WIND TUNNEL STUDIES OF TURNS BY FLYING DRAGONFLIES

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SUMMARY

High-speed movies of dragonflies turning in flight on flexible tethers show that there are two distinct modes of turning. In the 'conventional' mode, dragonflies use left–right asymmetries in the wing stroke amplitude, and occasionally in the angle of attack, to produce more lift and thrust on one side than the other. This causes the animal to roll into a bank, so that the lift vector has a sideward component; this sideward component produces the turn, much as in an aeroplane. This type of turn is probably most useful during fast forward flight.

The second mode of turning is the 'yaw turn'. Yaw turns are accomplished without banking, and the dragonfly's long axis may turn more than 90° in the period of two wing strokes. The kinematics of this turn could not be as closely analysed, but it appears that dragonflies use drag on the inner wing upstroke and the outer wing downstroke to turn, much like pivoting a rowing boat. This turn may be hampered by drag on the abdomen during fast forward flight and would be most useful at low speeds or during hovering.

INTRODUCTION

Flying insects must use their wings to control manoeuvring, as well as to produce lift and thrust. In spite of the large number of studies on insect flight (see Pringle, 1957, 1968, and Lighthill, 1975, for reviews), there have been relatively few on the physics of turning.

Most work on turning flight has focused on physiology: how either the muscles (e.g. Baker, 1979*c*; Burton, 1964; Zarnack & Möhl, 1977) or nervous and sensory systems (e.g. Blondeau, 1981; Gewecke & Philippen, 1978; Gettrup & Wilson, 1964; Goodman, 1965) bring about and control turns. Some of these studies also describe the wing motions produced by such neuromuscular activity (e.g. Baker, 1979*b*; Blondeau, 1981; Burton, 1964; Gettrup & Wilson, 1964). Although these studies have used wing movement observations during turns primarily as a sensory or neuromuscular assay, they have suggested several possible mechanisms for initiating turns or correcting unintentional course changes. For example, in Diptera,

Nachtigall & Wilson (1967) described flexing (partially or completely folding back) one wing, and Taylor (1981) described contralateral stroke angle differences for turn initiation. Researchers working with locusts disagree as to whether turns are produced by a reduction of the angle of attack (increased pronation) of the forewing to the inside of the turn (Baker, 1979b; Dugard, 1967; Gettrup & Wilson, 1964) or an increase in the stroke angle of the wings to the outside of the turn (Taylor, 1981). These studies on locusts, as well as that of Camhi (1970), also describe 'ruddering' movements of the abdomen and hindlegs. Studies on dragonflies (Hisada, Tamasige & Suzuki, 1965; Taylor, 1981) and beetles (Burton, 1964) also suggest that these insects produce turns by increasing the stroke angle (amplitude) of the outer wing.

Most previous studies on turning behaviour were not primarily concerned with the mechanics of turns, so unnatural experimental conditions (still air or non-pivoting tethers) were used, and wing movements were not quantified. Baker (1979b), however, flew locusts on a pivoting tether, and found angle of attack differences between the forewings and 'ruddering' with the abdomen and legs during turns; he found no consistent stroke amplitude asymmetries. Because of the locust's freedom of movement, Baker could not quantify wing movements in detail.

The goal of my study was to provide a detailed description of the wing movements that a highly manoeuvrable insect uses to initiate turns under the most realistic conditions that are practical. My primary focus was on initiation of a turn, when the unbalanced forces that cause a turn are first produced. Such a description can be used to elucidate the aerodynamic mechanism used for turning. I chose dragonflies (Odonata: Anisoptera) as experimental animals because most adult dragonflies are highly manoeuvrable and carry out most of their activities on the wing (Corbet, 1962). Because of their relatively simple wing articulation, dragonflies must manoeuvre by modifying their wingbeat pattern and cannot employ the dipteran method of flexing one wing. This study describes the wing movements during two different types of turns by flying dragonflies.

MATERIALS AND METHODS

In most experiments, I used a male dragonfly of either *Libellula luctuosa* (Burmeister) or *Celithemis elisa* (Hagen); female dragonflies will not fly as readily in the wind tunnel. I netted the dragonflies in the field and placed them in containers suspended over ice. While the dragonflies were still cold, I immobilized them on a pinning board with strips of modelling clay and cemented a 1·0 cm long, 0·2 cm diameter sleeve of aluminium tubing to the posterioventral part of the thorax with fast-drying epoxy cement ('Elmer's Super-Fast Epoxy', Borden Co.). The dragonflies were stored at 9 °C, in plastic boxes lined with wet paper towels to prevent desiccation, and were used in less than 48 h.

The dragonflies were flown in the 15-cm diameter working section of an open-throat wind tunnel. I used a conventional linear wind tunnel rather than a radial one such as that of Baker (1979a,b): although an insect in a radial wind tunnel can align itself with the wind direction no matter what direction the animal faces, this

arrangement precludes taking three-view photographs (see below). After a dragonfly starts to turn in a linear wind tunnel, it no longer faces directly into the air flow: this is different from turns in free flight. I have concentrated on the initiation of turns in order to minimize this problem; in addition, the first few degrees of turn should be quite similar to free flight conditions, aside from the problems of tethering (see Discussion). The velocity was nearly uniform across more than 90 % of the wind tunnel's diameter; no turbulence was detected with a pinhole vane anemometer (orifice diameter 3 mm, response time 0·2 s full scale). The diameter of the laminar flow region at the starting position of the dragonfly was about 14 cm.

In preliminary wind tunnel tests, I found that *L. luctuosa* and other large dragonflies preferred to fly at about $3·5 \, m \, s^{-1}$ and *C. elisa* preferred to fly at about $2·7 \, m \, s^{-1}$ when attached to a tethering system that allowed them to choose their own flying speed (balancing thrust and drag). During the rest of the trials, I left the wind tunnel speed fixed at $3·5 \, m \, s^{-1}$ for *L. luctuosa* and at $2·7 \, m \, s^{-1}$ for *C. elisa*, so that a pivoting tether (Fig. 1) could be used. Each dragonfly was attached to the pivoting tether by sliding the sleeve glued to its thorax over the shaft of bearing 'a' (Fig. 1A). The sleeve fitted tightly onto the shaft, and adhesion was aided by coating the shaft with a thin layer of Tackiwax (Cenco). The tether consisted of miniature ball-bearings [3/64″ (approximately 1·19 mm) shaft size; P-I-C Design Corporation] attached to aluminium tubing. The bearings allowed the dragonfly to rotate around the vertical (yaw) and longitudinal (roll) axes, as well as to move in a circle about the central support.

I filmed the dragonflies flying in the working section of the wind tunnel with a Locam II (Redlake Corporation) 16 mm, pin-registered high-speed ciné camera, on Kodak Tri-X film, using two custom-built, 1200-W lighting systems (Kier, 1982). Front-surface mirrors mounted above and also behind the dragonfly gave a top and a back image of the dragonfly in the field of view of the camera (Fig. 1B). *L. luctuosa* were filmed at $400 \, frames \, s^{-1}$ and *C. elisa* were filmed at $550 \, frames \, s^{-1}$.

Filming a sequence consisted of moving the perch of a tethered dragonfly into the wind tunnel working section, turning the tunnel and movie lights on, activating the camera, and pulling away the dragonfly's perch. As the movie lights were the brightest light source in the laboratory, most dragonflies turned towards the lights as soon as they began to fly, performing a right-hand turn. In a right-hand turn, the insect's left wings will be referred to as the 'outside' wings and the right wings as the 'inside' wings (all turns analysed in detail were right-hand turns). Animals flew and turned in a total of 73 sequences, including eight in which untethered dragonflies were released in the field of view of the camera.

To permit accurate measurements from a film sequence, several conditions had to be met: (1) the dragonfly's long axis should be lined up with the long axis of the wind tunnel, (2) the wings should be in the camera's plane of focus, (3) the wings should be in the field of view of both mirrors, and (4) the dragonfly should have a negligible bank angle, i.e. the mid-sagittal plane should be approximately vertical. In any other orientation, the apparent wing angles seen in the mirrors would not represent the true angles. Because initiation of turns is the focus of this study, only the first few

strokes of a turn need to be analysed; this is also when the air flow conditions are most realistic and the most accurate measurements can be made.

I analysed the films by projecting them at about three times life size with a L-W International Mark V film analyser: known dimensions of the tether served as length calibrations. With the magnification known, I could measure the apparent vertical dimensions of a wing to the nearest 0·1 mm with Vernier calipers, and calculate trigonometrically the wing's angle with respect to the horizontal ('geometric inci- dence'). I simultaneously determined the vertical and horizontal angular velocity of the wing by projecting the film onto large sheets of paper, sketching successive wing positions, and measuring the angle between successive positions with a protractor (accurate to ±1·5° based on repeated sketches). Dividing successive values by the frame interval gives the angular velocity, which can then be used to calculate tangential velocities. When summed over a half-stroke, these angles give the vertical or horizontal component of the stroke angle. Dragonflies actually beat their wings at
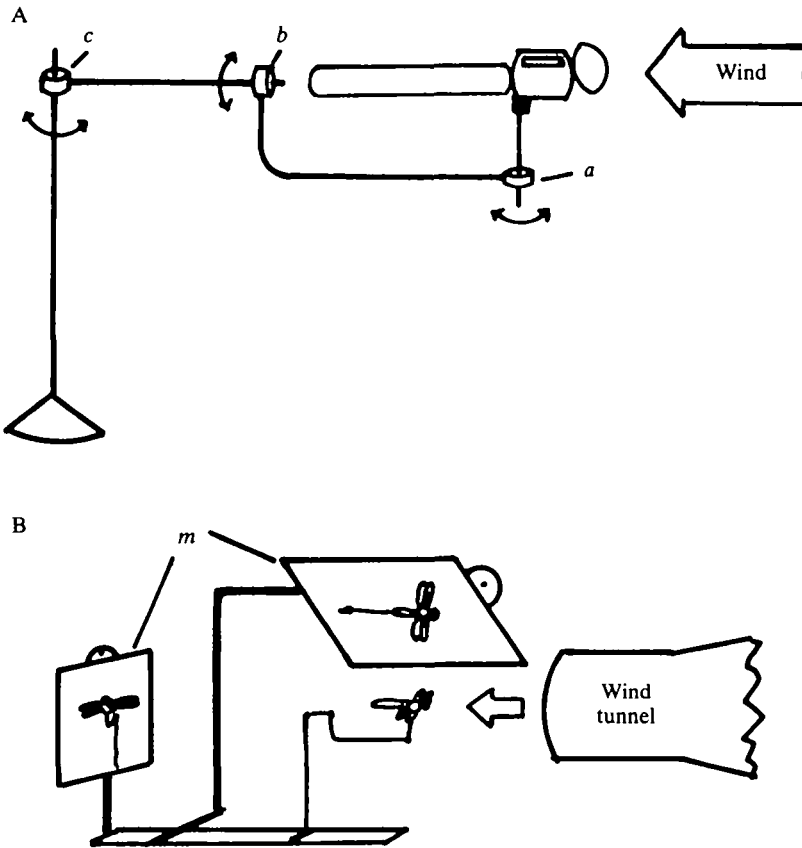

Fig. 1. Insect tethering and viewing systems. (A) The tether contained three bearings that allowed the insect to yaw (bearing *a*), roll (bearing *b*) and fly in a circle about the central support (bearing *c*). (B) Mirrors (*m*) arranged so as to provide back and top views of the insect.
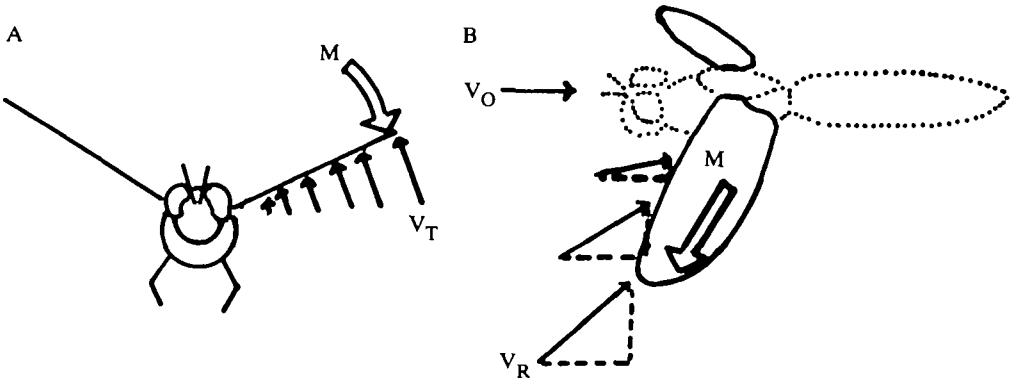
Fig. 2. (A) Diagrammatic front view of a flying insect: the tangential component of the velocity of the air moving over the wing (V_T) increases towards the tip due to the wing's flapping motion (M). (B) Diagrammatic side view of a flying insect: because of the change in tangential velocity along the wing, the magnitude and direction of the resultant air velocity over the wing also changes along the wing. M, wing motion; V_O, air velocity over the insect due to the movement of the whole insect through the air; V_R, resultant air velocity over the wing due to the wing's motion and the insect's forward velocity.

about a 30°–35° angle from the vertical (Neville, 1960; Norberg, 1975, and personal observation), but in this study I used the vertical projections of the extremes of the stroke, which I will refer to as the stroke angle, as a measure of the stroke amplitude. (The horizontal components of the stroke angle closely parallelled the pattern of the vertical components and provided no additional information.) The tangential velocity, and thus the actual angle of attack, varies along the span of a flapping wing. The tangential velocity adds vectorially to the animal's flying speed (the wind tunnel speed in this case) to give the resultant wind velocity vector, and the angle of this vector plus the geometric incidence gives the angle of attack at a given point on the wing (see Fig. 2). This is the angle of attack relative to the free stream, as commonly applied to aircraft wings; note that a detailed study of the flow patterns around the wing might require the 'effective angle of attack' (Bertini & Smith, 1979, p. 168). The effective angle of attack is somewhat lower than the angle of attack as I have defined it, because of the downwash induced by the wing's bound vortex. The angle of attack, as I have defined it, is useful for comparing similar wings or wing models, but may not be appropriate for calculations based on thin airfoil theory (Bertini & Smith, 1979; Von Mises, 1959). It is likely that the difference between these two angles is small compared to the changes in the angle of attack (Hoerner & Borst, 1975).

When a dragonfly turns in flight, it may rotate about its longitudinal and dorso-ventral axes simultaneously. Thus, it is extremely difficult to define accurately a 'horizontal' wing position (with respect to the insect) on which to base wing stroke angle measurements. Measuring wing position with respect to an external, fixed horizon would be misleading because the wing stroke angle would appear to increase on one side and decrease on the other, because of the rolling motion of the dragonfly's body. I have, instead, measured the wing's angular displacement between successive

film frames and called such measurements the 'positional angle'; no fixed reference points or reference points on the dragonfly were required for such measurements.

<div align="center">RESULTS</div>

Analysis of 73 turn sequences revealed that two distinctly different types of turns were used by the dragonflies. In 45 of the sequences, turns were initiated by changes in the wing stroke which caused the insect to roll about its longitudinal axis ('bank'). As this type of turn is analogous to turning a fixed-wing aircraft, I will refer to it as the 'conventional' turn. In 21 other sequences, the animal turned very quickly about its vertical axis ('yawing') with little or no bank, so I will refer to these as 'yaw' turns. Many sequences showed more than one turn, and seven sequences showed both a yaw turn and a conventional turn.

A flight turn is adjusted to fit the circumstances each time it is performed. A dragonfly probably adjusts its turn based on a large number of factors, so that details of the wing kinematics (stroke angle, angle of attack, etc.) are unique to each turn. It would thus be inappropriate to observe many turns and attempt to calculate 'average' values for such kinematic variables. (This contrasts with straight and level flight, which is so stereotyped that such averages can be used, e.g. Weis-Fogh, 1956; Vogel, 1967.) Thus, several individual turns are described below, so that both the similarities and variations can be seen.

Kinematic description of conventional turns

A conventional turn is characterized by an initial rolling movement into a banked attitude, which leads to sideways translation in one or two strokes. The animals also yawed into the turn, but yawing tended to lag behind rolling and translation. Thus, an animal usually moved in a noticeably different direction from the direction it was facing. In all film sequences showing conventional turns, one or both pairs of wings showed left–right asymmetries in the stroke angle, with the lower amplitude on the inside of the turn (Table 1). While the exact angle of attack cannot be calculated from these data, the geometric incidence angle was clearly higher on the outer wings in four cases (Table 1), but not obviously different in the other six cases. These relative differences in stroke angle and angle of attack between inner and outer wings can be achieved in several ways: dragonflies may change these stroke variables on one or both sides, and the forewing and hindwing strokes can be changed to different degrees. This variability can be seen in the conventional turn sequences described in detail below.

The first analysis is on a tethered turn by *C. elisa*. This animal started turning immediately after it began flying, and the data in Fig. 3 begin about three strokes into the flight. The forewings displayed strong asymmetry in stroke angle: the right (inner) wing flapped through an angle of about 10° to 20°, but the left (outer) wing flapped through an angle of about 40° (Fig. 3A). (In straight and level flight, dragonflies usually fly with a forewing stroke angle of 25°–35° and a hindwing stroke angle of 35°–45°, D. E. Alexander, unpublished.)

Fig. 3 also shows that the angle of attack of the outer forewing was higher than that of the inner forewing throughout most of the stroke, with the greatest difference during the downstroke when most of the lift should be produced. During the upstroke, the angles of attack of both forewings are low, suggesting that little force was being generated.

The hindwings displayed analogous, but more extreme, asymmetries. The right (inner) hindwing was essentially gliding, while the left (outer) hindwing flapped through an approximately normal stroke angle of about 35° (Fig. 3C). The angle of attack of the outer wing again was much higher than that of the inner wing (Fig. 3D) throughout almost the entire stroke.

Note that the wingtip of a flapping wing has the tangential velocity due to flapping added vectorially to the velocity of the animal's forward progress, which means that the air will strike the wingtip with a much higher speed than if the animal were gliding. Thus, in the middle of this downstroke, the outer forewing tip has a tangential velocity of $155 \, \mathrm{cm \, s^{-1}}$ compared to $102 \, \mathrm{cm \, s^{-1}}$ for the inner forewing tip; the outer hindwing tip has a tangential velocity of $146 \, \mathrm{cm \, s^{-1}}$, considerably higher than the inner hindwing tip's $35 \cdot 1 \, \mathrm{cm \, s^{-1}}$. When vectorially added to the $270 \, \mathrm{cm \, s^{-1}}$ forward velocity, the differences may not appear large; however, the aerodynamic forces are approximately proportional to the square of the velocity (Von Mises, 1959), so a considerable difference in lift will result.

Increasing the stroke angle also affects the angle of attack by increasing the vertical components of velocity, especially towards the tip. Under such conditions, when the vertical velocity is added vectorially to the other velocity components, the angle of attack is increased on the downstroke and decreased on the upstroke.

A detailed analysis of a turn by an individual of a different species (*L. luctuosa*) illustrates the variation possible within the 'conventional' mode of turning. As in the previous sequence, the forewings clearly showed asymmetrical stroke angles (Fig. 4A); the outer wing apparently increased its stroke amplitude while the inner

Table 1. *Summary of stroke angles from films of right-hand turns that met the criteria for analysis (see text)*

Sequence	Forewings		Hindwings	
	Left	Right	Left	Right
2–1*	56°	35°	69°	69°
4–2	54°	55°	51°	37°
4–3	57°	44°	60°	47°
5–1	42°	39°	50°	27°
7–1*	36°	23°	55°	72°
10–1*	48°	34°	29°	29°
10–2	39°	23°	27°	21°
10–4*	57°	36°	43°	24°
A–4	43°	40°	not visible	
B–3	35°	32°	not visible	

* Geometric incidence of forewings, hindwings, or both, clearly higher on left side by about 20 % or more.
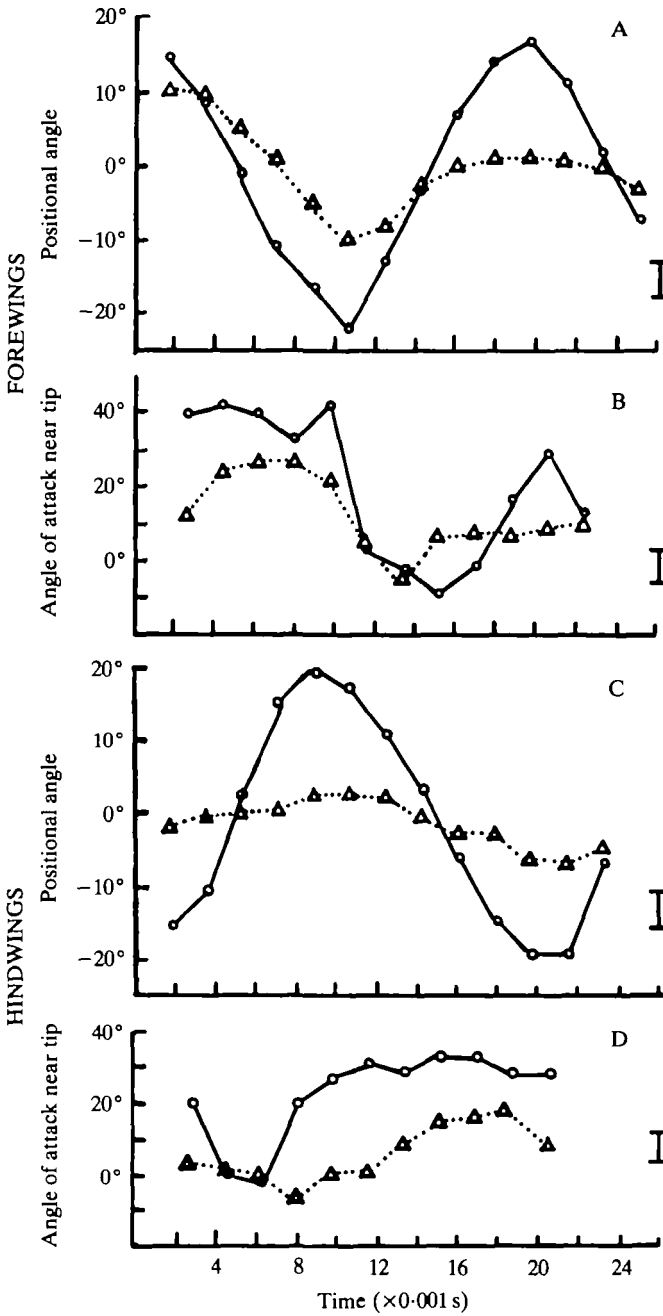
Fig. 3. Wing kinematics at the beginning of a turn by *Celithemis elisa*. In all sequences analysed, the dragonfly turned to the right; the left wings are to the outside of the turn and are represented by a solid line and the right wings are represented by a broken line. The frame rate in this sequence was 550 frames s^{-1}. The positional angle is defined as the vertical component of the angular displacement of the long axis of the wing when viewed from behind, and is thus independent of reference points: the zero on the positional angle axis represents approximately the midstroke point. The angle of attack is based on the resultant velocity vector and the geometric incidence 90 % of the span from the wing base (articulation). Each symbol is the mean value of four measurements from the same frame. The error bars are a measure of the repeatability of measurements from the films: the length of the bar shows the largest range for four measurements of the same angle in this sequence. (A), (B), forewings; (C), (D), hindwings.

wing maintained nearly the stroke angle seen in straight and level flight. In contrast, the angle of attack of both wings varied during the stroke, but neither wing consistently exceeded the other. Note, however, that at the top of the second
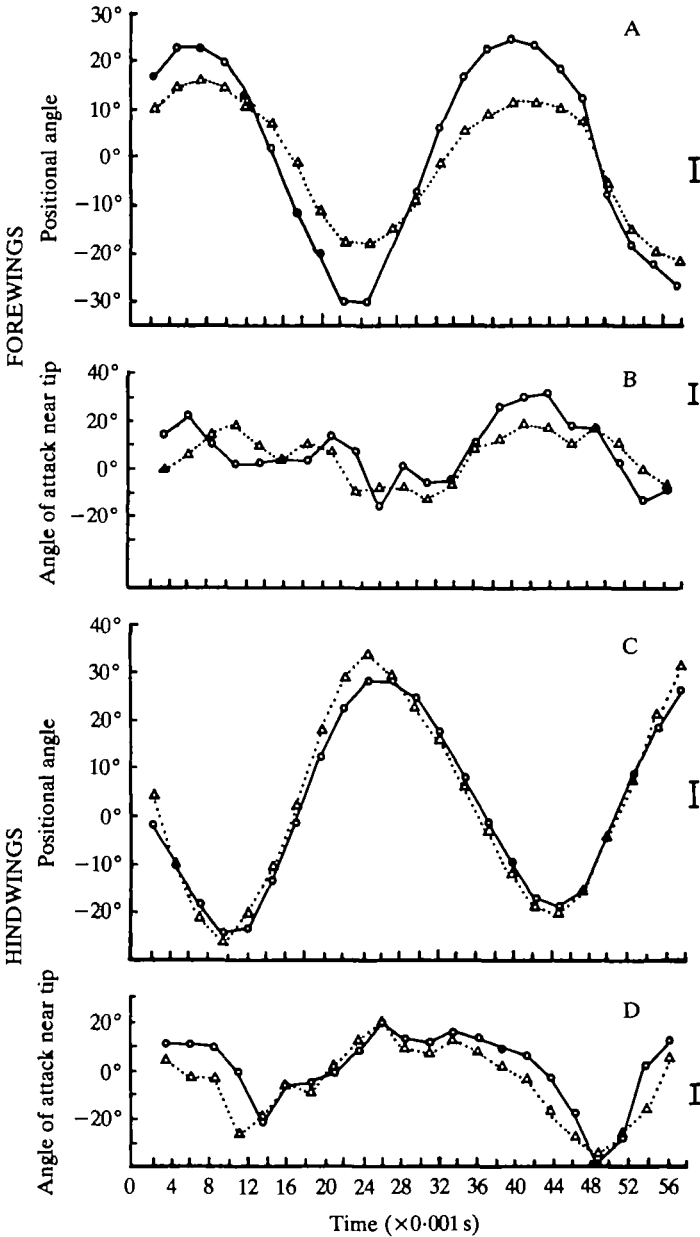

Fig. 4. Wing kinematics at the beginning of a right-hand turn by a specimen of *Libellula luctuosa*. Left wings are represented by solid lines, right wings by broken lines; frame rate was 400 frames s^{-1}. Variables defined in Fig. 3. (A), (B), forewings; (C), (D), hindwings.
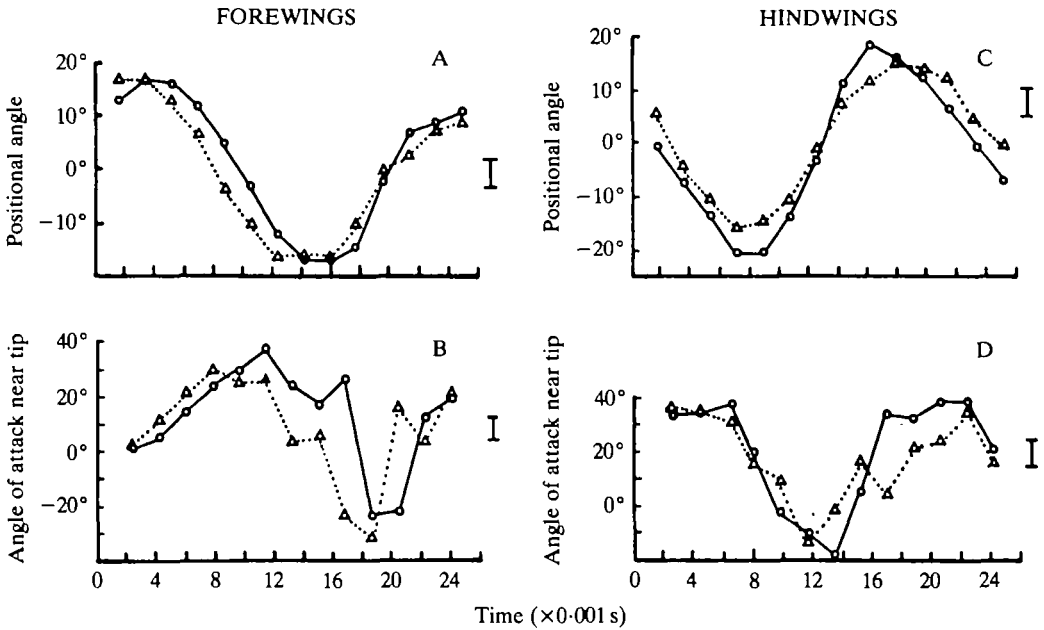
Fig. 5. Wing kinematics well into a turn by a specimen of *Celithemis elisa*. Variables and notation as in Fig. 3; frame rate was 550 frames s^{-1}. (A), (B), forewings; (C), (D), hindwings.

upstroke, the outer wing did maintain about a 12°–14° increase over the inner wing. If the quasi-steady approximation is valid, the higher angle of attack may indicate that the outer forewing starts into the downstroke with greater lift production; alternatively, it may be involved with some unsteady phenomenon, such as Ellington's (1984) 'flexion' mechanism. Also, both forewings displayed a negative angle of attack on the upstroke, suggesting some thrust production (Lighthill, 1975).

In contrast to the previous sequence, the hindwings showed very little asymmetry (Fig. 4C,D). The differences in stroke angle are of the order of 10% and thus near the limit of resolution of this analysis. The outer hindwing had a consistently higher angle of attack on the downstroke, but the difference between the right and left hindwings was not as dramatic as seen in Fig. 3.

The roll rates of the dragonflies in these two sequences generally correlate with the degree of asymmetry of their wingbeat patterns. The dragonfly in the first sequence displayed a very large difference between its left and right wingbeats and it rolled continuously through at least nine strokes; its roll rate during the analysed frames was 80° s^{-1} and two strokes later it was 180° s^{-1}. *Libellula luctuosa*, in the second sequence, displayed less extreme differences between its left and right wingbeats and it rolled at a rate of 60° s^{-1} during the analysed stroke which increased to 110° s^{-1} within two strokes; three strokes later it stopped flapping and glided out of the flow of the wind tunnel with a constant bank angle.

In a third sequence (using the same *C. elisa* as the first sequence) the dragonfly was in the proper orientation for analysis later in the turn, after the bank angle was well established. Fig. 5 shows that for the fifth stroke into the turn, the amplitudes of the

left and right forewings were nearly equal and there were only slight differences between the amplitudes of the left and right hindwings. There were no measurable differences in the angle of attack on the downstroke (Fig. 5C,D), and the differences in the angle of attack on the upstroke suggest there might have been a slight thrust asymmetry that would produce a yawing force into the turn; any such force evidently was quite small compared with that produced earlier in the turn.

Left and right forewing amplitudes are the same within the limits of this analysis. There appears to be some angle of attack asymmetry, but Fig. 5A indicates that the inner forewing led the outer forewing by about the interval of one frame so that if the curve for the inner forewing were moved one frame to the right, most of the asymmetry would disappear. Thus, even with the animal clearly in a bank and turning, the wingbeat was generally symmetrical, especially when compared to the wingbeat patterns used to initiate turns as shown in Figs 3 and 4.

Yaw turns

Apart from the lack of longitudinal rolling, yaw turns have other striking differences from conventional turns. Yaw turns are extraordinarily fast: in one free-flight sequence, the dragonfly turned about 180° in less than three wingbeats and in another it turned about 90° in two wingbeats; in tethered sequences, the insects commonly turned 90° in 4–6 strokes. This is three or four times faster than conventional turns. Additionally, in 25 of the 28 yaw turn sequences, the dragonflies beat their wings so that the anterior and posterior pairs were in phase, i.e. the forewings and hindwings reached the tops and bottoms of their strokes at the same time (Alexander, 1983); dragonflies usually beat their fore- and hindwings about a half-stroke out of phase (Chadwick, 1940). Of eight successful, untethered flight sequences, six clearly showed yaw turns and flapping in phase, which demonstrates that such behaviour was not an artefact of the tethering system.

A comprehensive kinematic analysis of yaw turns was impeded by the very high turn rates and common co-occurrence of flapping in phase. The following analysis on *L. luctuosa* is missing data for some frames (especially for the angle of attack) because the images of the forewings and hindwings occasionally overlapped, so that their images were partly obscured.

At the beginning of the analysed section, the forewings have a very similar amplitude (Fig. 6A), but comparison with Fig. 7 reveals that the fore- and hindwings are not really in phase until about frame 8. At that time, the amplitude of the forewings begins to diverge rapidly, with the outer wing assuming a much larger amplitude. There are extreme swings in the forewing angles of attack (Fig. 6C) with the outer wing at a peak during the downstroke and the inner wing higher on the upstroke with a peak at the top of one stroke. Unlike other sequences where the anterior–posterior components of the stroke amplitude simply followed the same pattern as the vertical components, the forewing in this case showed quite a different pattern. On the first stroke, there was a strong asymmetry in the horizontal stroke angle, in spite of very similar vertical components. On the second upstroke, the outer wing moved very little horizontally, which means that it moved almost straight up,

rather than in the normal up-and-back direction. Also, except on the second upstroke, the outer forewing had a much higher horizontal amplitude. Note that yawing of the body would exaggerate such horizontal motion; the body yawed less than 10° during the first stroke and less than 15° during the second stroke.

The pattern of the hindwings was considerably different. Initially, the inner wing had a higher vertical amplitude component; then as the fore- and hindwings moved into phase, the vertical components became very similar (Fig. 7A). The hindwing angles of attack showed less extreme swings than the forewings (Fig. 7C): although
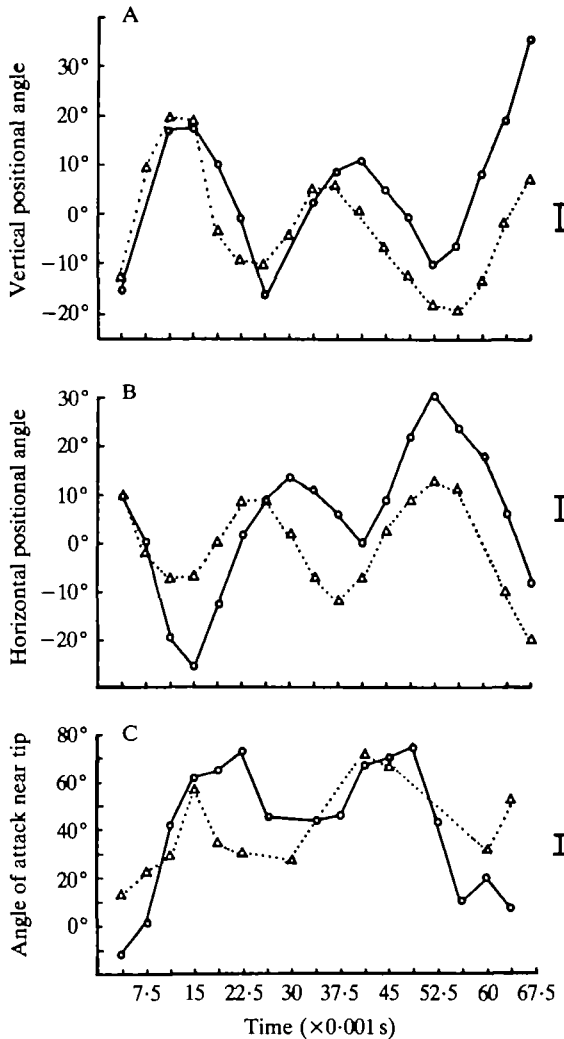

Fig. 6. Forewing kinematics of a yaw turn by a specimen of *Libellula luctuosa*. Frame rate was 265 frames s^{-1}. Horizontal positional angle was measured from the top view in a similar manner to vertical positional angle; other variables and notation as in Fig. 3. Positional angles or angles of attack could not be calculated for every frame due to overlapping wing images (see text).
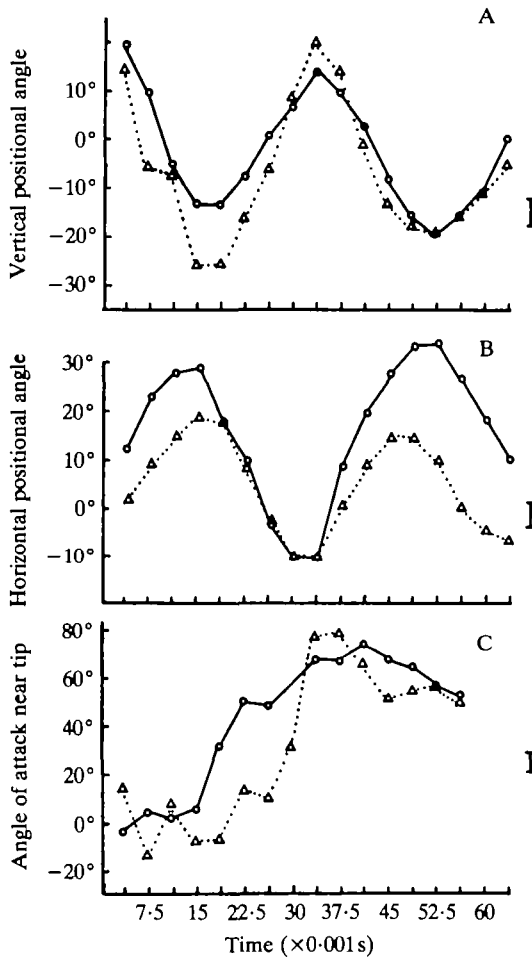
Fig. 7. Hindwing kinematics during a yaw turn by *Libellula luctuosa*. Same sequence and frame numbers as Fig. 6; notation as in Fig. 6.

there was no consistent pattern of asymmetry, the angles of attack increased throughout the analysed period.

In contrast to the vertical amplitude components, the horizontal components of the hindwings showed a consistent difference throughout the analysed segment, in spite of the fact that the vertical components were equal in the last half of the segment. The only way that the vertical components can be equal and the horizontal components unequal is for the wings to be flapping in different planes (i.e. for the wings to have different stroke plane angles, see Alexander, 1982; Jensen, 1956): in this case, the inner (right) wing stroke was closer to the vertical than the outer (left) wing. Actually, both hindwings displayed a more horizontal stroke plane than normal, the left wing being 43° and the right wing being 50° from the horizontal [the normal stroke angle is about 60° from the horizontal; Neville, 1960 (*Aeschna* spp.) and personal observation (*L. luctuosa* and *C. elisa*)].

DISCUSSION

Dragonflies can use two different manoeuvres to produce a turn: conventional turns and yaw turns. There seems to be little or no intergradation between conventional and yaw turns: they appear to be fundamentally different, rather than extremes on a continuum.

Conventional turns

Conventional turns by dragonflies seem to be analogous to turning in an aeroplane. The essential elements of initiating a simple level turn in an aeroplane are the following: (1) producing unbalanced forces to cause rolling into a bank; (2) neutralizing the controls once the desired bank angle is reached, at which time the net lift has a sideward component, and then (3) allowing this sideward lift component to change the aeroplane's direction (Perkins & Hage, 1949). Dragonflies clearly make use of banking to cause turns. In order to roll into a bank, they must produce unbalanced forces on one side with respect to the other. The high-speed films provide evidence that these unbalanced forces are produced by left–right asymmetries in the wing stroke angle and, to a lesser degree, the angle of attack. The third sequence analysed in detail demonstrates that once the bank angle is established, the dragonfly may return to a nearly normal stroke pattern, which has the same effect as neutralizing the controls of an aeroplane.

The unbalanced forces that produce a banked turn are generated by changing the amount of lift produced on one side or the other. Assuming that the quasi-steady approximation is valid for the dragonflies used in this study (Weis-Fogh, 1975), a simple interpretation of the kinematics of conventional turns can be made. Changes in the stroke angle (amplitude) affect the velocity of air over the wing (which has a strong effect on lift) and the instantaneous angle of attack (which has a smaller influence on lift). These effects are especially important on the distal part of the wing (Alexander, 1982). The dragonfly can also make further adjustments to the angle of attack with the wing articulations, which affect the whole wing equally, but these were less common than changing the stroke angle during turns and may be most important for turns while gliding. Differential changes in camber (wing profile), as found in locusts, could also be used to produce unbalanced lift and initiate a turn (Nachtigall, 1981; Weis-Fogh, 1956). Dragonflies do not appear to use changes in wing camber to affect lift; the only major camber changes shown in the films occurred when the flexible trailing edge occasionally bent up or down slightly during the rapid pronation or supination at the top or bottom of a stroke. Thus, during flapping flight, the amplitude changes are probably the main control input, with angle of attack changes for fine tuning. In some instances, the differences in angle of attack undeniably have the dominant role. Dragonflies in 18 sequences performed banked turns in the wind tunnel entirely or partially by gliding. During a glide, with no amplitude to adjust, the only control mechanism available with the wings is angle of attack adjustment.

Ellington (1984) has recently challenged the validity of the quasi-steady approximation even for large insects, suggesting that unsteady effects may be important for them as well. In the conventional turn, an increase of the amplitude of the wing stroke on one side with respect to the other would increase the acceleration of the wing as well as its speed. The differences in acceleration may be important for unsteady mechanisms like Ellington's (1984) chordwise 'flexion'; the insect could use this mechanism to generate more lift on one side than the other, causing a bank, and thus a turn, just as outlined above. My evidence does not clearly favour either the quasi-steady or the unsteady interpretations: flexing can occasionally be seen during pronation (although this cannot be quantified from my films) but the changes in angle of attack during pronation tend to be gradual, rather than abrupt as one might expect with the flexing mechanism. Whether or not unsteady effects are dominant, it is clear that increasing the amplitude on one side should increase the force produced on that side.

Note that flying animals produce thrust with a slight forward tilt of the resultant force vector throughout most of the stroke, so that an increase in stroke angle should increase the thrust as well as lift on one side, if no other changes are made to the stroke pattern. This unbalanced thrust tends to yaw the animal into the turn, which supports Baker's contention that it is artificial to try to separate the production of roll and yaw in flying insects (Baker, 1979*b*): indeed, asymmetrical stroke amplitude has been reported to produce both rolling (Srinivasan, 1977) and yawing (Götz, 1968) forces in flies (Diptera). Baker argued that trying to separate roll and yaw production in insects is a result of thinking in terms of aeroplane control, and during initiation of a conventional turn, this is clearly true. The yaw turn, however, does not fit Baker's scheme.

The conventional turn mechanism should produce a smooth, moving turn that would be most useful during fast, forward flight; at high speeds, a high bank angle can produce a very sharp turn if the magnitude of lift is increased appropriately (Perkins & Hage, 1949). At very low flight speeds, this type of turn should be less effective: a small bank angle would cause the dragonfly to move laterally, but relatively large pitching and yawing moments would be required to align the insect's body with the new direction of flight.

Clearly, the variations evident in the films demonstrate that many combinations are possible within the conventional turn mode. Either the hindwings or forewings or both can show large asymmetries, and dragonflies can employ many combinations of amplitude and angle of attack asymmetries. If dragonflies in nature use the variations displayed in the films, they are capable of producing turns along a continuum, from using shallow bank angles to produce wide, sweeping turns, to higher bank angles which produce sharper, faster turns.

Yaw turns

Yaw turns are fundamentally different from conventional turns because they are performed with little or no bank. In the yaw turn, there is no need for a force to move

the whole animal to the side; instead, unbalanced aerodynamic forces cause the animal to pivot about a vertical axis (which probably runs through the centre of mass). Because of the difficulty of analysing this type of turn, caused by the high turning rates and overlapping wing images, the description presented above may not be complete.

The outstanding features of the yaw turn are that the outer forewing had a very high angle of attack on the downstroke and a nearly vertical upstroke, whereas the inner forewing had a high angle of attack during a very fast downstroke. The hindwing pattern is less clear, but the difference in horizontal positional angle suggests that fore-and-aft wing movements may be important.

The extremely high angles of attack, as well as the large changes in angle of attack during the yaw turns suggest that unsteady effects may be important. In addition to the 'flexion' mechanism, Ellington (1984) also pointed out that delaying the pronation at the beginning of the downstroke can enhance the effect of flexion. Because of the overlapping wing images, I could not determine whether flexion occurred in the turn described by Figs 6 and 7, but Fig. 6C does show a delay in pronation of the outer forewing. A dragonfly might take advantage of this effect to increase thrust on the outer wings. Negative thrust could be produced by the inner wings with appropriate flexion at the beginning of the upstroke, but such flexion was not apparent on this film sequence.

Comparison of the two types of turns

In all 73 sequences (many showing several turns), there is only one sequence that appears to involve both conventional and yaw turns simultaneously. I projected this sequence at a very slow frame rate (about $2\,\text{frames}\,\text{s}^{-1}$) and discovered that a bank was initiated as in conventional turns for a stroke, then there were two strokes of yaw turn, and then the bank angle again was increased in the conventional fashion. This suggests that the two types of turn cannot be used during the same stroke, but by being used in such rapid succession their effects can be almost simultaneous. It is obvious that these two types of turn involve different mechanisms: by definition, the conventional turn requires a banked attitude and pitching and yawing, while the yaw turn requires only yaw. The conventional turn is clearly the type of turn that Baker (1979b) had in mind when he argued that roll and yaw cannot be functionally separated during insect flight, but his argument apparently does not apply to yaw turns, especially in slow flight or near hovering.

Conventional and yaw turns are probably used under different circumstances. Forward speed requires rolling into a bank to prevent side-slipping, so the conventional turn should be used most in fast forward flight, especially when the dragonfly is not stimulated to face immediately to the side (see below). A dragonfly would move over a substantial distance (several body lengths) in this type of turn. The large amount of variation available suggests that dragonflies are capable of doing a large amount of adjusting to tailor this type of turn to their immediate requirements.

Because of the drag on the elongated abdomen, which increases with the square of the velocity, the yaw turn would be most effective at low flight speeds. Thus, the yaw

turn should be preferred during hovering and slow flight. Indeed, all films taken during hovering (parts of several free-flight sequences) depict yaw turns. This type of turn would also be very useful in situations where the dragonfly is stimulated to face a different direction suddenly, such as during territorial disputes or prey capture. Finally, this type of turn is probably used on take-off, when the perch does not face the desired direction of flight. The last suggestion is supported by several free-flight sequences which show yaw turns during the first few strokes after take-off. Yaw turns would not be very effective during fast flight, due to side-slipping and the large amount of asymmetrical drag on the abdomen.

In this study, I have concentrated on initiation of turns because that is when the unbalanced forces that produce turns should be greatest; it is also the least difficult phase for which to simulate natural conditions. When studying the fine details of wing movements during a manoeuvre, one should be aware that a given tethering system can only mimic some aspects of free flight. The most significance should be attached to the broader results; in this case, the presence of two distinct types of turns, and the general features of each type. Further studies of the details of wing kinematics will be necessary before a complete analysis of the aerodynamics of turning can be performed, particularly for yaw turns.

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