FURTHER OBSERVATIONS ON DIPTERAN FLIGHT: DETAILS OF THE MECHANISM

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Summary

1. We took high-intensity flash photographs of the wing base during tethered flight of Lucilia sericata. These show that the radial stop and the pleural wing process separate during the upper part of the wing beat and then mate together on the downstroke.

2. Using tungsten needle probes attached to wire strain gauges, we measured the movements of the parascutal shelf (PSS), of the lateral and dorsal scutum, and of the scutellum during tethered flight. We made a detailed study of the wing base sclerites and associated muscles in order to answer criticisms of our original model (Miyan & Ewing, 1985a,b).

3. The PSS rotates upwards about its hinge with the lateral scutum at the start of the downstroke.

4. The dorsal scutum and medial edge (at the hinge) of the PSS are held down, presumably as a result of dorsoventral muscle activity.

5. As the downstroke progresses, the whole of the PSS and dorsal scutum are lifted together suggesting the action of a locking mechanism.

6. At the bottom of the downstroke there is an opposite, downward rotation of the shelf about its hinge that follows the start of downward scutal movement at the beginning of the upstroke. This is followed by downward movement of the whole PSS and scutum.

7. Movements of the lateral scutum exactly follow scutellar and lateral PSS movements and are probably dictated by the articulation.

8. Scanning electron micrographs illustrate the probable components of the wing base–PSS locking mechanism. Rotation of the first axillary sclerite, brought about by the rising scutellar lever arm, results in mating of its medial arm with a recess in the PSS. This prevents further rotation of the PSS which is now held at two points by the sclerite and is lifted by further movement of the lever.

9. There is no evidence that the third axillary muscles act as wing pronators. Scanning electron micrographs show a mechanism that maintains the line of action of the muscles on the posterior edge of the wing.

Key words: Diptera, flight, mechanism.
Introduction

We published two papers (Miyan & Ewing, 1985a,b) which proposed a model for dipteran flight that did not incorporate the thoracic ‘click’ mechanism first put forward by Boettiger & Furshpan in 1952. Pfau (1987) defends the original ‘click’ mechanism with morphological observations and further analysis of CCl4-anæsthetized flies. Modifying the original model, Pfau proposes direct muscular control over wing pronation–supination at the top and bottom of the wing beat in cooperation with the wing base mechanism. Ennos (1987) revives the idea of whole thoracic distortions originally proposed by Chabrier (1822, reviewed by Pringle, 1957), but incorporating the radial stop mechanism described in our model. Ennos (1987) proposes that the indirect flight muscles act to distort the dorsal thorax and so produce the horizontal and vertical movements of the lateral scutum that cause the wing to beat about the basal sclerites. In agreement with us, Ennos finds that contact between the radial stop and pleural wing process forms a limit for the downstroke past which the wing can bend. Cyclical changes in angle of attack are thought to be largely passive and determined by torsional compliance and basal weakenings of the radial wing vein with limits set by mechanical stops.

Criticisms of our model

The relationship between the radial stop (RS) and pleural wing process (PWP)

Ennos describes essentially the same relationship as that described by us, but Pfau states that this is incorrect. He maintains that the RS contacts the PWP at the top of the upstroke only momentarily in order to allow the third axillary muscles to pronate the wings for the downstroke. Under certain conditions, in which the pleurosternal and tergopleural muscles are not strongly contracted, he finds that the two structures do not make contact at all, the RS passing frontolaterally of the PWP. Pfau (1987) also argues that for our model to operate there must be a switch in wing-pivot from the ventral joint of the second axillary sclerite (Ax 2) to the dorsal crest of the PWP and that this is impossible because the joint is immovable and, furthermore, that any such mechanism should be observed as marked velocity changes in the wing beat itself.

The relationship between the first axillary sclerite (Ax 1), the parascutal shelf (PSS) and the scutum

Miyan & Ewing (1985a,b) give details of the structural elements. Pfau and Ennos both failed to find a locking of Ax 1 onto the PSS during the downstroke and consequently no direct lifting of the scutum or stretching of the dorsoventral muscles (DVM) as we described.

The role of the third axillary muscles

Pfau maintains that these muscles are responsible for wing pronation at the beginning of the downstroke and that the tendon of these muscles is actually stretched during the downstroke. He claims also that the external manifestation of
Fig. 1. High-intensity flash photograph of *Lucilia sericata* in tethered flight with the wing caught at the top of the upstroke (note that the wing is supinated). There is a clear separation of the radial stop (RS) and pleural wing process (PWP) highlighted in the tracing (B). For details of the other structures see Miyan & Ewing (1985b). Scale bar, 100 μm.

A ‘click’ is concealed by the effects of aerodynamic, muscular and elastic forces acting on the wing. He has proposed muscular control of pronation and supination, implying wing-synchronous activity of certain direct flight muscles. Ennos proposes no muscular control at all, believing instead that the pronation–supination characteristics of the wing beat are purely a function of inertial forces acting upon the longitudinally flexible wing, following the removal of aerodynamic forces at the end of each half stroke.

In our recent studies we have sought to clarify these three issues and present here our findings, which substantially support our original model.

**Materials and methods**

Morphological examinations were made of specimens of *Lucilia sericata* (Meigen), *Sarcophaga argyrostoma* (R.-D.) and *Glossina morsitans* (Westwood). Freshly killed specimens were used to observe the effects of wing and thoracic manipulations on wing base structures and for dissections of the wing base. Some
Fig. 2
Dipteran flight

233

specimens were fixed in phosphate-buffered glutaraldehyde (2.5%), rinsed in buffer, dissected and critical point dried for scanning electron microscopy in a Phillips 505 scanning electron microscope. All the experiments involving tethered flight were performed on specimens of *Lucilia sericata*, which is the best flier under these conditions. To examine and measure the relative movements of the various wing base structures, it is essential to ensure that there is no general body movement in space. The only attachment points we found to meet this criterion were the pronotum and the sternum; in our experiments, therefore, we routinely glued flies to a tungsten wire positioned on the sternum between the legs.

Using wire strain gauges and amplifiers (EPIL260A) connected to tungsten needle probes, we were able to perform two sets of experiments. (1) We monitored the movements of different points of the thorax and wing base structures. Recordings were only accepted for analysis if the needle tips remained located at a particular point at the start and end of flight. (2) We studied the functional relationship of the structures in flight. We used recordings of thoracic vibrations and the variable delay function of a Digitimer DS9A stimulator to trigger a high-intensity strobe light (EMI type 4 stroboscope) at any point in the wing beat arc. This allowed a detailed study of the functional relationships of the structures. To photograph events at the wing base we employed a point-source xenon arc bulb (Thorn FA5) driven at 2.5 kV by a high-voltage power unit (Leland Instruments Ltd) fed through a 15 µF photoflash condenser for single flashes. A 340 mm concave reflector was used to focus the light to a 1 cm spot with its centre over the wing base of the fly. Photographs were taken with an Olympus OM-2 camera fitted with bellows and a Zuiko MC macro 1:3.5 (f = 20 mm) lens and using Ilford HP-5 film force-processed to 800 ASA. Although these photographs were

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Fig. 2. Thorax of *Sarcophaga* with wings, sclerites and pleural wing process (PWP) removed to show the sites from which transducer measurements were taken. The traces show recordings from the medial (mPSS), and lateral (IPSS) edges of the parascutal shelf (PSS) during normal (upper traces) and low-amplitude (lower traces) wing beats, the dorsal scutum above the wing base, and the lateral scutum. The bottom trace in each recording is taken from the posterior end of the scutellum (Sc) as part of the scutellar lever (SL). The time mark in each trace is 2 ms. Arrows show upward movement direction for all the records except for the lateral scutum where the arrow shows outward movement. Notice the delay between upward movement of the IPSS and upward movement of both the mPSS and dorsal scutum. This indicates a rotation of the PSS upwards around its medial hinge with the scutum but only for a small angle, after which the whole shelf along with the dorsal scutum rises. The marked phase difference between lifting of the lateral PSS and downward movement of the scutellum is not seen in low-amplitude beats and suggests a bending of the scutellar lever at higher amplitudes as the wing lags behind basal movements. There is a near perfect synchrony between lateral scutal movements and movements of the lever. Also, it can be seen that although the amplitude of scutellar movement is decreasing across the record, lateral scutal movements remain at constant amplitude. This suggests a mechanical limit to lateral scutal movements which is further evidence for a locking of the PSS, preventing lateral movements past the lock and lifting the whole scutum.
difficult to obtain, the events are easily observed with any laboratory stroboscope and stereomicroscope.

Results

What are the relative movements of the pleural wing process and radial stop?

The answer to this question is crucial in testing the validity of the modified click mechanism proposed by Pfau (1973, 1987) or the models of Miyan & Ewing (1985a,b) and Ennos (1987). Fig. 1 illustrates the relationship between the RS and PWP during the upper part of the wing beat. As the wing rises we observed that the distal end of the RS was located in one or other of the recesses of the PWP, and
was bent at its proximal end to be nearly horizontal, pointing posteriorly. Subsequently, above the wing's horizontal position, the RS straightened to point ventrally, normal to the radial vein. The events at the upper end of the wing beat were found to depend upon the amplitude of the beat. In beats of less than 90° in amplitude, the RS did not separate from the pleural crest recess as it reached the top of wing movement. In any wing beat that exceeded a 90° amplitude, which is typical of normal flight, there was a clear vertical separation of the two structures (Fig. 1). They mated during the downstroke, a few degrees above the horizontal position of the wing. Mating with one or other of the recesses of the PWP was accomplished by fore and aft movements of the pleural plate effected by the tergopleural muscle (Pfau, 1973). This is the only muscle attached to the dorsal end of the pleural plate and so has the requisite geometric relationship. Thus, its function remains the same as that proposed by us but it acts to move the pleural plate (as described by Pfau, 1973, 1987) and not the scutum, its distal attachment.

We observed no beat in which the RS and PWP did not mate during the downstroke. Surgically removing the radial stop from one wing produced no effect on events in the upper half of the wing beat, but the lower part was affected. There appeared to be a loss of amplitude control, the wing was observed to 'jitter' between different end positions of the downstroke and all beats fell into the large-amplitude class. The contralateral wing was unaffected.

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**Fig. 3.** Movements of the various wing base components plotted against a common trace of scutellar movement (Sc). Vertical movements of the lateral (IPSS) and medial (mPSS) edges of the parascutal shelf (PSS) during low-amplitude wing beating (A). A relative rotation is seen between the IPSS and mPSS at the top and bottom of wing movement. There is an upward rotation at the start of the downstroke and a downward rotation at the start of the upstroke. During the rest of each stroke, the shelf moves fixed in a particular attitude suggesting a locking mechanism. The lateral edge of the PSS (IPSS) moves in synchrony with the scutellum (Sc), as would be expected from the tight articulation between the end of the lever, the first axillary sclerite (Ax 1) and the lateral PSS. There are also synchronous movements of the lateral scutum (B). A clear indication of a locking mechanism is seen in records of the PSS during high-amplitude beats (C). As the lateral edge of the PSS is lifted (after line 2) there is a short period of deceleration (between lines 3 and 4) which is probably the point at which the lock of Ax 1 is engaged. It is only after locking that the medial edge is seen to be lifted (line 4). It is also at this point that the dorsal scutum is observed to rise (line 4 in B). The striking phase difference between movements of the lateral PSS (IPSS in C) and scutellum (Sc) at high amplitudes contrasts with the near synchrony at low amplitudes (A). This can be explained by the strains resulting from the larger bending forces imposed on the wing, a consequent lag in wing movements relative to wing base events, and a bending of the scutellar lever. Such a bending does occur during high-amplitude beating (unpublished observation). It can be seen that, whereas the lateral scutum moves in synchrony with scutellar movements (B), movements of the dorsal scutum (B), which is under constant downward force due to the action of the fibrillar muscles, appear to depend upon the action of the locking mechanism of Ax 1 onto the PSS (compare lines 3 and 4). Arrow indicates upward movement of each component except for the lateral scutum where it indicates outward movement.
What is the movement of the parascutal shelf during the wingbeat?

To validate either our model or that of Ennos (1987) it is necessary to establish the relative movements of various thoracic elements. Pfau and Ennos both describe an upward rotation of the PSS contrary to that predicted by the locking of
Ax 1 onto the PSS. Pfau incorporates this movement into a bistable system, while Ennos argues that the movement is a localized distortion of the scutum producing the lateromedial and dorsoventral forces that move the wings via the sclerites. In our model, we proposed that the dorsal longitudinal muscles (DLMs) actuate the scutellar lever and that all movements at the wing base are a direct result of the forces applied by the lever through Ax 1 and its articulation with the other structures of the joint.

It is clear from our recordings (Figs 2, 3) that the PSS does rotate in the direction observed by Ennos and Pfau but that this rotation is limited by the locking of Ax 1 onto the shelf. It is also apparent that the dorsal scutum is probably under constant downward force as it was not observed to rise until after the locking of Ax 1 onto the PSS. This ensured the observed upward rotation of the PSS as its medial edge was held down, while its lateral edge was raised by Ax 1. It is significant that lateromedial movements of the lateral scutum (Figs 2, 3) were exactly in phase with movements of the scutellar lever and lateral PSS, suggesting that this component of movement was largely dictated by the articulation and was not itself the driving force for wing movement. Once Ax 1 has locked onto the lateral edge of the PSS, however, all three components – the lateral and medial edges of the PSS, and the dorsal scutum – were observed to rise together. At the bottom of the downstroke, there was a rotation of the PSS in the opposite direction following the start of downward movement of the dorsal scutum (Fig. 3, line 6). This was followed by a locking of the shelf that was seen as movement of both lateral and medial PSS together with the dorsal scutum. Scanning electron micrographs show a relationship between the PSS and Ax 1 that clearly allows for the operation of such a locking system (Fig. 4). This arrangement has the advantage of a positive stretching of the DVMs and a consequent positive linkage for the upstroke and stretching of the DLMs.

Is pronation active or passive?

Our present observations do not answer this point. However, it is clear that as there was separation of the PWP and RS at the top of the wing beat (Fig. 1), contact between them cannot be implicated in wing pronation as proposed by Pfau.
(1987). Furthermore, the third axillary muscles do not have the requisite geometry to act as pronators of the wings, since their tendons, stretched on the upstroke, are attached to the posterior edge of the wing and their line of action is maintained by the cuticular stop illustrated in Fig. 4C.

Discussion

Any credible model must explain the observed thoracic and wing movements and incorporate those aspects of active control within the fly’s central nervous system, as well as those occurring as an automatic consequence of the articulation. It is puzzling that kinematic analysis of dipteran flight has failed to demonstrate the action of a click mechanism (Ellington, 1984; Miyan & Ewing, 1985a). Of the various explanations proposed to account for this, the most widely accepted is the dampening effects of inertial and aerodynamic forces acting on the wing itself, together with elastic strain forces within the flight muscles (see Alexander & Bennet-Clark, 1977, for an analysis). In the absence of a click mechanism, such forces would produce a simple harmonic motion of the wings; the effect of a click is said to reduce the forces over the middle section of the stroke and produce the constant velocity observed together with the abrupt direction changes at each extreme of wing movement (Alexander & Bennet-Clark, 1977). However, this analysis ignores the presence of a radial stop which should have dramatic consequences for the system. Moreover, on the upstroke the wing is feathered to slice through the air, reducing drag/wind resistance which should reveal any bistability that might be operating, yet none is observed. To date there has been no direct measurement of the movements of the wing base components. Whereas movements of the wings may be masked by inertial and aerodynamic forces etc., there should be some indication of a bistable system at the wing base. The results presented in this study show no such movements, indicating instead an operation consistent with the mechanism proposed by Miyan & Ewing (1985a,b). Fig. 5 illustrates the differences between the observed movements of the PSS (Fig. 5A) and those expected according to the classical click mechanism (Fig. 5C). The

Fig. 5. Comparison of observed movements (Aii) of the lateral (LPSS) and medial (mPSS) edges of the parascutal shelf (PSS) with those expected from the click mechanism (Ci) plotted against recorded movements of the scutellum (B). Notice that there are relative movements between the LPSS and mPSS only at the top and bottom of the wing beat which contrast with the continuous changes, and the 180° phase difference, expected from the bistable click model. The observed movements support the model illustrated in Ai which incorporates a locking mechanism of the first axillary sclerite onto the PSS and provides a positive coupling between the fibrillar muscles and wing movements. Cii illustrates the click mechanism and its ‘toggle switch’ bistability. Both Ai and Cii show proposed arrangements at the points in the downstroke indicated by the dotted lines. Note that movements of the scutellum are in the opposite direction to movements of the lever at the wing base. The point of action of the lever is indicated by the arrow in the middle drawing of both Ai and Cii. Arrows numbered 1 and 2 in the third drawing indicate the medial and lateral edges of the PSS, respectively.
observed movements cannot be reconciled with the click mechanism but do fit with the operation of a locking mechanism acting upon the PSS.

There is now convincing morphological and mechanical evidence for the existence of a locking mechanism involving Ax1 and the PSS. There is no requirement for any drastic changes in articulation and there is a compelling argument for elastic energy storage, consequent on the wing bending, for release at the start of the upstroke. The release of elastic energy stored on the downstroke is evident in records of the movements of the PSS, particularly during high-amplitude wing beats (Fig. 3C), and occurs just before the start of the upstroke. Because of the positive linkage between the two sets of fibrillar muscles, there will be a greater contribution of their elastic/strain forces, and their active contraction forces, to movements of the wing base. Previous models have relied upon thoracic distortions to stretch the DLMs and DVMs alternately, whereas the mechanism proposed by us involves a positive linkage between the two sets of fibrillar muscles through the wing base articulation.

Two possible mechanisms could be operating to cause cyclical wing twisting: (1) passive effects due to inertial and aerodynamic forces acting upon wings with compliant bases and flexible veins (e.g. Ennos, 1987) and (2) automatic cyclical changes brought about by the relative movements of wing base sclerites during the wing beat (e.g. Boettiger & Furshpan, 1952; Pringle, 1957; Miyan & Ewing, 1985b). Both mechanisms allow for tonic changes in wing beat characteristics by the action of the direct, non-fibrillar muscles, although these are likely to be more profound in the latter case. It is probable that both mechanisms operate. The wings do indeed have torsional compliance and basal flexion lines (e.g. Wootton, 1981) and there is also a clear relationship between Ax4 and Ax3 that will result in cyclical effects upon the posterior edge of the wing causing changes in pronation-supination of the base (Miyan & Ewing, 1985b). The relative importance of the two mechanisms will only become clear with further detailed investigations.

We must agree with Pfau (1987) that the separation and mating of the radial stop and pleural wing process in every wing beat demand an incredible accuracy of the mechanical and muscular systems involved. The fact that this does occur can only increase our admiration of the system and stimulate continued efforts to understand its control. It is our opinion that a proper understanding will only result from a physiological study of the intrinsic controls operating during flight. Such a study has long been overdue although a few preliminary reports have been published (e.g. Nachtigall & Wilson, 1967; Heide, 1971, 1975, 1983). We are now beginning to tackle this problem and are developing a preparation with which to examine the internal organization of the dipteran flight motor system.

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