

The forewing tegulae: their significance in steering manoeuvres and free flight in *Locusta migratoria*

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Abstract: The flight system of *Locusta migratoria* is widely used to investigate the principles of sensory–motor control. The four tegulae are proprioceptors of the flight system that are active during the downstroke and provide afferent input to flight-system neurons. While the role of the hindwing tegulae in the flight motor pattern has been well characterized, the role of the forewing tegulae is unclear. We tested whether the forewing tegulae may be more important for the generation of intentional steering manoeuvres than for generation of the basic flight motor pattern. Following ablation of the forewing tegulae, tethered flying locusts continued to generate characteristic intentional steering manoeuvres in open-loop conditions. In contrast, we found that locusts were less likely to sustain unrestrained free flight following ablation of the forewing tegulae. We also found that the number of spikes in a forewing depressor muscle increased, as did the hindwing to forewing delay in elevator-muscle activation after ablation of the forewing tegulae. We conclude that the forewing tegulae promote free flight in locusts and we discuss the role they may play in locust flight.

Résumé : Le système de vol de *Locusta migratoria* sert souvent de base à la recherche des principes du contrôle sensoriel moteur. Les quatre tégulas sont les propriocepteurs du système de vol et elles sont actives durant l'abaissement des ailes et envoient des influx afférents aux neurones du système. Le rôle des tégulas des ailes postérieures dans la fonction motrice du vol est assez bien compris mais le rôle des tégulas des ailes antérieures n'est pas clair. Nous avons tenté de déterminer si les tégulas des ailes antérieures avaient un plus grand rôle à jouer dans les manoeuvres volontaires directionnelles que dans le fonctionnement moteur de base du vol. Après l'ablation de leurs tégulas antérieures, des criquets aux ailes attachées ont continué de faire leurs manoeuvres directionnelles volontaires caractéristiques au cours de vols en boucle ouverte. En revanche, nous avons constaté que les criquets étaient moins enclins à entreprendre des vols libres soutenus après l'ablation de leurs tégulas antérieures. Nous avons également constaté que le nombre de contractions du muscle dépresseur de l'aile antérieure et le délai entre l'activation du muscle élévateur de l'aile postérieure et celui de l'aile antérieure augmentaient après les ablations. Nous concluons que les tégulas de l'aile antérieure favorisent le vol libre chez les criquets et nous examinons le rôle qu'elles peuvent jouer dans le vol des criquets.

[Traduit par la Rédaction]

Introduction

The orthopteran flight system has long been an important model for studying central nervous system control of behaviour, including extensive investigation into the role of sensory information in modulating the motor output (e.g., Weis-Fogh 1956; Wilson and Gettrup 1963; Pearson and Wolf 1987; Wolf and Pearson 1987; 1988). The forewing and hindwing tegulae form one of the principal proprioceptive organs of the flight system of *Locusta migratoria*. The tegulae are cupola-shaped organs located on soft cuticle at the anterior margin of each wing hinge. Each tegula contains about 40 sensory hairs, each innervated by a single sensory afferent and an associated

chordotonal organ innervated by an additional 40 afferents (Kutsch et al. 1980). Every interneuron and motoneuron of the flight system that has been examined receives either direct or indirect input from at least one of the four tegulae (Kien and Altman 1979; Pearson and Wolf 1988; Ramirez and Pearson 1991). During flight, the tegulae afferents become active shortly after the upper stroke reversal and remain active throughout the downstroke (Neumann 1985). Activity from the tegulae strongly excites elevator motoneurons, inhibits depressor motoneurons, and can reset the flight rhythm on a cycle-by-cycle basis (see Neumann et al. 1982; Wolf and Pearson 1988).

Removal of the hindwing tegulae decreases the wingbeat frequency (Kutsch 1974), owing to an increase in the time interval between activation of depressor muscles and the succeeding activation of elevator muscles (Büschges and Pearson 1991). This change in timing of the flight motor pattern prolongs the time during which the wings occupy the aerodynamically unfavourable position at the lower stroke reversal, resulting in a loss of lift production (Wolf 1993).

The role of the forewing tegulae during flight is unclear. In the intact locust, ablation of the forewing tegulae does not affect wingbeat frequency, has no effect on the phase relationship of antagonistic hindwing muscles, and causes only a small delay in the initiation of forewing elevator activity (Büschges and Pearson 1991; Büschges et al. 1992b; Gee and Robertson

Received September 4, 1997. Accepted November 13, 1997.

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1996). After the hindwing tegulae are ablated, the forewing tegulae mediate recovery of the flight system and take over the role previously subserved by the hindwing tegulae (Büschges and Pearson 1991). The fact that removal of the forewing tegulae in intact locusts does not affect the timing of the flight motor pattern has led to the suggestion that the forewing tegulae are of little importance for flight-pattern generation (Büschges and Pearson 1991). Nevertheless, it is doubtful whether the forewing tegulae, which are complex sensory structures, would exist solely to effect recovery in the unlikely event that the two hindwing tegulae would be damaged. During flight, movement of the hindwings is thought to supply most of the power required to keep the locust aloft, whereas movement of the forewings plays an important role in stabilizing the locust and controlling the direction of flight. We hypothesized, therefore, that the forewing tegulae are not necessary for straight and level flight, but play a role in steering, a behaviour that is accompanied by changes in the downstroke of the forewings, about which the tegulae inform the central flight circuitry.

Mechanisms of steering have been widely studied in locusts (for review see Kammer 1985; Rowell 1988). In response to a laterally placed heat lamp being turned on and (or) off, tethered flying locusts will attempt steering manoeuvres by deflecting the abdomen, generating shifts in asymmetry between left–right pairs of forewing depressor muscles and changes in wing kinematics (Robertson et al. 1996; Shoemaker and Robertson 1997). We tested whether the forewing tegulae are necessary for steering by determining whether ablation of the forewing tegulae prevented tethered locusts from generating shifts in forewing depressor muscle asymmetry in response to thermal stimuli. In addition, we tested whether the forewing tegulae were necessary for sustained free flight and we examined motor patterns recorded from locusts shortly after removal of the forewing tegulae to determine whether there were changes in any parameters of the motor pattern apart from the timing of elevator and depressor muscle activation.

Methods

Throughout this study we used adult male *Locusta migratoria* obtained from a crowded colony maintained at Queen's University. All locusts were at least 2 weeks past the imaginal moult, to ensure that the flight system was fully mature. Tethered flight was always investigated under open-loop conditions.

Steering experiments

Attempted steering responses to thermal stimuli were examined in 24 tethered locusts. Briefly, locusts were rendered blind and deaf prior to testing to ensure that any attempted steering manoeuvres observed were in response to the thermal stimuli presented. After the legs were removed at the coxa–trochanter joint, the locusts were affixed by the pronotum to a rigid tether via a drop of hot wax. A total of four electromyograph (EMG) electrodes were inserted through the cuticle into forewing depressor muscles, the left and right m97s (forewing first basalar muscles) and left and right m99s (forewing subalar muscles) (nomenclature according to Snodgrass 1929) and held in place with a drop of wax. The locusts were suspended in front of a windstream (~2.5 m/s; ambient temperature 22–25°C) and muscle activity generated during tethered-flight sequences was digitized using a Neuro-corder (Neuro Data®, Delaware Water Gap, Pa.) and recorded to VHS videotape. The locusts were also videotaped from behind

(60 frames/s) to allow us to examine asymmetries in wing position and changes in abdomen position elicited by the stimuli.

After approximately 1 min of tethered flight, a 250-W heat lamp positioned 7.5 cm to the right of the locust was turned on for 5–15 s. The times of stimulus onset and offset were monitored with a BAT-12 thermometer (Sensortek®, Clifton, N.J.) via a copper–constantan thermocouple placed 1 cm directly above the locust's head. After the stimulus was presented, the windstream was stopped and either the forewing tegulae were removed by pinching them off with a pair of forceps ($N = 20$) or the locust was sham-operated ($N = 15$) by making a hole in the cuticle away from the wing hinge with the forceps without removing the EMG electrodes. The windstream was then restarted and a second thermal stimulus presented to the locust. Electrode placement was confirmed by postmortem dissection. Locusts were not included in the analysis if the electrodes were not found in the targeted muscles or if the muscle potentials could not be clearly distinguished in the electrical records.

The time of activation of each muscle throughout the flight sequence was determined using DataWave® Technologies Experimenter's Workbench (Longmont, Colo.). Asymmetries between the time of activation of right and left muscle pairs were then computed for each wingbeat cycle by subtracting the time of occurrence of the first muscle potential in the right muscle from the time of occurrence of the first muscle potential in the left muscle. A value greater than zero indicates that the right muscle was activated before the left muscle, whereas a negative asymmetry value indicates earlier activation of the left muscle in the wingbeat cycle.

Forewing asymmetry (FWA) and abdomen position were determined from frame-by-frame analysis of approximately 130 frames from the videotaped flight sequence encompassing the stimulus with the aid of Peak Performance Technologies hardware and software (Englewood, Colo.). From each frame, we digitized the positions of the tether, the intersection of the tether with the locust, the four wingtips, and the abdomen. The pixel coordinates were then used to calculate the angle between each wing and the line of the tether and the lateral deflection of the abdomen. FWA is the angular difference between the forewings and is equal to the angle of the right forewing minus the angle of the left forewing. A positive FWA value means that the right forewing is depressed relative to the left forewing. During the downstroke, the hindwings lead the forewings (Wilson and Weis-Fogh 1962); we therefore determined the FWA values that corresponded to downstrokes by selecting frames in which the hindwings were more depressed than the forewings.

Free-flight test

Three separate tests of free-flight ability were undertaken. Locusts were either left untreated (intact), had the forewing tegulae removed by pinching them off with a pair of forceps, or were sham-operated by using the forceps to make a hole in the cuticle of a size similar to that left by removing the tegulae. Locusts were treated at least 2 h before testing on the day of the test. Each locust was assigned a number, which was written on the forewing with a permanent-ink marker, and a key was kept of the numbers and the corresponding treatment.

The locusts were placed on a wooden platform on a balcony approximately 7 m above the floor in a room roughly 20 × 20 × 15 m with natural and artificial light. The room temperature was between 22 and 25°C. Flight was initiated when the locusts jumped from the platform. A few locusts landed on nearby wall fixtures immediately after taking off and were excluded from the analysis. Most of the locusts opened their wings and flew towards the far end of the room, flew around the room, or dropped to the floor in front of the balcony. Locusts were then ranked according to free-flight ability as follows: (1) nonflyers jumped and landed on the floor in less than 4 s; (2) poor flyers jumped and began to fly but landed in less than 8 s; (3) good flyers jumped and sustained flights lasting more than 8 s. Only after locusts were classified was the key used to determine to which treatment group each locust belonged. There was no difference in the

Table 1. Numbers of sham-operated locusts and locusts with the forewing tegulae ablated, showing changes in depressor asymmetry shifts and wingbeat frequency during attempted steering responses to stimulation with the heat lamp.

	Depressor asymmetry			Wingbeat frequency		
	No change	Larger shift	Smaller shift	No change	Larger change	Smaller change
Sham-operated ($N = 10$)	1	2	7	1	4	5
Forewing tegulae ablated ($N = 13$)	1	5	7	3	9	1

distribution of flight abilities on separate days of testing or between the intact and sham-operated locusts (not shown), therefore the results from the three tests were pooled and the intact and sham-operated locusts were combined.

Motor patterns during straight flight

EMG recordings collected from forewing and hindwing elevator and depressor muscles during tethered flights were reanalyzed (for other parameters see Gee and Robertson 1996). EMG electrodes were implanted in a forewing elevator (m83) and depressor muscle (m97) and a hindwing elevator (m113) and depressor muscle (m127) on one side of the body (for electrode placement see Pearson and Wolf 1987). Each locust was affixed to a rigid tether as described above and placed in a windstream (~2.5 m/s). Muscle activity was recorded for 2–4 min from the intact locusts and again from the same individuals after the forewing tegulae were removed (as above).

The average number of muscle potentials (spikes) per wingbeat cycle was determined for each individual by playing back the recorded electrical signals to a digital storage oscilloscope and holding the display at 10- to 15-s intervals throughout the flight sequence. The spikes were then counted in each of the two to five cycles displayed. We counted spikes from a minimum of 5 stored oscilloscope sweeps and a maximum of 17, depending on the duration of flight sequence that was recorded, and calculated the average number of spikes per cycle for each muscle in each individual. For each locust, the averages recorded in the intact condition were then subtracted from the averages recorded after ablation of the forewing tegulae to determine the change in the number of spikes per cycle due to ablation of the forewing tegulae.

From the same data set we also determined the mean delay between the first hindwing elevator spike and the first forewing elevator spike for each locust. Previously, we had calculated the mean hindwing to forewing depressor delay and the mean depressor to elevator intervals for both the hindwings and the forewings from locusts before and after the tegulae were ablated (see Gee and Robertson 1996). We determined the hindwing to forewing elevator delay by subtracting the mean hindwing to forewing depressor delay from the mean hindwing depressor to elevator interval, then subtracting this value from the mean forewing depressor to elevator interval.

Statistics

Appropriate parametric or nonparametric statistical tests were performed with the aid of SigmaStat statistical software (Jandel Scientific, Corte Madera, Calif.). Significance was assumed when $p \leq 0.05$. Values reported are the mean \pm standard error of the mean (SEM) unless otherwise specified.

Results

Effect of ablating the forewing tegulae on attempted steering manoeuvres

The responses of 4 of 24 locusts to either the onset or offset of a thermal stimulus are shown (Fig. 1). We recorded from two pairs of depressor muscles (m97, m99) to ensure that bulk shifts in depressor muscle asymmetries were occurring in response to the stimulus. In some cases, the m99s were inactive

during part of the flight sequence (e.g., the two sham-operated locusts shown). It is not uncommon for some flight muscles to be inactive during some wingbeat cycles (for example, see Wilson and Weis-Fogh 1962; Waldron 1967; Zarnack 1988). Table 1 is a summary of the relative effects of the treatments on stimulus-induced shifts of depressor muscle asymmetry and wingbeat frequency. We did not quantify either the shifts in depressor asymmetries or the changes in wingbeat frequency, owing to the fact that the stimuli had to be presented sequentially and we could not control for the possibility that the second response was either habituated or facilitated. Neither the sham operations nor ablation of the forewing tegulae prevented the generation of shifts in right–left depressor muscle asymmetries in response to stimulation with the heat lamp. Three of the locusts shown responded to either lamp-off (Figs. 1A, 1C) or lamp-on (Fig. 1B) by generating positive shifts in the depressor muscle asymmetry and increasing wingbeat frequency, indicating that they had attempted to turn right. The fourth locust responded to lamp-on with small negative shifts in depressor asymmetry and increases in wingbeat frequency (Fig. 1D).

We also examined whether other parameters that are known to change during attempts at steering manoeuvres were affected by ablation of the forewing tegulae. Figure 2 shows data for one individual that attempted to steer right after lamp-off both before and after the forewing tegulae were ablated. The abdomen deflected to the right (up), the FWA increased during the downstroke (thick line), indicating that the right forewing was depressed relative to the left forewing, the number of spikes per burst increased in the right m97 and decreased in the left m97, and m97 depressor asymmetry increased, indicating that the right muscle was activated before the left. This repertoire of changes in response to the stimulus did not change after the forewing tegulae were ablated (Fig. 2), and is the same as intentional steering responses reported elsewhere (e.g., Robertson and Johnson 1993; Dawson et al. 1997; Shoemaker and Robertson 1997).

Effect of ablating the forewing tegulae on free-flight ability

The distributions of free-flight ability differed between the intact/sham-operated locusts and the locusts with the forewing tegulae ablated (Fig. 3; Mann–Whitney test, $T = 1759.5$, $p = 0.012$). There were many more good flyers and poor flyers than nonflyers among the intact and sham-operated locusts, whereas there were more nonflyers and poor flyers than good flyers among the locusts with the forewing tegulae ablated (Fig. 3). It appears that in many cases, the nonflyers and poor flyers were slow to open their wings and properly initiate flight, especially following ablation of the forewing tegulae. Unfortunately, we were not able to study this, as it requires the use of high-speed videography to resolve.

Fig. 1. Forewing depressor muscle asymmetries typical of attempted steering manoeuvres that continued to be generated by tethered flying locusts following ablation of the forewing tegulae. Depressor asymmetries in the timing of activation between contralateral pairs of m97 and m99 (top and middle) and wingbeat frequency (WBF) (bottom) are shown for 10 s of a flight sequence containing a response by four individuals to a thermal stimulus. Shaded areas indicate that the heat lamp placed to the right of the animal was on. (A) Depressor asymmetries shifted to more positive values in response to lamp-off, indicating that the locust was attempting to steer towards the heat lamp. WBF also increased as the locust reacted to the stimulus. Similar depressor asymmetry shifts were seen both in the intact locust and after a sham operation (sham), although the response to the second stimulus was of a lower magnitude. The left m99 was not activated during every wingbeat cycle, which accounts for the missing data points in the middle traces. (B) Depressor asymmetries shifted to more positive values in response to lamp-on, accompanied by increases in WBF. The magnitude of the depressor asymmetry shift was smaller after the sham operation, whereas WBF changed more dramatically. (C) Depressor asymmetries shifted to more positive values both in the intact locust and after ablation of the forewing tegulae (-fwt) in response to lamp-off. There was also a small change in WBF in response to the stimuli. The depressor asymmetry shift was smaller after the forewing tegulae were ablated. (D) Depressor asymmetries shifted to more negative values, indicating an attempted turn away from the lamp in response to lamp-on, accompanied by increases in WBF. In this individual the magnitude of the responses was greater following ablation of the forewing tegulae in response to the second stimulus presentation.

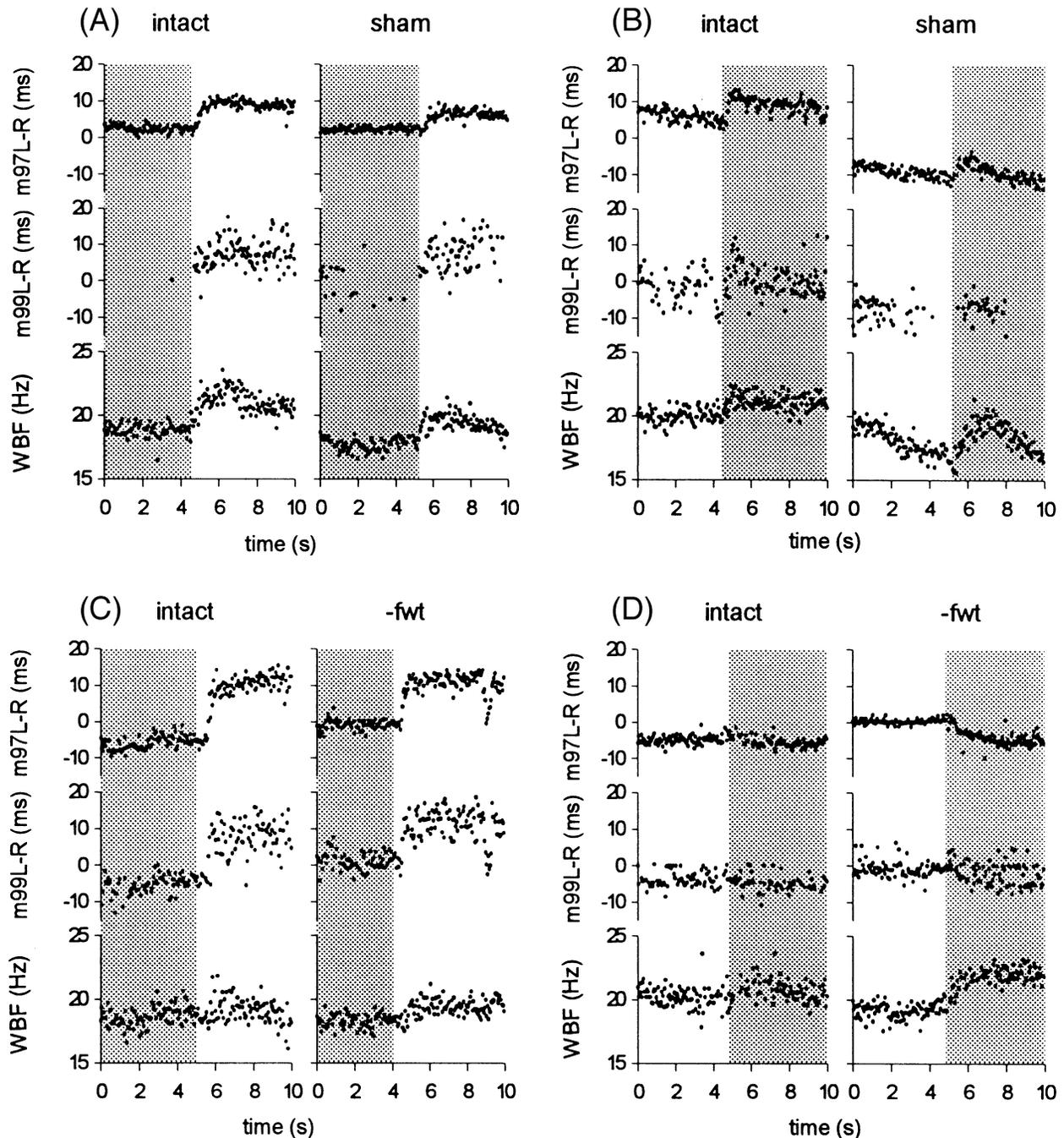
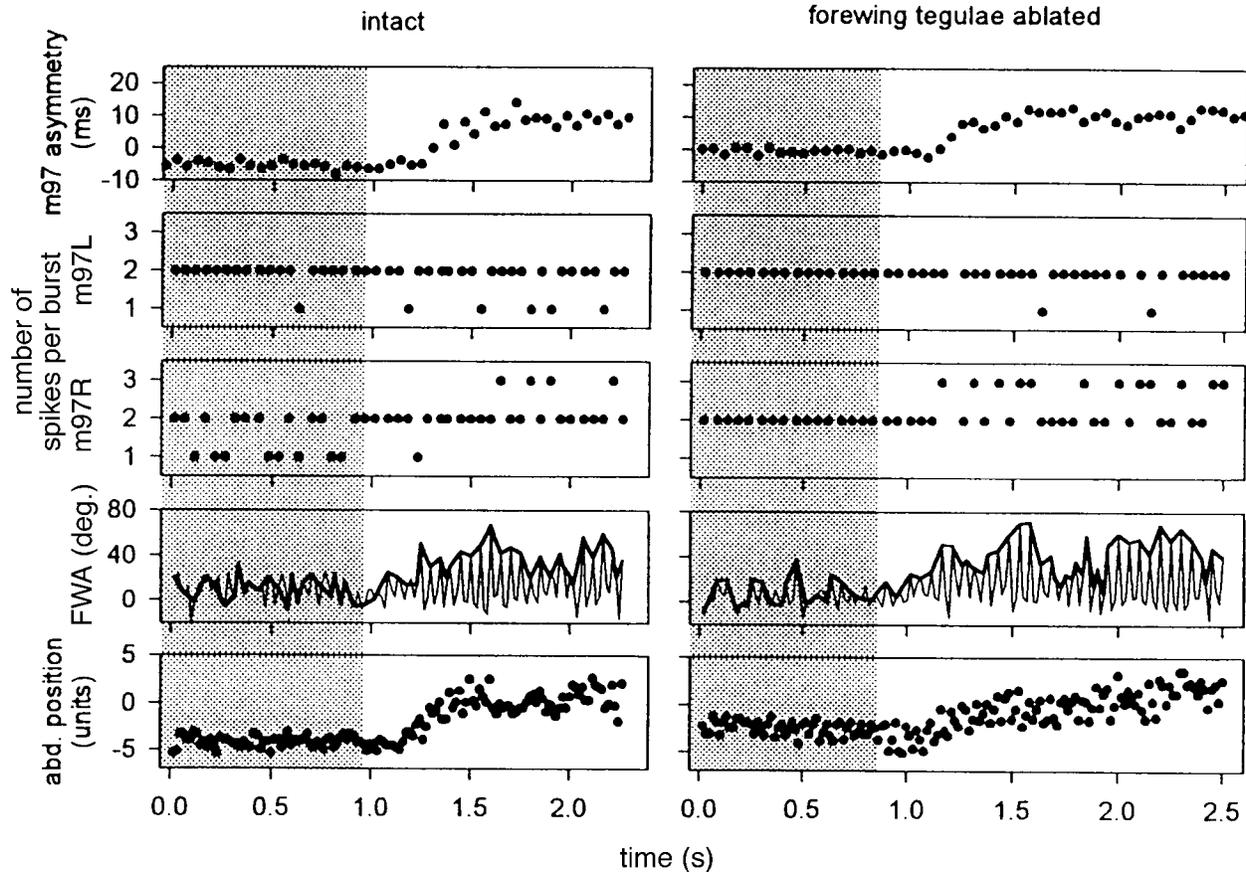


Fig. 2. Coincident changes in m97 left–right depressor asymmetry, number of spikes per burst, forewing asymmetry (FWA), and position of the abdomen in response to the heat lamp being turned off in one individual before and after the forewing tegulae were ablated. The heavy line in the forewing asymmetry trace indicates the angular asymmetries measured only during downstrokes. Position of the abdomen shows a value of zero when in line with the attachment point of the tether and is offset to the left when negative and to the right when positive. Note that the time alignment of abdomen position and FWA with the stimulus is unequivocal, while the alignment with muscle asymmetry and number of spikes per burst is ± 50 ms. There is no difference in any of these parameters due to ablation of the forewing tegulae.



Effect of ablating the forewing tegulae on the number of muscle potentials per cycle

When we found that free-flight ability was reduced in locusts following removal of the forewing tegulae, we reexamined EMG recordings of flight motor patterns from locusts that were intact and after the forewing tegulae were removed in the same individuals. It is well documented that there is no significant effect on the relative timing of depressor and elevator muscle activation for the hindwings and only a small effect for the forewings within each wingbeat cycle due to ablation of the forewing tegulae (Büschges and Pearson 1991; Büschges et al. 1992b; Gee and Robertson 1996). We therefore examined whether ablation of the forewing tegulae caused changes in other aspects of the flight motor pattern.

We determined the average number of muscle potentials (spikes) per wingbeat cycle both before and after ablation of the forewing tegulae from one depressor and one elevator muscle for both the forewing and hindwing of 28 locusts. The EMG data were collected during a previous study in which this was the control group, and other parameters of the motor patterns are published elsewhere (Gee and Robertson 1996). Figure 4 shows the mean changes in the average number of spikes per cycle after ablation of the forewing tegulae. We found a

significant increase in the average number of spikes per cycle following ablation of the forewing tegulae only for the forewing depressor muscle (Fig. 4; paired *t* test, $T = 2.35$, $p = 0.026$, $df = 27$). There was no significant difference between the average numbers of spikes before and after ablation of the forewing tegulae for any of the forewing elevator, hindwing depressor, or hindwing elevator muscles (Fig. 4; paired *t* test, $p \geq 0.87$). While we do not have a sham-operation comparison for this group, during the steering experiments there was either no change or a slight decrease in mean depressor spike number per burst following the sham operations for three locusts.

We found that activity in the forewing elevator muscle (m83) lagged behind activity in the hindwing elevator muscle (m113) in the intact locusts (Figs. 5A, 5B; paired *t* test, $T = 4.660$, $p = 0.00006$, $df = 29$; $T = 3.540$, $p = 0.0076$, $df = 8$). Immediately after the forewing tegulae were ablated there was a significant increase in the hindwing to forewing delay between elevator muscle activation (Fig. 5A; paired *t* test, $T = -4.074$, $p = 0.0003$, $df = 27$). For comparison we also examined the change in hindwing to forewing elevator delay after ablation of the hindwing tegulae and found that the forewing elevators now led the hindwing elevators; again the effect was significant (Fig. 5B; paired *t* test, $T = 3.521$, $df = 7$, $p = 0.0097$).

Fig. 3. Reduction in free-flight ability following ablation of the forewing tegulae. Free flight was initiated when the locusts jumped from a platform. The numbers of locusts classified as nonflyers, poor flyers, and good flyers (see Methods) are shown for the combined intact/ sham-operated condition ($N = 37$) and after ablation of the forewing tegulae (-fwt; $N = 43$) performed approximately 2 h prior to testing.

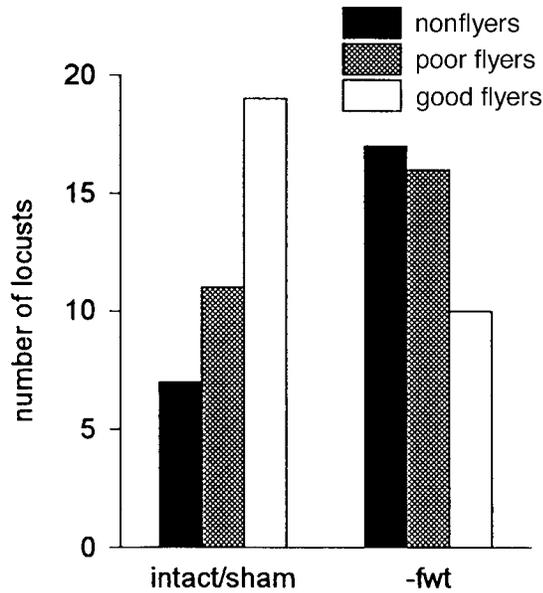
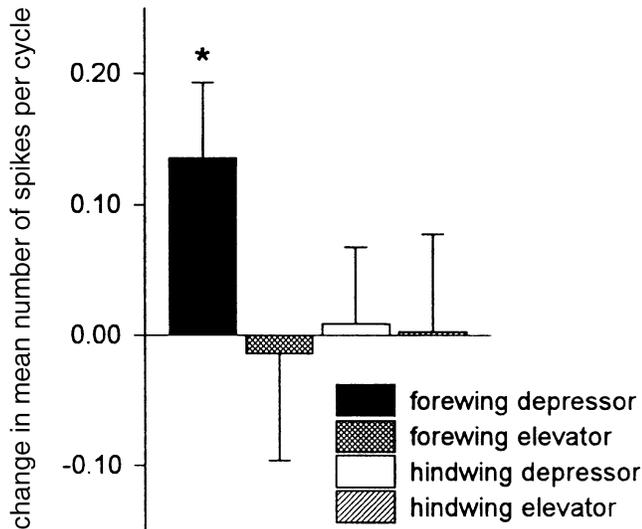


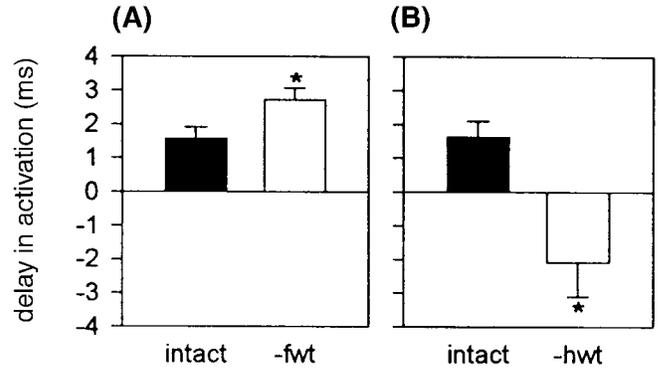
Fig. 4. Changes in the number of muscle potentials (spikes) per wingbeat cycle in a forewing depressor muscle (m97) but not in a forewing elevator muscle (m83) or hindwing depressor (m127) or elevator muscle (m113) after ablation of the forewing tegulae.



Discussion

The forewing tegulae have extensive input into the locust flight central pattern generator (Büschges et al. 1992a; Wolf and Büschges 1997), but their role in the control of flight has not been characterized. Ablation of the forewing tegulae does not affect the flight motor pattern in *Locusta* spp. except for slightly increasing the time interval between activation of the

Fig. 5. (A) Increase in the delay between activation of the hindwing elevator muscle (m113) and activation of the forewing elevator muscle (m83) after ablation of the forewing tegulae (-fwt). (B) Reversal of the hindwing to forewing elevator delay after ablation of the hindwing tegulae (-hwt), so that, on average, activation of the forewing elevator muscles led activation of the hindwing elevator muscles.



forewing depressor muscle and subsequent activation of the ipsilateral forewing elevator muscle (Büschges and Pearson 1991). We speculated that the forewing tegulae may play a more important role in the control of forewing position during steering rather than during straight flight. M97 is an important depressor and pronator of the forewings that inserts on the basalar sclerite and is highly involved in steering manoeuvres. Activity in m97 rotates the sclerite, which in turn affects the position of the tegula, presumably allowing the tegula to closely monitor activity of this muscle. When the forewing tegula is stimulated during flight it has a strong inhibitory effect on m97 (Neumann et al. 1982). This suggests that the forewing tegulae may be in a position to play a role in monitoring and modulating steering manoeuvres. We found that ablation of the forewing tegulae did not prevent the generation of shifts in forewing depressor muscle asymmetry in response to stimulation by the heat lamp. We also observed changes in the number of spikes per burst in the forewing depressor muscles induced by the stimulus, which were unaffected by ablation of the forewing tegulae. Wing and abdomen positions were also unaffected by ablation of the forewing tegulae. We therefore conclude that for tethered flying locusts, the forewing tegulae are not necessary for attempting normal steering manoeuvres

We also tested whether locusts with the forewing tegulae ablated were less likely to sustain unrestrained free flight. We found that some locusts with the forewing tegulae ablated sustained free flight; however, the majority did not fly well. We did not expect to see a deficit in free flight of the locusts with the forewing tegulae ablated because it has been documented that the timing of depressor and elevator activity of the motor pattern is unaffected by ablation of the forewing tegulae, except for a small delay in the initiation of forewing elevator activation (Büschges and Pearson 1991). The reason why some of the locusts did not sustain free flight has not been determined. It is interesting that in some locusts, free-flight ability was not compromised by loss of the forewing tegulae, whereas in other individuals it was. This behavioural difference suggests that the afferent input from the forewing tegulae may be

organized differently within the flight circuitry in different individuals. In fact, this has been seen at the level of flight interneurons that are variably contacted by afferents from the forewing tegulae in intact locusts (Büschges et al. 1992a). In this study we have not been able to examine the mechanisms behind the loss of free-flight ability. Loss of the forewing tegulae may decrease flight ability because of a deficit in the ability to either initiate flight or maintain it. Many of the locusts that did not fly appeared to jump and tumble, or appeared to have difficulty opening their wings, rather than jumping forwards and immediately spreading their wings to start flying. It is known that the forewing tegulae are stimulated by breathing in addition to flight, and the activity of m98 during walking should move the basalar sclerite onto which it inserts and activate the forewing tegula (Neumann 1985). It is possible that when the locust jumps to initiate flight, the tegulae are activated and, in turn, activate the elevator motoneurons to assist with opening of the wings and the initiation of flight. Activity in the tegula nerve has been seen to precede flight in tethered locusts (Neumann 1985). In addition, EMG recordings of tethered locusts always show activity in the forewing elevator muscles prior to activation of the depressor muscles at the beginning of a flight sequence (e.g., Wilson 1961). As the tegulae have excitatory input onto elevator motoneurons, and elevation of the wings must occur to initiate flight, the forewing tegulae may be important for opening the wings at the start of flight, and loss of the forewing tegulae may prevent locusts from getting started rather than prevent them from sustaining flight. Further work requiring the use of high-speed videography will be necessary to determine whether, in fact, the forewing tegulae are required for flight initiation.

We also found a small increase in the number of muscle potentials in the forewing depressor muscle, while there was no change in the number of spikes in the forewing elevator or the hindwing elevator or depressor muscle. This suggests that there may be some change in forewing kinematics after ablation of the forewing tegulae. Wolf (1993) has shown that after ablation of all the tegulae, the downstroke proceeds at a slightly faster rate than in intact locusts and the wings spend somewhat more time near the lower reversal point. The higher number of spikes in the forewing depressor muscle may contribute to a similar effect after the forewing tegulae are ablated. The downstroke of the forewings may occur more rapidly than in intact locusts, which, when combined with a slight delay in elevator muscle activation (Büschges and Pearson 1991), would be expected to result in the forewings spending somewhat more time in the aerodynamically unfavourable down position.

While it is well documented that the forewing tegulae are involved in recovery of the flight motor pattern after ablation of the hindwing tegulae, we have now demonstrated that they promote flight. Whether they are necessary to sustain flight or are primarily involved in initiation of flight remains to be determined.

Acknowledgements

Funding for this work was provided by the Natural Sciences and Engineering Council of Canada (NSERC) and the Whitehall Foundation Inc. Student fellowships were provided by

Ontario Graduate Scholarships and NSERC to C.E.G. and by the School of Graduate Studies, Queen's University, to K.L.S.

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