAGNER, 1925); an aerofoil starting from rest must travel several chord lengths before reaching its steady state lift values beyond the influence of the starting vortex.

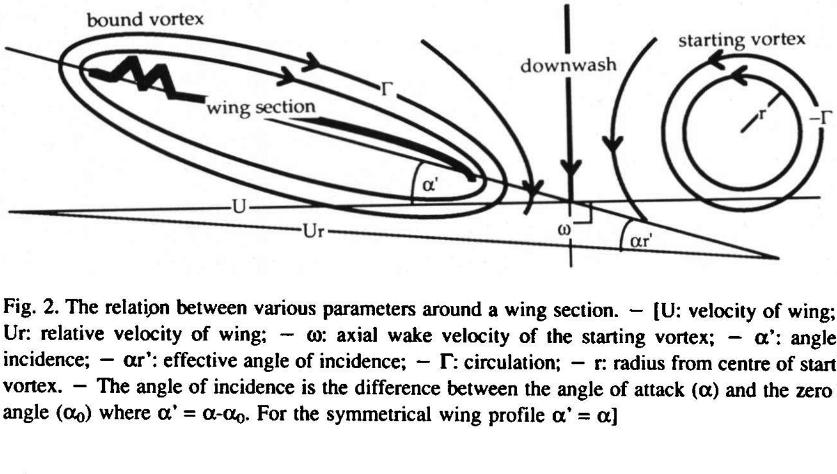

Fig. 2. The relation between various parameters around a wing section. – [U: velocity of wing; – Ur: relative velocity of wing; – ω: axial wake velocity of the starting vortex; – α': angle of incidence; – $\alpha r'$: effective angle of incidence; – Γ: circulation; – r: radius from centre of starting vortex. – The angle of incidence is the difference between the angle of attack (α) and the zero lift angle (α_0) where $\alpha' = \alpha - \alpha_0$. For the symmetrical wing profile $\alpha' = \alpha$]

The Wagner effect is an extreme example of wake vorticity effects. When an aerofoil accelerates, its circulation must change to satisfy the Kutta condition. An equal and opposite vortex will tend to be shed into the wake at the trailing edge of the aerofoil and this will delay the change in lift due to the acceleration (in a similar manner to the Wagner effect as described above).

The unsteady effects of wake vorticity and the Wagner effect tend to delay the onset of new lift forces on an aerofoil when it is changing velocity or starting from rest.

DELAYED STALL

At angles of incidence greater than the stalling angle the bound vortex separates from the aerofoil; once the circulation has been lost no lift can be generated (equation 5). FRANCIS & COHEN (1933) observed that when an aerofoil is moved from rest, at higher than stalling angles of incidence, the circulation slowly builds up (similar to the Wagner effect) to a level higher than the steady state level for the aerofoil, before it then stalls. This phenomenon is known as delayed stall and is the only conventional unsteady mechanism that can produce circulatory lift in excess of the maximum observed for steady motion (ELLINGTON, 1984d).

Delayed stall permits operation of the wings at large angles of incidence over the short distance travelled in each half-stroke, generating enhanced circulations to compensate for the Wagner effect (ELLINGTON, 1984d). the wings of a hovering *Aeshna juncea* only travel 2.5 chord lengths during each half-stroke (data from NORBERG, 1975), so it is possible that they can benefit from an enhanced circulation before the onset of stalling. Yaw turns in *Libellula luctuosa* and *Celithemis elisa* characteristically have high angles of attack (ALEXANDER, 1986), implicating the use of delayed stall mechanisms. The wings of *Sympetrum frequens* gradually increase angle of attack, and hence angle of incidence, throughout each half-stroke (AZUMA et al., 1985), to values well above steady state stalling; again it would seem that dragonflies can utilise the delayed stall effect.

Stall can also be delayed by applying a positive rotational velocity to a wing (ELLINGTON, 1984d), i.e. during downstroke and subsequent supination. Rotational velocity gives a wing rotational circulation, Γ_r, that in turn generates lift (equation 5). This again can give enhanced values for $C_{L\max}$.

FLING AND FLIP MECHANISMS

The fling mechanism (WEIS-FOGH, 1973; LIGHTHILL, 1973) was proposed to explain the high lift coefficient for the wasp *Encarsia*. Before beginning each downstroke the wings are clapped together dorsally, they then 'fling' apart about their trailing edges. The flow of air into the gap in the centre creates an equal and opposite circulation around each wing; this circulation is created before and independently of translation of the wing and it occurs without a starting vortex to cause the Wagner effect. The fling mechanism has been noted in many insects that allow their wings to touch at the end of the half-strokes. ALEXANDER (1984) studied 91 high speed film sequences of dragonflies in tethered flight (mainly *Libellula luctuosa* and *Celithemis elisa*); in only one of the sequences did he see evidence for this clap-fling mechanism. There have been no other reports of this in dragonflies.

WEIS-FOGH (1973, 1975) proposed the flip mechanism for Syrphinae and Odonata, insects hovering with an inclined stroke plane and unusually high lift coefficients. This mechanism suggested that as the wing 'flips' at pronation and supination, the flexible posterior part of the wing would lag behind due to its inertia. The wing would effectively flex along its centre with the flexion propagating out along the wing length to the wing tip. Although it is now known that the dragonfly wings may show twisting at pronation and supination due to inertia (NEWMAN, 1982), the actual flip mechanism was only conjectural and there are lines of evidence against it; here are three: (1) ELLINGTON (1984d) points out that any increase in vorticity as the wing flexes in a clap type motion would be reversed as the wing straightens again at the end of pronation or supination. – (2) The wing tip path of a hovering *Aeshna juncea* was not elliptical (NORBERG, 1975), another requirement for the mechanism. – (3) Agrionid and anisopteran Odonata show a relatively slow reverse wave from the wing tip to the wing base through the deformable areas of the wings (WOOTTON, 1981), this wave is opposite to that proposed for the flip mechanism. The flip mechanism, as a way of enhancing lift production, has not been pursued since its introduction.

ISOLATED ROTATION AND THE FLEX MECHANISM

The wing is rotated at the end of each half stroke, so that it is run upside down for half of the cycle. For the upstroke the morphologically dorsal side of the wing faces the direction of wing motion, and for the downstroke the ventral side of the wing faces the direction of the wing motion. The circulation accordingly changes polarity for each direction of the wing movement. Thus the circulation from a half stroke must be shed and a new circulation of the opposite sense generated for the subsequent half stroke.

Translational circulation may be retained as rotational circulation during the wing rotation at the end of each half stroke. This prolongs the time that lift is generated and postpones the shedding of that circulation. This circulation is in the same polarity as the subsequent starting vortex, that is opposite to the circulation of the next half stroke. If the circulation from a half stroke is retained throughout wing rotation to the start of the next half stroke then it will be shed as an enhanced starting vortex. Although the lift generated by any half stroke would be enhanced by such a phenomenom the lift from the subsequent half

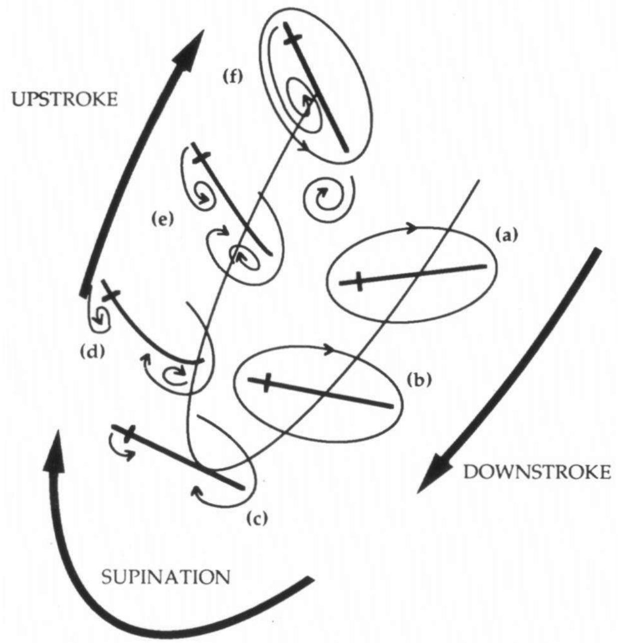

Fig. 3. The vorticity patterns suggested for the flex mechanism in isolated rotation (adapted from ELLINGTON, 1984d). – [See text for explanation]

stroke would be retarded by an exaggerated Wagner effect.

ELLINGTON (1984d) proposed a 'flex' mechanism to get around this problem (Fig. 3). At the end of the downstroke (a-b) the wing starts to rotate as it enters supination (c). The wing flexes during this rotation and the trailing edge is left stationary while the leading edge continues to move. As the trailing edge is almost stationary, new rotational vorticity is produced at the moving leading edge (d) whilst the previous vorticity rolls up at the trailing edge (e). When the wing straightens and accelerates into the upstroke, the leading edge vortex should attach to the morphologically ventral surface of the wing while the previous bound vortex breaks away from the trailing edge (f) as a combined starting and stopping vortex.

This rotation and flex mechanism falls well within the rotational coefficients measured in Diptera (ENNOS, 1989) and a sharp lift pulse is observed when the wing of *Drosophila melanogaster* is rotated at supination (ZANKER & GOTZ, 1990), both these reports support the 'flex' idea. In most insects supinatory twisting is partly an active process but in Odonata it is assisted, perhaps even wholly driven, by the momentum of the wing behind the torsional axis (WOOT-

TON, 1992, see also ENNOS, 1988b). This passive twisting suggests that the trailing edge lags behind as the wing rotates. Measurements from *Aeshna cyanea* and *Sympetrum striolatum* show that the wings do indeed rotate about their trailing edge during supination (data from NEWMAN, 1982) making them ideal candidates for the flex mechanism.

For insects hovering with an inclined stroke plane, like the dragonfly, upstroke circulation is small, if not zero. The trailing edge of the wing must become stationary near the start of pronation so vortex shedding occurs at the leading edge, and a useful separation bubble is to be generated for the downstroke. Hoverflies can advance or delay the rotation at pronation (ELLINGTON, 1984d) and this will affect the amount of vorticity that is shed at the leading edge. Dragonflies may also have this control over the timing of wing rotation. This could explain their extreme aerial manoeuvrability (ELLINGTON, 1984d).

Flow visualisation tests were performed on a two-dimensional flat plate model of a dragonfly wing in water (SAVAGE et al., 1979). Based on NORBERG's (1975) low speed film data for hovering *Aeshna juncea* the wing kinematics were averaged over many cycles. The subsequent downstroke modelled was deemed to have a fast 'scull' phase followed by a slower 'pause' phase. It is unlikely that dragonflies do actually have such a downstroke, as the inertial costs for wing accelerations would be high; also a relatively sinusoidal stroke has been shown for *Sympetrum frequens* (AZUMA et al., 1985). Nevertheless they did show large vortex shedding during rotations, producing lift larger than for the translationary part of the downstroke. They also showed a build up of a strong leading edge vortex during the rapid 'scull' phase that was not shed during the following 'pause'; this may be interpreted as delayed stall in translation. The model used may seem far removed from live dragonflies but it does outline the importance that rotary mechanisms probably play in lift generation for hovering dragonflies.

FORE AND HINDWING INTERACTIONS

Unsteady flows are generated around each wing pair and help augment the maximum lift that the individual wings can generate. Interactions between the two wing pairs are important, however, to the extent that some phase differences are predicted to lead to unstable pitching moments (AZUMA et al., 1985). Force measurements on a tethered *Libellula luctuosa*, while counterstroking, suggest that there is a single large lift peak that occurs during each stroke period (SOMPS & LUTTGES, 1985). This may indicate that lift generation is dominated by the integrated interactions between the wings rather than the unsteady effects initiated by each of the four wings. Aerodynamic analysis has not, as yet, been performed on parallel stroking dragonflies, yet this mode may produce even higher aerodynamic forces than counterstroking (ALEXANDER, 1984, 1986; RÜPPELL, 1989), probably due to flow interactions between the wing pairs.

CONCLUDING REMARKS

Dragonflies show wide ranging flight behaviours, from gliding and fast forward flight at the one extreme to hovering at the other. Gliding and fast forward flight have the steady forward velocity component as the predominant motion, and so the main aerodynamic forces involved are steady state and can be modelled with classical aerodynamic theory. Hovering, on the other hand, involves entirely unsteady motion and the clasical quasi-steady approach to animal hovering proves inadequate to model the forces involved. Steady state and unsteady theory are not mutually exclusive, however, and it is more than likely that they can both contribute to our understanding for all flight behaviours, the key difference being the relative importance that each mechanism has for generating the required aerodynamic forces.

Current studies have noted that the phasing between the wings appears important, with parallel stroking during flight generating extraordinary forces, even by dragonfly standards. All the detailed aerodynamic studies, however, have concentrated on counter stroked flight. The ability to alter the phase difference between the pairs of wings during flight is an ability shared by very few other flying insects. It hardly needs stressing that, if our understanding of dragonfly aerodynamics is ever to near completion, then an appreciation of the relative costs and benefits of the interactions caused by different wing phasing is also required.

Many studies on dragonflies and other insects have converged on the view that wing rotations may be critical in the generation of unsteady lift forces. The 'flex' idea seems plausible for the dragonfly, but as yet is unconfirmed. What is needed to test this, and other ideas, is a detailed kinematic analysis, adequate to resolve dragonfly wing motions down to the level of the centre of torsion of each section of the wing stroke. Whether such an approach is feasible can only wait the course of time.

As a final cautionary note I would like to outline a comment by Professor G. Rüppell at the British Dragonfly Society meeting in 1992. He recently filmed the species of *Mnais pruinosa* and *M. navaii* in Japan; both these species have two distinct forms differing only in that one form has clear, hyaline wings while the other form has orange markings on its wings. When each individual species is considered, if the two forms fly in isolation from each other then they showed similar flight patterns, except that the wing strokes of the coloured form were much larger than for the hyaline form. It is thought that this difference is because the wings of the coloured form act as visual flags and hence are 'waved' more in front of conspecifics. This shows how the aerodynamics of a dragonfly may be affected by factors other than purely lift generating capability and efficiency. Any aerodynamic study, if it is to be relevant to the dragonfly in its natural habitat, must be put into the perspective of the overall behaviour of that animal.

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