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THE LOCUST TEGULA: SIGNIFICANCE FOR FLIGHT RHYTHM GENERATION, WING MOVEMENT CONTROL AND AERODYNAMIC FORCE PRODUCTION

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Summary

The tegula, a complex sense organ associated with the wing base of the locust, plays an important role in the generation of the flight motor pattern. Here its function in the control of wing movement and aerodynamic force production is described.

The vertical component of forewing movement was monitored while recording intracellularly from flight motoneurones during stationary flight. First, in accordance with previous electrophysiological results, stimulation of hindwing tegula afferents was found to reset the wingstroke to the elevation phase in a well-coordinated manner. Second, recordings made before and after removal of fore- and hindwing tegulae were compared. This comparison demonstrated that the delayed onset of elevator motoneurone activity caused by tegula removal is accompanied by a corresponding delay in the upstroke movement of the wings.

The consequences of this delayed upstroke for aerodynamic force production were investigated by monitoring wing movements and lift generation simultaneously. A marked decrease in net lift generation was observed following tegula removal. Recordings of wing pronation indicate that this decrease in lift is primarily due to the delayed upstroke movement – that is, to a delay of the wings near the aerodynamically unfavourable downstroke position.

It is concluded that the tegula of the locust hindwing signals to the nervous system the impending completion of the wing downstroke and allows initiation of the upstroke movement immediately after the wings have reached the lower reversal point of the wingstroke. The functional significance of tegula feedback and central rhythm generation for locust flight control are discussed.

Introduction

The role of sensory feedback in the control of rhythmic motor acts varies greatly, depending on the requirements of the behaviour under consideration. One extreme of the spectrum is represented by centrally generated motor programmes that are not modulated by signals of sensory origin (e.g. swimming of the pelagic pteropod *Clione limacina*, Arshavsky *et al.* 1985*a*,*b*). At the other end of the spectrum, signals from sense organs

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provide both timing and shaping cues for the specific movement and are essential for the generation of rhythmicity itself (e.g. in walking stick insects; Bässler and Wegner, 1983; Bässler, 1993). More common than these extremes, however, are situations in which central circuits capable of rhythm generation interact with sensory feedback loops to generate a motor pattern. Locust flight is a well-studied example of such an interaction (Altman, 1983; Wendler, 1985). Central rhythm-generating networks and numerous sense organs, in particular proprioceptors of the wing base, have been shown to contribute to the generation of the flight motor command (e.g. Wendler, 1974, 1985; Reye and Pearson, 1987, 1988; Pearson and Wolf, 1988). The flight motor command is further modified by exteroceptive inputs, for instance during compensatory steering (Reichert and Rowell, 1985; Hensler, 1988), an issue that will not be addressed here.

The tegula, a complex receptor organ of the locust wing base, has proved to be of particular importance for flight pattern generation (Neumann *et al.* 1983; Wolf and Pearson, 1988). This sensory structure inserts on the soft cuticle associated with the anterior part of the wing hinge and consists of a knob-shaped hair field and internal chordotonal sensillae (Kutsch *et al.* 1980). During flight, the tegula is excited by the downstroke movement of the wing. The afferent receptor axons discharge a few milliseconds after the wing has passed the upper reversal point and may remain active through much of the downstroke movement (Neumann, 1985). A discharge of the tegula afferents, in turn, initiates a burst of action potentials in the wing elevator motoneurones. This activation of elevator motoneurones (and the concomitant suppression of depressors) by tegula input occurs significantly earlier than the discharge of elevator motoneurones driven by the central oscillator of a dissected ventral cord preparation – or by the otherwise intact flight system of a locust with excised tegulae. Tegula input thus overrides timing cues from the central oscillator. Strong parallel projections of tegula afferents onto *all* known interneurones of the central oscillator, together with the tegula afferents' ability to elicit plateau potentials in elevator interneurones, may explain this effect (Ramirez and Pearson, 1991*a*). It is apparently by virtue of this immediate access to central oscillator components that the tegula resets the oscillator in every wingbeat cycle if and when it is stimulated, restarting the rhythm with an elevator discharge (see Fig. 1; reviewed by Wolf, 1991). I describe the properties of the hindwing tegulae only, because the organs of the forewings are of minor, if any, importance in the context considered here (Büschges *et al.* 1992*a*,*b*). This means that the hindwing tegulae, by exerting their influence on flight pattern generation, contribute to the control of both hind- and forewing movements.

Despite our knowledge about the interaction of hindwing tegula input with central rhythm-generating networks and its role in flight pattern generation, the ultimate function of the tegula remains unclear: what is the role of this proprioceptive organ in the control of wing movement and the resulting generation of aerodynamic force during flight? To address this question, the movement of the forewings and the production of lift, together with muscle or motoneurone activity, were monitored during tethered flight. A comparison of wing movements in locusts before and after removal of all tegulae revealed that the upstroke of the wings is delayed with regard to the preceding downstroke by about 13ms as a result of proprioceptor ablation. This corresponds to the observation that tegula input initiates elevator motoneurone activity and overrides the timing of the central flight oscillator. Stimulation of hindwing tegula afferents was able to produce a coordinated resetting of the wingstroke to the elevation phase, demonstrating the physiological action of the tegula input.

Tegula removal substantially affected net lift generation. Analysis of the angular setting of the wing and the lift force generated in the course of the wingbeat cycle indicated that this is due to the delayed upstroke movement. The wings are halted near the lower reversal point of the wing stroke – an aerodynamically unfavourable attitude which may result in the generation of negative lift and, probably, drag (Nachtigall, 1981). The following delayed upstroke movement is more rapid and apparently adds to the generation of negative lift. In addition, the prolonged stay of both fore- and hindwings near the downstroke position may disrupt their normal aerodynamic interaction.

Materials and methods

Animals

Adult male and female *Locusta migratoria* (L.), between 3 and 4 weeks after the imaginal moult, were used for the experiments. Animals showing good flight performance were selected from a crowded breeding colony maintained at the University of Konstanz. Data for the present investigation were obtained from 32 individuals.

Recording technique

Wing movement

Up and down movements of one forewing were recorded using an optoelectronic camera adapted from that of von Helversen and Elsner (1977). A piece of reflective (Scotch light) tape was rolled to form a small (approximately 1mm by 1mm) cylinder and glued to the anterior margin of one forewing with the axis of the cylinder being parallel to the wing margin. The Scotch light marker was both illuminated and monitored *via* a semi-reflecting mirror in front of the animal. The cylindrical shape of the reflective foil ensured that part of its surface was always roughly perpendicular to the optoelectronic camera, allowing its image to be projected onto a position-sensitive photodiode. Signals from the photodiode were processed by a custom-made amplifier (U. Koch, Kaiserslautern). Only the vertical component of wing movement was monitored. Wing position traces in the figures therefore represent a sine function of the wing's upstroke angle, the horizontal wing position corresponding to 0˚. Right and left wing movements may be regarded as symmetrical for the purpose of the present investigation because, first, the locusts were illuminated from an anterior and slightly dorsal direction (except for photogrammetry) and did not show overt steering behaviour during the experiments and, second, changes in wing movement associated with steering activity (Thüring, 1986; Waldmann and Zarnack, 1988; Zarnack, 1988; see review by Rowell, 1988) are small compared with the changes in overall motor pattern considered here.

Wing pronation

Angular settings of the fore- and hindwings were observed – together with the vertical components of their movements – using photogrammetry. A detailed description of the procedure and the evaluation of data is given by Wolf (1990). The animal's eyes and ocelli were lacquered in these experiments to avoid steering towards the stroboscope light. A marker line was drawn across the upper and lower surface of the forewing and across the central field (delimited by the subcostal and anal vein) of the hindwing. The marker was monitored at 2.5ms intervals with a stroboscope light (see Fig. 8).

Lift

Lift force produced by locusts during stationary flight was recorded using a laser flight balance constructed according to Heinzel (1989; see also Dombrowski and Wendler, 1989). The animal was glued to the end of a horizontal stainless-steel rod (length 8cm, diameter 2.5mm) mounted on a solid holder. The rod acted as a spring and was bent up or down by the lift component of the aerodynamic forces produced during flight. Movements of the rod were in the micrometre range and were monitored by a laser beam. The laser beam was focused from below onto a small piece of mirror glass attached horizontally to the lower surface of the supporting rod, under the locust's centre of gravity. This mirror reflected the beam onto a distant position-sensitive photodiode. The small movements of the rod were thus amplified by the long lever arm of the laser beam and were recorded by the photodiode. The flight balance was calibrated using the precision weights of a pharmacist's balance. The resonant frequency of the balance arrangement was about 230Hz, i.e. more than 10 times the locust wingbeat frequency. A small piece of sheet metal attached to the end of the supporting rod was immersed in silicone oil of high viscosity. By varying the depth of the oil, damping was adjusted to a value just below the aperiodic limit. This allowed lift generation to be recorded over the course of the wingbeat cycle. Fluctuations in the force recording resulting from minor resonant oscillations were eliminated by averaging (see Figs 5, 6).

These lift recordings represent the sum of aerodynamic forces generated by wing movement and of inertial forces produced by the deceleration and acceleration of the wings near the reversal points. A correct measure of aerodynamic net lift is obtained by integrating the forces generated during a wingbeat cycle since the inertial forces cancel out in the course of one cycle of steady flight (see Fig. 7; e.g. Zarnack, 1983). Only qualitative analysis is possible with regard to phase-related effects since the contribution of inertial forces cannot be determined for shorter sections of the wingbeat cycle (see Results).

Electromyograms

Electromyogram (EMG) wires (stainless steel, 20 μm in diameter, insulated except for the cut end) were inserted into the sternal attachment sites of forewing flight muscles 83, 84 or 97 (tergosternals and first basalar muscles; numbering according to Snodgrass, 1929) in a bipolar configuration (Pearson and Wolf, 1987).

Intracellular motoneurone recordings

Intracellular recordings from flight motoneurones were made according to Wolf and Pearson (1987*a*). The locust, in an inverted position, was glued to a fork-shaped holder by its thoracic sternites. The thoracic nervous system was exposed by removing a small flap of sternal cuticle, the underlying trachea and the salivary glands. Supporting the meso- or metathoracic ganglion with a steel spoon allowed intracellular recordings to be made from motoneurone somata during tethered flight.

Stimulation of tegula afferents

The dissection for intracellular motoneurone recordings also exposed nerves 1 of the pterothoracic ganglia and their proximal branches. Bipolar hook electrodes insulated with Vaseline were placed bilaterally on nerves 1C (Campbell, 1961) of the metathoracic ganglion for electrial stimulation of the afferent axons arising from the hindwing tegulae. Trains of four voltage pulses, 0.1ms in duration, were delivered at a repetition rate of 200Hz to mimic a natural discharge of the receptor organs. The stimulus-related occurrence of excitatory postsynaptic potentials in elevator motoneurones was noted, and the stimulus voltage for reset experiments was adjusted to 1.3 times the threshold value necessary for eliciting synaptic potentials in the ipsilateral motoneurones (Pearson and Wolf, 1988).

Experimental procedure

For intracellular recording of motoneurone activity, the legs of the animal were severed (Wolf and Pearson, 1987*b*). Locusts used for photogrammetry experiments and those flown on the flight balance were intact; however, legs were later removed from some individuals to examine the possible effects on the flight pattern. No such effects were found. Flight was elicited either by removing a small styrofoam ball held by the locust's tarsi or by directing a wind stream (approximately $3\,\mathrm{m\,s^{-1}}$) onto the animal's head. Measurements were made after the wind stimulus had been terminated and the locust had settled into stable flight. Although overall lift production was smaller in this situation (compare Gewecke, 1975), locusts were flown in still air because both cycle-to-cycle and individual variability were noticeably reduced (Wolf and Pearson, 1987*b*; Pearson and Wolf, 1989) compared with locusts flown in a wind tunnel. Segments of flight sequences in which wingbeat frequency was low, i.e. between approximately 8 and 15Hz, were preferentially recorded in intact locusts. This was necessary to provide data for a comparison based on matching wingbeat frequencies, because flight sequences were short and wingbeat frequency rarely exceeded 15Hz after tegula removal. Only hindwing tegula afferents were stimulated for reset experiments (see Fig. 1; Wolf and Pearson, 1988; Büschges *et al.* 1992*a,b*) whereas the tegulae of all four wings were removed in the remaining experiments.

Evaluation of data

Electrophysiological data, wing position recordings and signals from the flight balance were stored on magnetic tape (Racal Store 4 DS) for later display on a chart recorder (Gould ES 1000). Wingbeat period and the intervals between upstroke and downstroke were determined on a digitizing oscilloscope (Tektronix 5223). Signal-averaging of wing position and lift recordings was performed on a combined averager/oscillosope (Gould 1425). The positive lift impulse associated with the downstroke and the negative impulse related to the upstroke of the wings were calculated by digitizing averaged curves of flight balance signals (see Fig. 6) on a digitizing pad (Hewlett Packard 9874A with computing facility 9000/226). For statistical analyses, data from the same individual recorded before and after removal of all tegulae were compared using two-tailed Student's *t*-tests.

Results

Forewing movement

The tegula organs of the hindwing play a specific role in the production of the locust flight pattern. Recordings from individual motoneurones have demonstrated that a discharge of the tegula afferents initiates a depolarization in wing elevator motoneurones and is able to reset the flight rhythm to the elevator phase of the wingbeat cycle (Wolf and Pearson, 1988). Fig. 1A,B demonstrate that stimulation of the hindwing tegula afferents leads to well-coordinated resetting of the entire flight motor. The electrical stimulus (bottom trace in Fig. 1A) not only elicits a depolarization in the recorded elevator motoneurone (supplying the metathoracic anterior tergocoxal muscle; Snodgrass, 1929) but also affects the overall movement of the wing, which is controlled by nine main stroke muscles. If, for instance, the stimulus takes effect during the downstroke movement (Fig. 1A), stroke velocity is first decelerated and then reversed into a premature upstroke movement. The initial deceleration is presumably caused by the rapid inhibition of existing depressor activity (note the missing depressor discharge after the second stimulus train in the EMG of Fig. 1A; Pearson and Ramirez, 1990), whereas the inversion of stroke direction is a result of the activation of elevator inter- and motoneurones (Pearson and Wolf, 1988; Wolf and Pearson, 1989; Ramirez and Pearson, 1991*a*). The smooth transition

Fig. 1. Reset of the flight rhythm by hindwing tegula input. (A) A section of a flight episode recorded in a semi-intact locust preparation during stationary flight. Forewing position (top trace), elevator motoneurone activity (second trace, intracellular soma recording) and flight muscle discharge (third trace, EMG of muscles 97 and 83, depressor discharges marked by dots) were monitored. The two stimulus trains delivered bilaterally to the hindwing tegula afferents (bottom trace) reset the flight rhythm to the elevator phase of the wingbeat cycle. (B) Wing position records (top trace) from four consecutive stimulus presentations are superimposed with regard to the electrical stimulus (bottom trace; the reference point for the superposition is indicated by the arrowhead). Stimulus trains were delivered to the hindwing tegula afferents at arbitrary phases of the wingbeat cycle, but the resetting leads to close matching of the superimposed traces after a latency of 50–65ms. (C) The connectivity pattern of tegula afferents with interneurones of the flight oscillator circuitry offers an explanation of the reset effected of hindwing tegula stimulation. The diagram summarizes data presented by Pearson and Wolf (1988), Wolf and Pearson (1989) and Büschges *et al.* (1992*a*). Filled circles represent inhibitory interneurones. Only those interneurones of the pattern-generating circuitry ('CPG') proposed by Robertson and Pearson (1983, 1984, 1985*a*,*b*) are indicated, which are assumed to make direct synaptic connections to motoneurones. As an exception, interneurone 301 is included because, together with neurone 501, it is thought to form the core of the central part of the flight pattern generator. Not all interneurones are essential elements of the pattern generator; for instance, they are not all able to reset the flight rhythm. The dashed lines enclose neurones that are active in the fictive wingbeat rhythm of deafferented locusts. *E*, wing elevation; *D*, wing depression.

of the wing movement during the reset and its subsequent undisturbed continuation (Fig. 1A,B) indicate that all flight muscles involved in the reset are coordinated and that the entire rhythm-generating network is therefore affected by the stimulus.

Hindwing tegula afferents apparently reset the flight rhythm by virtue of their strong parallel influence on the central interneurones of the flight pattern generator. Fig. 1C

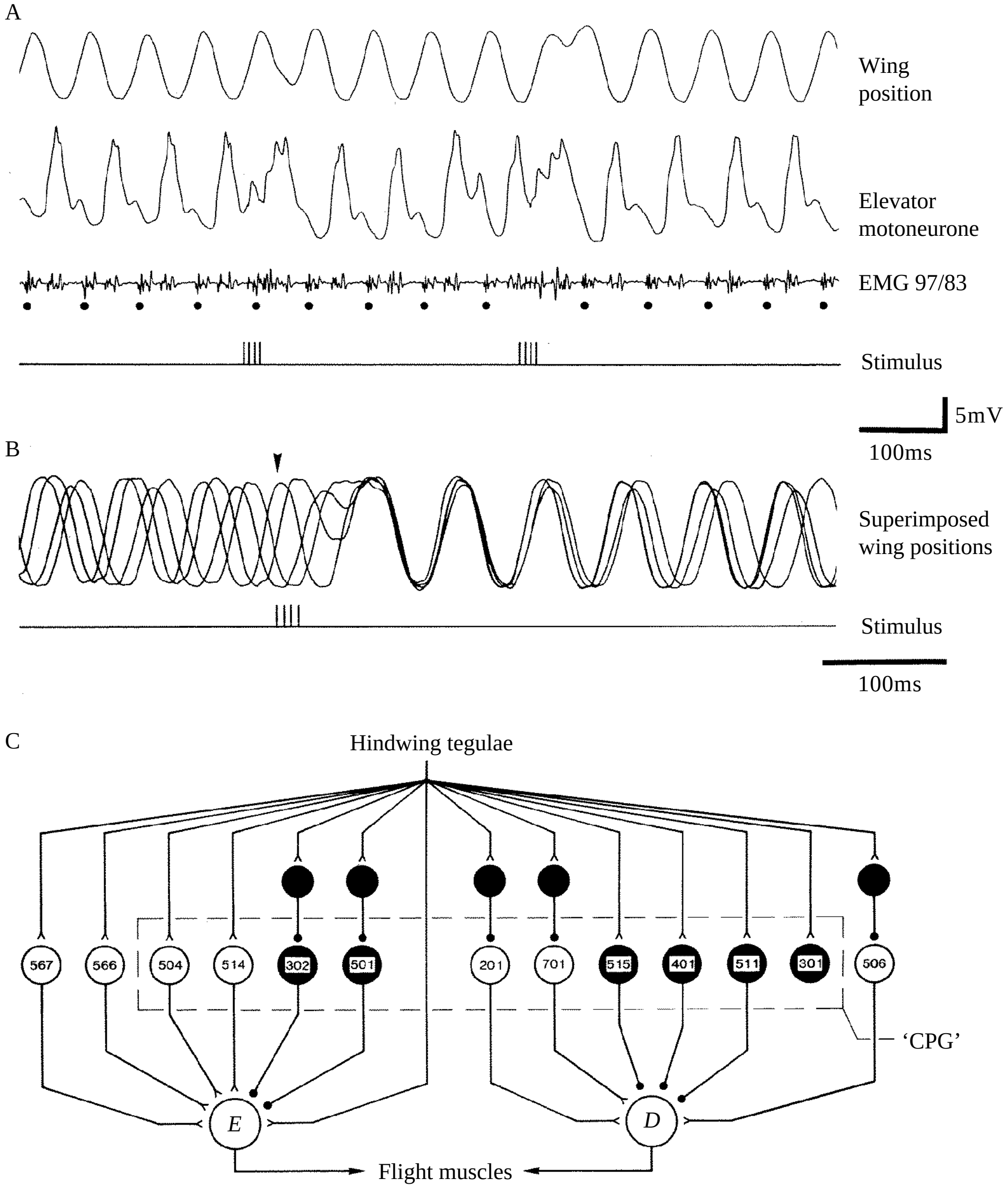

Fig. 1

summarizes the results of previous studies which revealed a very consistent pattern of efficient synaptic connections between hindwing tegula afferents and flight interneurones (Pearson and Wolf, 1988; Wolf and Pearson, 1989; Büschges *et al.* 1992*a*,*b*): tegula afferents produce a net excitation of elevator motoneurones, either directly (motoneurones in the same hemiganglion), by excitation of excitatory premotor interneurones, or by inhibition of inhibitory premotor interneurones. The reverse pattern of connectivity holds for the depressor motoneurones. Excitation by the tegula afferents elicits plateau potentials in several elevator interneurones and, in this way, initiates the elevator phase of the wingbeat cycle (Ramirez and Pearson, 1991*a*). This connectivity pattern applies to the interneurones of the central oscillator circuitry proposed by Robertson and Pearson (1983, 1984, 1985*a*,*b*), particularly to interneurones 301 and 501, but also to all other interneurones examined so far that are active in the (fictive) wingbeat rhythm observed in deafferented preparations (dashed line in Fig. 1C). It also applies to interneurones that contribute to pattern generation only in the intact animal (Wolf and Pearson, 1989; Wolf, 1991).

During normal flight, the hindwing tegula discharge is responsible for the generation of a characteristic, early depolarization of wing elevator motoneurones. Removal of tegula input thus delays the onset of elevator activity (Pearson and Wolf, 1988; Wolf and Pearson, 1988). The vertical component of forewing movement was recorded, together with the activity in flight muscles and motoneurones, to detect possible changes in movement pattern resulting from these alterations in motoneurone activity.

In Fig. 2, traces recorded at different wingbeat frequencies are superimposed to illustrate the characteristics of the movement patterns recorded in intact animals (Fig. 2A,B) and after removal of the tegula of both fore- and hindwings (Fig. 2C). The middle of the downstroke was used as a reference point for superposition. For the purpose of the following description, the cycle of wing movement is divided very roughly into four phases: downstroke, upstroke and the transition periods near the reversal points. These phases are not clearly delimited, of course, and during the transition from up- to downstroke and *vice versa* the wings do not remain motionless near the reversal points. Instead, these are the phases of deceleration and acceleration and of rotation of the wing from the supinated upstroke into the pronated downstroke position, and *vice versa* (see Fig. 8; Weis-Fogh, 1956; Pfau and Nachtigall, 1981). Depending on wingbeat frequency and the particular phase, one of these phases may account for 10ms to more than 50ms of the wingbeat period (see below).

In the intact animal (Fig. 2A,B), changes in wingbeat frequency were brought about mainly by changes in the length of time the wings dwelt near the upstroke position and, to a smaller extent, by changes in the duration and velocity of the upstroke movement. Duration and velocity of the downstroke movement and the time spent near the downstroke position were relatively constant, particularly at wingbeat periods above 100ms. Downstroke and subsequent upstroke movements coincided almost perfectly in the superposition of recordings made at these long wingbeat periods (e.g. Fig. 2B).

These frequency-dependent changes in the pattern of wing movement closely reflected corresponding changes in motoneurone activity described previously (Pearson and Wolf, 1987, 1989; see middle traces in Fig. 2A,B). Namely, the duration of the discharge in

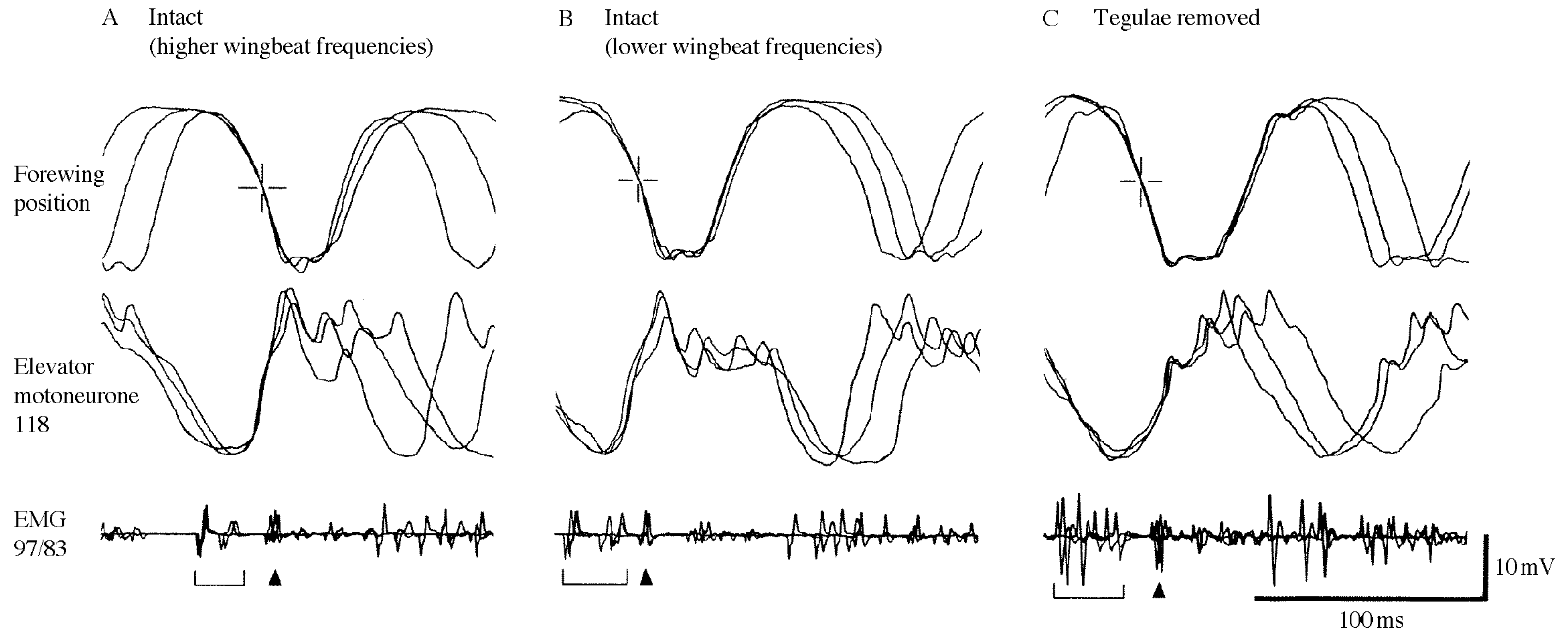

Fig. 2. Forewing movement (top traces) and elevator motoneurone activity (middle traces) recorded in intact locusts (A,B) and after removal of the hind- and forewing tegulae (C). In the bottom traces, electromyographic recordings of forewing depressor (97, spike bursts indicated by brackets) and elevator (83, first action potentials in burst indicated by arrowheads) discharges are shown. Three traces recorded at different wingbeat periods are superimposed in each diagram, taking the middle of the downstroke (cross marks) as a reference point. These sample recordings illustrate the characteristic frequency-dependent changes in motoneurone activity and wing movement pattern associated with tegula removal (for details see text). All recordings are from one individual.

elevator motoneurones was correlated with the time spent by the wings near the upstroke position and varied with wingbeat frequency (Fig. 3; correlation with the duration of elevator depolarizations was less strict; compare Pearson and Ramirez, 1990). By contrast, the interval between depressor activity – and thus the downstroke movement (Fig. 2A,B) – and the onset of elevator activity remained relatively constant, particularly at low wingbeat frequencies.

After removal of all tegulae (Fig. 2C), wingbeat frequency rarely exceeded 15Hz. As for corresponding wingbeat frequencies in the intact animal, a further decrease in wingbeat frequency was primarily due to the increased time that the wings spent near the upper reversal point of the wingstroke and to the corresponding changes in the duration of elevator motoneurone discharges. Downstroke, upstroke and the interval between them showed relatively little variation. The interval between downstroke and subsequent upstroke, however, was significantly increased compared with the intact situation ($P<0.01$, $N=201$) and, in intracellular recordings, the initial rapid depolarization elicited by tegula input was missing (middle trace in Fig. 2C). In the intact locust the interval from mid-depression to mid-elevation was about 25–45ms, depending on wingbeat frequency; it ranged from about 35 to 70ms after tegula removal. Because of this frequency-dependence, the delay in upstroke is best detected by a comparison based on matching wingbeat frequencies. In Fig. 4A, two recordings, made just before and just after all four tegulae of the locust had been severed, are superimposed. The two recording segments were selected for matching wingbeat periods and are aligned with respect to the middle of the wing downstroke. Both the abolition of the initial part of the elevator

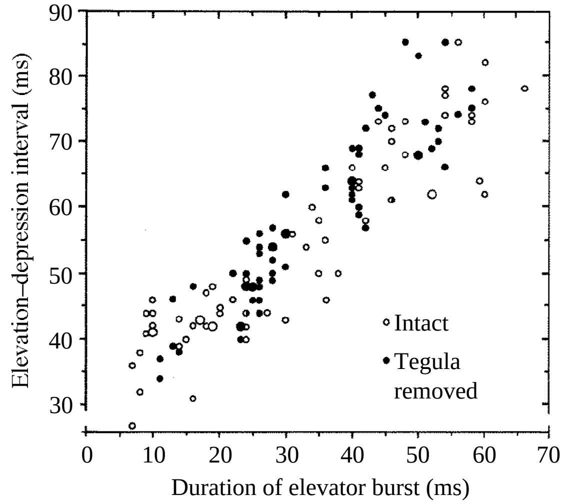

Fig. 3. Correlation between forewing upstroke duration (ordinate, measured from mid-elevation to mid-depression) and elevator motoneurone discharge (abcissa, interval between first and last action potential in a spike burst of motoneurone 118). Each circle represents 1–3 measurements, according to its size. The correlation is good considering that at least six motoneurones contribute to the upstroke movement of a wing (same animal as in Fig. 2, 131 wingbeats evaluated, correlation coefficient 0.91).

motoneurone depolarization and the delay of the wing upstroke by about 12ms are discernible. Two other changes, although less conspicuous, were often observed as a result of tegula removal. First, the amplitude of the wingstroke was sometimes increased and, second, the upstroke movement was often more rapid when tegula input was missing (see also superimposed wing position traces in Fig. 6C,D).

The graphs in Fig. 4B,C give a quantitative comparison of the intervals between wing depression and wing elevation for the observed wingbeat periods ranging from 50 to 130ms. Tegula removal delayed the upstroke movement by an average of 13ms regardless of wingbeat frequency (Fig. 4B; there were significant differences at wingbeat periods between 70 and 120ms, $P<0.01$). At frequencies above 10Hz, the pattern of wing movement was often close to phase-constant; at wingbeat frequencies below 10Hz, by contrast, an almost constant latency between downstroke and upstroke movement was often observed. The time during which the wings were elevated above the horizontal, i.e. the interval between mid-upstroke and mid-downstroke, increased almost linearly with increasing wingbeat period, with a slope of 0.7 (Fig. 4C). This demonstrates that variation in the time spent near the upstroke position is the locust's main means of changing wingbeat period. Again, these data are in agreement with previous descriptions of the flight motor pattern based on electromyographic and intracellular motoneurone recordings (e.g. Wolf and Pearson, 1987*c*; Robertson, 1988; Ronacher *et al.* 1988).

Lift generation

The experiments described in the previous section have established that the tegula sense organs are responsible not only for the generation of an early rapid depolarization of elevator motoneurones but also for a corresponding early upstroke movement of the (fore)wings. This raises the question of the functional relevance of an early upstroke movement, and thus of its control by the hindwing tegulae, in flight performance. The lift component of the aerodynamic force produced by a flying locust was determined in an attempt to address this question. Measurement of lift was chosen because this is not only the largest of the aerodynamic force components generated but is also the most important one for keeping the locust airborne.

Lift recordings reflect inertial forces produced by the deceleration and acceleration of the wings near the reversal points, in addition to aerodynamic forces. A correct measure of aerodynamic net lift is obtained by averaging the forces generated during a wingbeat cycle since inertial forces cancel out in the course of a cycle of steady flight (see Fig. 7; e.g. Zarnack, 1983). Phase-related analysis of lift force and correlation with changes in wing movement appear to be necessary for an intelligible interpretation of the aerodynamic effects of tegula removal. Such an interpretation can only be qualitative because of the unknown contribution of inertial forces. It is evident, however, that the inertial component of lift recordings will show a positive peak shortly before and after the upper reversal point and that a negative peak will be generated just before and after the lower reversal point of the wingstroke. A rough estimate based on the recordings of wing movement suggested that at wingbeat frequencies below 20Hz the peak values of inertial force do not exceed 4mN and are usually lower. These limitations should be borne in mind when interpreting the following results.

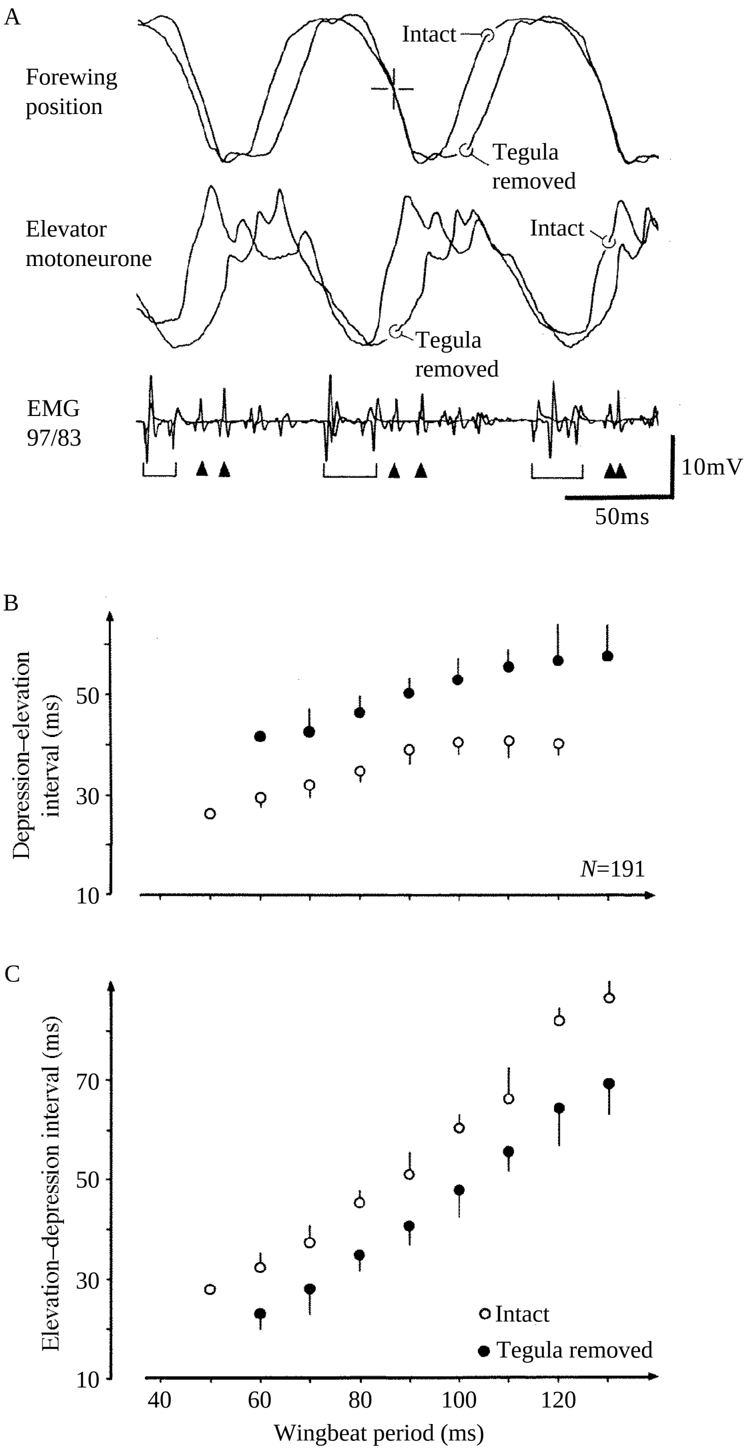
A
Forewing position
Intact
Tegula removed
Elevator motoneurone
Intact
Tegula removed
EMG 97/83
10mV
50ms
B
Depression–elevation interval (ms)
50
30
10
N=191
C
Elevation–depression interval (ms)
70
50
30
10
40
60
80
100
120
Wingbeat period (ms)
○ Intact
● Tegula removed

Fig. 4

The diagrams in Fig. 5A,B show superimposed recordings obtained at different wingbeat frequencies. The frequency-dependent changes in wing movement described above are discernible, as is the delayed upstroke caused by tegula removal (Fig. 5B). The lift recording shows that a positive lift force is produced by the wing downstroke. Force generation peaks during the early part of the downstroke of the forewings, the peak probably containing significant inertial force components. When interpreting the time relationship between forewing movement and force production it must be considered that in the intact animal, as well as after partial or complete deafferentation, hindwing movements precede corresponding forewing movements by 5–10ms (see Fig. 8; Weis-Fogh, 1956; Wilson and Weis-Fogh, 1962; Schwenne and Zarnack, 1987). Like the downstroke movement itself, the course of the generated lift force appeared to be relatively constant and independent of wingbeat frequency. Even after tegula removal no major changes were discernible. Negative lift was generated during the interval between the end of the downstroke and the end of the upstroke. Negative force generation peaked just after the start of the upstroke. The overall production of a negative lift component varied with the frequency-dependent changes in the interval between the end of one downstroke and the beginning of the next one. This is illustrated in Fig. 5A, in which recordings representing a broad range of wingbeat periods (approximately 60–110ms) are superimposed.

The fluctuations in the force recording make a more detailed analysis based on individual recordings difficult. The salient features of lift force generated in the course of the wingbeat cycle and possible differences in force production between the intact situation and after tegula removal are more reliably judged from averaged recording traces. In the diagrams of Fig. 6A,B, data are presented in the same arrangement as in Fig. 5A,B, but averaged, instead of individual, recordings are shown. In Fig. 6C,D, matching wingbeat periods were evaluated before and after tegula removal and the resulting averages superimposed. Signal-averaging verified most of the results seen in the individual recordings.

(i) The time course of lift force generated during the downstroke of the forewings was relatively constant, although both downstroke velocity and peak force slightly decreased with decreasing wingbeat frequency, particularly in the intact animal.

(ii) Negative lift was generated mainly between the end of the downstroke and the end of the subsequent upstroke. The shape of the force recording was therefore dependent on wingbeat frequency. Lift production was most negative between the end of the downstroke and the beginning of the upstroke. Inertial forces would be expected to

Fig. 4. Changes in forewing movement resulting from tegula removal. (A) Superposition of forewing movement (top trace) and elevator motoneurone activity (middle trace) recorded before and after removal of all tegula organs. The bottom trace represents the corresponding superposition of electromyograms recorded from forewing depressor muscle 97 (spike bursts indicated by brackets) and elevator muscle 83 (initial spikes of discharges recorded before and after tegula removal are indicated by arrowheads). Recordings are aligned with respect to the middle of the second downstroke (cross marks). (B,C) The intervals between the middle of the downstroke and the middle of the subsequent upstroke (B), and *vice versa* (C), are plotted *versus* wingbeat period for the intact (open circles) and partially deafferented (filled circles) preparation. Data are from one individual; standard deviations are indicated.

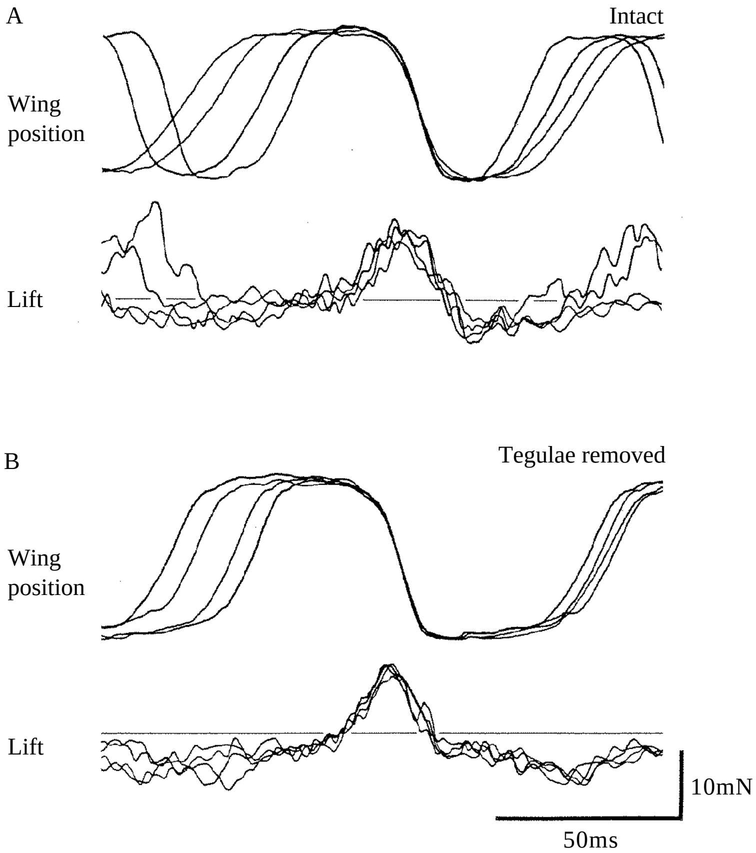

Fig. 5. Forewing movement (top traces) and the lift component of aerodynamic force (bottom traces) recorded before (A) and after (B) removal of fore- and hindwing tegulae. Four traces recorded at different wingbeat frequencies are superimposed in A and B, taking the middle of the downstroke as a reference point. The horizontal line indicates zero lift.

contribute negative lift mainly at this point. In the intact locust, peak negative force was larger at higher wingbeat frequencies. Nevertheless, a smaller negative lift impulse (Fig. 7) was produced because negative force was generated during a shorter interval at the higher frequencies.

(iii) Superposition of traces recorded before and after tegula removal (Fig. 6C,D) showed that all phases of the wing movement were affected by the partial deafferentation. Tegula removal had the following effects. (1) The downstroke movement was slightly more rapid and a larger peak lift was generated. However, because the generation of positive lift force commenced later in the wingbeat cycle and was thus restricted to a shorter time interval, a smaller lift impulse was produced after tegula removal (Fig. 7). (2) The upstroke movement commenced later and, although it too was more rapid, the wings remained near the upstroke position for a shorter interval. This extended the period during which negative lift was generated and, in addition, the more rapid upstroke was correlated with an increased negative peak force. The negative lift impulse generated was thus always significantly larger, comparing the equivalent wingbeat frequencies, in locusts with excised tegulae than it was in intact animals. Inertial forces will contribute to the lift recorded near the end of the downstroke and at the beginning of the upstroke, but generation of negative lift during the extended stay of the wings near the downstroke position must be attributed to aerodynamic effects.

The consistency of these observations in different animals is illustrated in Fig. 7. Force recordings obtained from eight animals are summarized; the generation of positive and

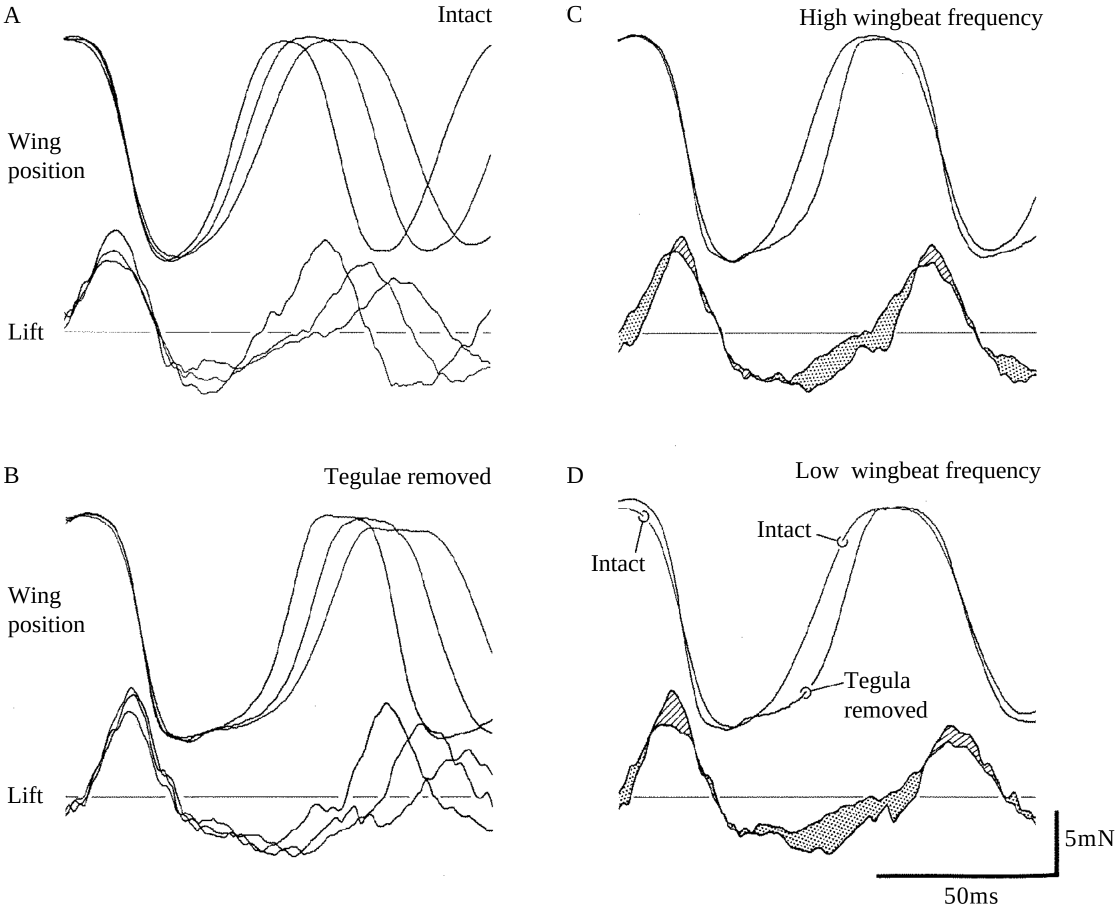

Fig. 6. Forewing movement (top trace) and lift force (bottom trace) recorded before (A) and after (B) removal of fore- and hindwing tegulae. Each trace represents the average of 32 recordings. The middle of the wing downstroke served both as a trigger point for averaging and as a reference for superposition. Wingbeat periods ranging from 50 to 62.5ms, from 62.5 to 75ms and from 75 to 87.5ms were evaluated for the three traces superimposed in A; periods between 62.5 and 75ms, 75 and 87.5ms, and 87.5 and 100ms were evaluated in B. In C and D, the respective intervals were 62.5–75ms and 75–87.5ms. Data recorded before and after tegula removal are superimposed. Hatched area: averaged lift force was larger after tegula removal; dotted area: lift force was larger before tegula removal.

negative lift force during the respective phases of the wingbeat cycle is listed separately (left ordinate and bars in Fig. 7). Tegula removal consistently reduced positive lift production and increased negative lift production. Integration of the lift forces generated during a wingbeat cycle was used to eliminate inertial force components and to obtain net lift (right ordinate and circles in Fig. 7). This demonstrated that, in all cases, smaller, and sometimes negative, net lift was generated after the locust's tegulae had been removed, as a result of the effects of tegula removal outlined above.

Angular setting of the wing

The results presented in the two previous sections suggest that the main effect of tegula removal is to delay the wing upstroke and to decrease net lift production, apparently because of a delay of the wings near an aerodynamically unfavourable downstroke position. This interpretation might be flawed, however, if major changes occur in the angular setting of the wing as a consequence of tegula removal. The generation of aerodynamic force is determined not only by the up- and downstroke movements of the wing but also by its aerodynamic angle of attack (and the phase relationship between the movements of hind- and forewings; M. Wortmann and

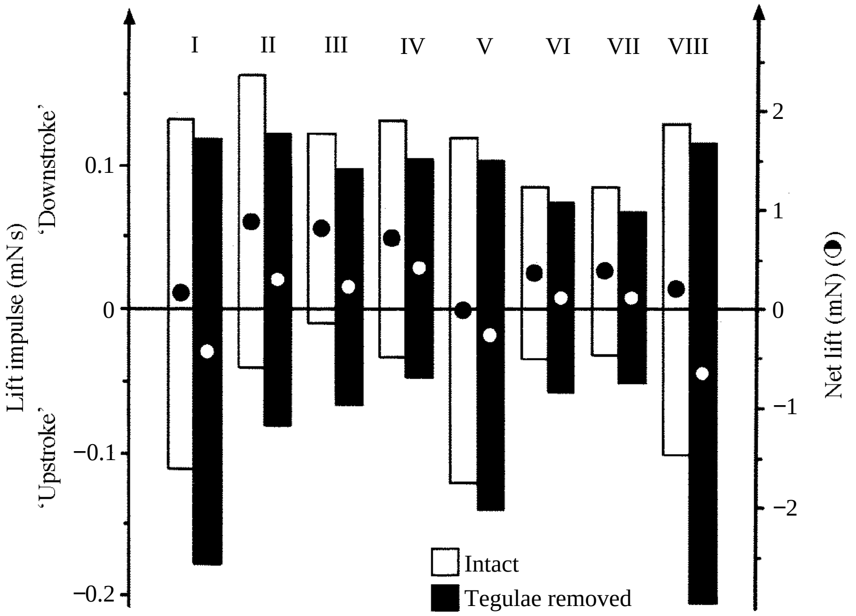

Fig. 7. Generation of positive and negative lift force during different phases of the wingbeat cycle in intact locusts (open bars) and after removal of fore- and hindwing tegulae (filled bars). Positive and negative lift forces were integrated separately over the appropriate time intervals, corresponding roughly to the down- and upstroke movements (left ordinate). The lift force generated during the wingbeat cycle was integrated to obtain net lift and to eliminate inertial force components generated by the acceleration of the wings near the reversal points (filled and open circles, right ordinate). Wingbeat periods between 62.5 and 75ms were used for averaging (see Fig. 6) and subsequent evaluation. Force recordings were obtained from eight animals (I–VIII).

W. Zarnack, in preparation; reviewed by Rowell, 1988). In the case of simultaneous changes in wingstroke variables and angular setting, it becomes unclear what each contributes to the over all changes in lift production. Changes in the angular setting of the wing might ensue if tegula removal were to affect the subtle relative timing among powerstroke muscles, in particular the first basalar and subalar, or the activity of the ‘flight steering’ or pleuroalar muscles (Pfau, 1977, 1978, 1983; Heukamp, 1984; Schmidt and Zarnack, 1987; Zarnack, 1988). For these reasons, the angular settings of the hind- and forewings were recorded, together with their movement trajectories, during flight before and after tegula removal.

The two photographs traced in Fig. 8 were taken before (Fig. 8A) and after (Fig. 8B) removal of the animal’s four tegulae to monitor the angular setting of the right fore- and hindwing during a wingstroke. Images of the wing profiles were produced by a stroboscope flash every 2.5ms (i.e. 24 images of the wing profile during a 60ms wingbeat period). The overall changes in angular setting during a wingstroke can be read from this figure. Both wings are pronated by an angle of up to 40° during the downstroke and they are supinated, often by more than 60°, during the upstroke (values cannot be read directly from Fig. 8A,B because prismatic distortions must first be corrected; see Wolf, 1990). Near the lower reversal point, the wings are rapidly turned from the pronated downstroke to the supinated upstroke attitude, and the reverse occurs near the upper reversal point. It is evident from a comparison of Fig. 8A,B that both fore- and hindwings stay near the lower reversal point for longer, and in a more horizontal attitude, after tegula removal. In addition, the two pairs of wings dwell near the downstroke position during overlapping time intervals as a result of the delay of the upstroke movement. In the intact animal, by contrast, the rapid transitions between down- and upstroke, together with the fact that the movement of the hindwings precedes that of the forewings by 5–10ms, prevent such a coincidence (arrowheads indicate corresponding profiles of hind- and forewings in Fig. 8A,B).

In Fig. 8C,D, the data from 72 wingstrokes of the animal shown in Fig. 8A,B are evaluated and wing pronation is plotted *versus* the vertical component of wing movement. The resulting graph provides a fairly typical picture of the changes in wing pronation produced by tegula removal. As a rule, the wings were slightly more pronated during the downstroke after tegula removal. This change may be related to the increased downstroke velocity noted in Figs 5 and 6 since stronger activation of the basalar depressor muscles may lead to increased downstroke pronation (however, the subalar depressor muscle antagonizes downstroke pronation; Pfau, 1983). By contrast, upstroke supination of the wing is delayed and often weaker after tegula removal, particularly in the hindwings.

It is unlikely that these changes in the angular setting of the wings account for the reduced generation of net lift observed as a result of tegula removal. This is evident from the fact that changes in wing pronation, although often similar to those shown in Fig. 8A,B, were quite variable between animals and were not consistently related to lift production. In some individuals, downstroke pronation was actually decreased after partial deafferentation while a reduction in net lift was consistently observed. In animal I of Fig. 7, both the angular setting of the forewing and the generation of lift were determined during flight before and after tegula removal. Although excision of the proprioceptive organ produced only minor, if any, changes in the angular setting of the wing (data not shown), the resulting decrease in net lift production was among the most pronounced recorded.

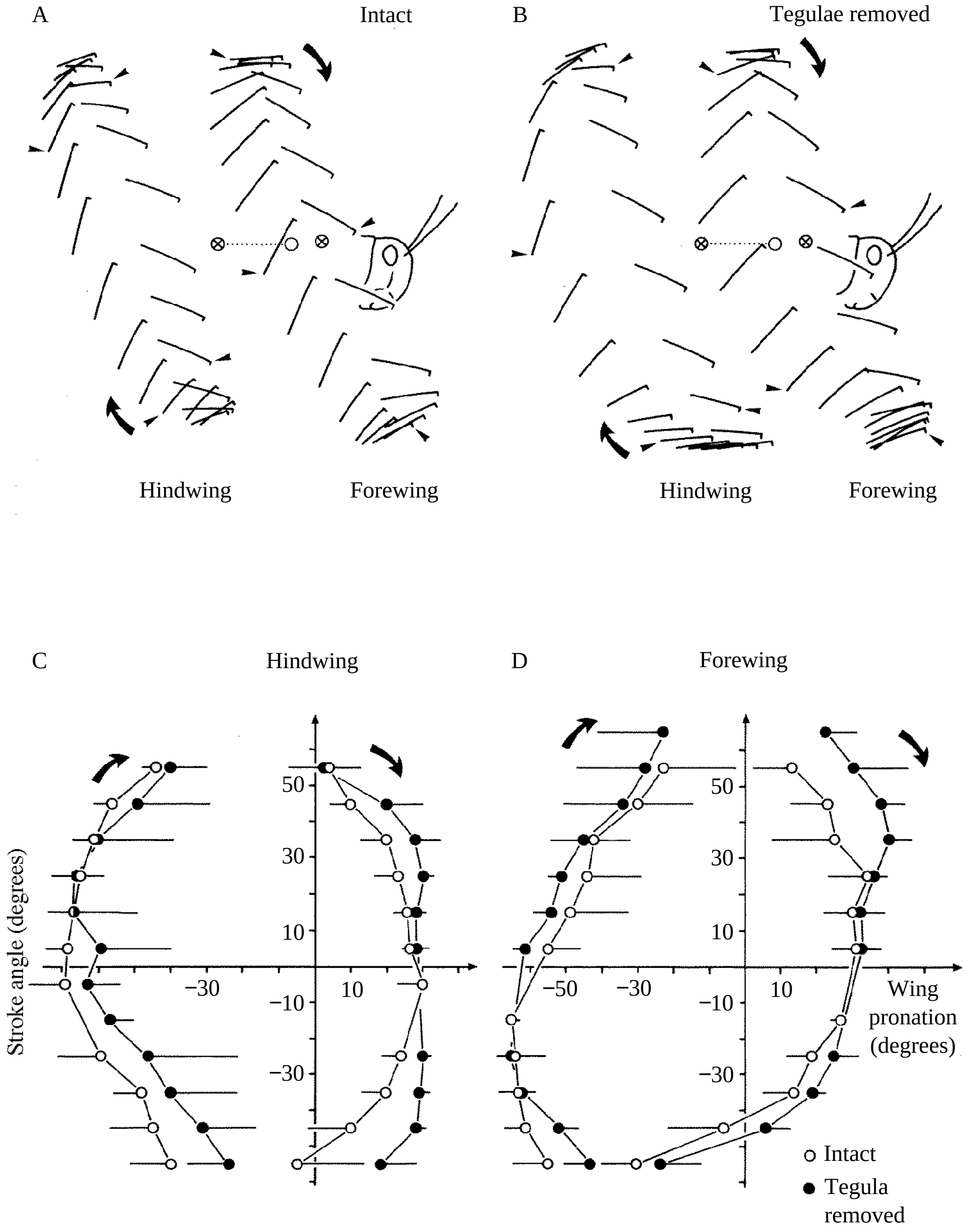

Fig. 8

Discussion

The function of the locust tegula organs during flight has been investigated with respect to control of wing movement and the generation of aerodynamic force. An important role of the tegulae in normal flight performance has been indicated in previous electrophysiological studies (reviewed by Wolf, 1991) and is demonstrated by the data presented in Fig. 1A,B. Discharge of the hindwing tegula afferents, elicited by electrical stimulation of nerve 1C, is able to reset the flight rhythm at any phase of the wingbeat cycle by depolarizing elevator motoneurones and by suppressing existing depressor motoneurone activity. The entire flight motor is affected by the resetting and all flight muscles apparently contribute to it in a coordinated manner. Analyses of the connectivity of the tegula afferents with central flight interneurones (Fig. 1C; Pearson and Wolf, 1988; Wolf and Pearson, 1989; Büschges *et al.* 1992*a*) and of the cellular properties of these interneurones (Ramirez and Pearson, 1991*a*,*b*) have provided some understanding of the cellular basis of tegula action.

Wing movement

The present study shows that the tegulae are responsible for the generation of an early upstroke movement of the wings (Figs 2, 4). Tegula removal delays the upstroke by an average of 13ms with regard to the previous downstroke and causes the wings to pause near the lower reversal point. This result agrees closely with the observation of a delayed onset of elevator motoneurone activity after tegula removal or complete deafferentation (in the case of tegula removal by about 15–20ms; see Fig. 14 of Pearson and Wolf, 1988). The onset of elevator discharges is delayed because the hindwing tegulae are responsible for the generation of a characteristic, early depolarizing component in the elevator motoneurones of both pterothoracic segments (Wolf and Pearson, 1988; Ramirez and Pearson, 1991*a*,*b*).

Only movements of the forewings were examined in detail in the present investigation, but there is little doubt that the results hold true for movements of the central field of the hindwing (however, there is a delay of 5–10ms between the movements of hind- and forewings; e.g. Weis-Fogh, 1956). For instance, preliminary position recordings of the hindwings during flight (data not shown), the data presented in Fig. 8 and numerous studies employing EMG (Pearson and Wolf, 1987, 1989; Ronacher *et al.* 1988) and intracellular motoneurone recordings (Wolf and Pearson, 1987*b*,*c*) have all demonstrated

Fig. 8. Effect of tegula removal on the angular setting of the wings. Profiles of the locust's right pair of wings were photographed (2.5ms flash interval, exposure time 1/15s) in the intact animal (A) and after removal of the fore- and hindwing tegulae (B). Positions of the wing hinges are indicated (crossed circles); profiles of the hindwing are displaced posteriorly from the position marked with an open circle (dotted line) to avoid interference with the forewing recording. Corresponding profiles of hind- and forewing are marked by arrowheads. The movement of the hindwing preceded that of the forewing by about 7.5ms. The direction of wing movement is indicated by arrows. Note that, after tegula removal, the wings remained near the downstroke position in almost horizontal attitudes for several milliseconds. The angular settings (abscissae) of the hindwing (C) and forewing (D) were examined before (open circles) and after (filled circles) tegula removal (72 wingstrokes and 1843 wing profiles evaluated) and plotted *versus* the stroke angle (ordinates). Standard deviations are indicated.

that the coordination of fore- and hindwings and flight muscles remains almost unaffected even by complete deafferentation.

Despite a generally unchanged coordination of the movements of fore- and hindwings, a delay near the lower reversal point in both pairs of wings (Fig. 8B) may affect their normal aerodynamic interaction in which the forewings act as leading flaps controlling the flow of air towards the hindwings (Zarnack, 1983). The corresponding reduced speed of the wings' flip from the pronated downstroke into the supinated upstroke attitude may also have adverse effects on non-steady-state aerodynamics such as vortex shedding. Finally, in contrast to the central field, the highly flexible anal field of the hindwing does not lend itself to kinematic analysis and has rarely been investigated, although this part of the wing is assumed to contribute significantly to the generation of aerodynamic force (Schwenne and Zarnack, 1987; M. Wortmann and W. Zarnack, in preparation). Interpretations of the aerodynamic results of the observed changes in wing movement must remain tentative for these reasons and because a reliable description of the non-steady-state aerodynamics of locust flight is not available (Zarnack, 1983). The observations that changes in wing movement caused by tegula removal were very consistent and larger than the variations observed in the context of steering manoeuvres (Thüring, 1986; Waldmann and Zarnack, 1988) challenge an interpretation of the most prominent aerodynamic effects associated with tegula removal (see also Wortmann and Zarnack, 1993).

Aerodynamic force

Tegula removal results in a marked decrease in net lift generation (Fig. 7). The combined recordings of wing position and lift force (Figs 5, 6) suggest that this decrease in net lift is an immediate consequence of the delayed upstroke movement of the wings. Following tegula removal, the wings are delayed near the downstroke position by an average of 13ms. In this position, considerable negative lift force is produced. Since inertial forces will contribute to the recorded negative lift predominantly near the end of the downstroke and at the beginning of the upstroke, the wings must produce negative lift while they are almost stationary near the downstroke position. The generation of negative force is probably due to the fact that the wings are almost horizontal, particularly towards the beginning of the upstroke, or may even remain pronated during part of the time that they spend near the lower reversal point (Nachtigall, 1981; the profile observed in Fig. 8 was roughly in the middle of the wing but, since the wing blade is twisted, its more distal part remains more pronated as long as the wing has not clicked into the upstroke profile; Pfau, 1983; Zarnack, 1983, 1988). Considerable negative lift is also generated during most of the upstroke. Although the upstroke movement is, as a rule, more rapid after tegula removal (Figs 5, 6), in terms of lift generation, this does not compensate for its delayed onset. By contrast, the negative peak force is increased, apparently as a result of the accelerated upward movement, and the wings arrive near the upper reversal point later than in the intact locust (Fig. 6C,D).

It is only in the upstroke position that positive lift can be generated without the wings actually moving relative to the insect's body – as occurs in gliding locusts (Baker and Cooter, 1979). This is because the wings remain supinated and thus generate lift

(Nachtigall, 1981) when held in the upstroke position. The pronated attitude observed during the downstroke is initiated only by contraction of the downstroke muscles and is effected by the mechanics of the wing hinge (Pfau, 1983). This appears to be the reason why the transition from upstroke to downstroke movement is much less critical than the reverse transition. Positive lift is generated when the wings rest in the upstroke position, so variation in the time interval between the end of the upstroke and the beginning of the downstroke may be employed without detriment to adjust wingbeat frequency, as is in fact observed, particularly if wingbeat frequency drops below 16Hz (Fig. 2; Wolf and Pearson, 1988).

In summary, the delayed onset of elevator activity caused by tegula removal prolongs those phases of the wingstroke in which negative lift is produced and does so at the expense of the phases that contribute to the generation of positive lift (Fig. 7). The result is a significant reduction of the net lift generated during flight, sometimes leading to negative values.

Preliminary experiments show that the effects of tegula removal are enhanced if the locusts are flown in a wind stream of about $3\,\mathrm{m\,s^{-1}}$, which corresponds to their normal flight speed (Baker *et al.* 1981; Gewecke, 1983). This is because the generation of both negative lift in the downstroke position and positive lift in the upstroke position are increased with stronger front wind. This is immediately evident from the wing profile recordings shown in Fig. 8 (see also Nachtigall, 1981; Pfau and Nachtigall, 1981). Therefore, it becomes even more important at higher wind speeds that the transition from down- to upstroke movement is performed quickly, whereas dwelling in the upstroke position becomes less critical. The present experiments were performed with the locusts experiencing only their self-generated airstream because the effects of tegula removal are more clearly observable at lower wind speed (Pearson and Wolf, 1989) and cycle-to-cycle variability is considerably reduced, particularly at the low wingbeat frequencies analyzed in the present study (Wolf and Pearson, 1987*b*). Net lift generation was between 0 and 25% of body weight when intact animals were flown in still air (Fig. 7).

Function of locust tegulae

The results of this study suggest that it is the function of the locust tegula to signal to the nervous system the impending completion of the wing downstroke and to elicit an immediate subsequent upstroke movement. In this way, a disadvantageous delay of the wings near the lower reversal point can be avoided. Apparently, the central programming of a fixed shorter delay between depressor and elevator discharges does not constitute a functional alternative to feedback control *via* the tegulae. There are two reasons for this. First, exact timing of the upstroke is critical for effective locomotion: a premature initiation of the upstroke movement is probably as detrimental for flight performance as is a delayed one. Second, the actual execution of the wing movement in response to a given neural command is variable and will depend on numerous parameters – on internal ones, such as hormonal status (e.g. Whim and Evans, 1988; Orchard *et al.* 1993), muscle fatigue and wing wear, and on external perturbations, such as turbulence.

The present findings do not rule out the possibility that the tegula organs transmit to the nervous system information beyond the aspects investigated here or that they subserve other, and probably more subtle, functions in the control of wing movement. This is suggested, for instance, by the results of Neumann (1985) and by the apparent lack of functional significance of the forewing tegulae in pattern generation (Büschges *et al.* 1992*a*,*b*).

Owing to the rapid cycle frequency of the locust wingbeat and the limited conduction velocity of insect axons, the tegulae must be stimulated several milliseconds before the downstroke position has actually been reached in order to fulfill their task of initiating an elevator motoneurone discharge. Indeed, tegula discharge commences a few milliseconds after the start of the downstroke movement (Neumann, 1985; Wolf and Pearson, 1988). One might expect, therefore, that activity of the tegula organs relays information about downstroke velocity and thus allows a prediction as to when the wings will reach the lower reversal point. Similar velocity coding has been demonstrated, for instance, for sensillae of insect femoral chordotonal organs (Hofmann and Koch, 1985; Hofmann *et al.* 1985).

The spectrum of mechanisms employed in the generation of motor programmes for the control of locomotion ranges from almost pure central programming to relaxation oscillators that contain sensory signals as decisive elements (see Introduction). Locust flight is in the middle of this spectrum, since central oscillator networks and sense organs interact closely in the generation of the functional motor pattern. Although the significance of sensory signals has been addressed in this study, the generation of a continuous wingbeat rhythm independent of sensory signals, as is provided by the inherent oscillator properties of the central network, might prove important in situations where sensory feedback from the wing receptors is missing or abnormal. In order for a locust to remain airborne it would appear essential that the alternating movement of the wingbeat should not be terminated as a result of an occasional lack of appropriate sensory signals under unusual cicumstances. Tegula input, for example, might be absent during the initial wingbeat cycles at the start of flight and for several wingbeat cycles following collision with other locusts in the swarm.

It appears to be a general principle in motor control that functionally critical transitions between the phases of a (cyclic) movement are controlled by sensory feedback. This was shown here for the transition from the downstroke to the upstroke of the wings in locust flight. It is also true of the transition from upstroke to downstroke, which is controlled by the wing hinge stretch receptor (albeit allowing adjustment of wingbeat period; Reye and Pearson, 1988; Wolf and Pearson, 1988; Pearson and Ramirez, 1990) and for walking in a variety of animals. The stick insect (Bässler, 1983) and the cat (Grillner and Rossignol, 1978) are probably the best known examples here. In walking, the transitions between swing and stance phase are under strict sensory control. In the stick insect, the transition from swing to stance occurs if receptors on the tarsus signal that contact has been made with the supporting substratum (Bässler, 1985; Bässler, 1993); the transition from stance to swing is triggered by receptors monitoring posterior leg positions and load (Cruse, 1985). Sensory control is essential in these cases for reasons very similar to those cited for locust flight. A purely central programme provides neither the flexibility required for locomotion on uneven or discontinuous surfaces nor the possibility of recalibrating the motor system in response to changes in the components of the system itself (e.g. Möhl, 1988, 1989).

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