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Flight motor pattern in flying and non-flying Phasmida

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Summary. The insect order Phasmida comprises species with a broad spectrum of wing morphism and flight ability. By monitoring the electrical activity of several pterothoracic muscles the motor output during tethered flight was recorded for several Phasmida, ranging from excellent fliers to non-winged species. Both winged and non-winged species can generate a motor pattern as judged by criteria used to identify the locust flight pattern. However, in non-fliers the probability of expressing this pattern, its duration and precision are reduced. The antagonistic activity of the chosen muscle pairs is clearly different from the motor output during leg movements, which argues for specific motoneuronal coordination released for different behavioural performances. The demonstration of flight motor output in all tested Phasmida indicates that neural structures including their functional connectivity can be maintained independently of the appropriate peripheral structures. With respect to evolution this supports the idea that central neuronal interactions can be more conservative compared to changes in the periphery.

Key words: Phasmida – Wing reduction – Flight motor programme – Muscle bifunctionality – Neural conservatism

Introduction

It is now generally accepted that the flight motor output of intact locusts depends on a central flight oscillator influenced by peripheral sense organs (Robertson 1985; Stevenson and Kutsch 1987; Reye and Pearson 1988; Kutsch 1989; Möhl 1989). Robertson (1987) observed "that the flight system of locusts and crickets share a fundamental feature of interneuronal organization". This result is of interest in relation to studies concerning the evolutionary origin of flight (Kukalová-Peck 1978, 1986; Robertson et al. 1982; Dumont and Robertson 1986; Robertson and Olberg 1988).

We chose to study the insect order Phasmida for the following reasons: 1) They exhibit a wide range of different wing morphism, from developed wings to non-winged species. 2) Among the winged species representatives are known, from active fliers to non-fliers. 3) Phasmida belong to the Orthopteroidea; hence, all knowledge accumulated for locust flight (see below) can be compared with results of Phasmida. Therefore, this group appears to be suited to study whether changes in the periphery result in a modification of the circuitry underlying a specific motor output. Is the reduction of the wings during evolution paralleled with a change in the function of the relevant neuronal circuitry, reflecting adaptive differences (Robertson 1987)? Can reorganization in the periphery occur concurrently with a conservatism of its relevant central neural system?

For mature locusts several criteria have been listed describing the basic flight motor output (Wilson 1968; Kutsch and Stevenson 1984, 1988; Stevenson and Kutsch 1987):

(1) Identified motor units are activated rhythmically.

(2) Serially homologous motor units of both wing pairs are activated at the same frequency, and muscles of the hindwings lead their forewing homologues by several milliseconds.

(3) The muscles of a segment are divisible into two groups, correlated with wing elevation and depression.

(4) The phase of the elevator within the depressor cycle remains constant, independent of the duration of wing-beat cycle.

For a general description of Phasmida and their flight ability see Brunner von Wattenwil and Redtenbacher (1908); Beier (1968); Bedford (1978); Clark (1974); Carlberg (1986).

Abbreviations of species names and indication of sexes are given in the first paragraph of Results

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Materials and methods

Animals. For the present investigation adult males and/or females of the following 5 species were studied: *Acrophylla wuelfingi* Redtenbacher; *Carausius morosus* Br.; *Extatosoma tiaratum* MacLeay; *Phyllium bioculatum* Gray; *Sipyloidea sipylus* Westwood. These animals were raised from eggs in our laboratory, under a light/dark regime 12:12 h, at a room temperature of 18°–23 °C, at relative humidity 70–80%. They were fed on blackberry and oak leaves.

Tethered flight condition. A small copper holder was glued to the tergite along the anterior part of the mesothorax with a mixture of resin/beeswax. Heavier species, such as females of *Acrophylla* and *Extatosoma,* were glued with dental wax to a holder along the sternum of the meso- and metathorax. The first tarsal segments with the claws were amputated to prevent them gripping or clinging to objects, otherwise the animals remained unimpaired. The holder was attached to a clamp system allowing free movement of the wings, legs and abdomen.

Various stimuli were applied to initiate flight activity. With the diverse species it became apparent that different conditions and stimulus combinations were required for adequate excitation. Experiments were performed under a warm, red light (ambient temperature approx. 30 °C). The animal was tethered in a warm air stream (25 °C), velocity 2.5 m/s. For satisfactory performances, the wind speed occasionally had to be reduced. Light usually induces thanatosis in Phasmida (see Bässler 1983), characterized by aligning the middle- and hindlegs backwards along the body and pointing the stretched forelegs forewards. Thanatosis could be overcome by stroking the clamp system (see Results). The basic rhythm of the wings' movements could be monitored by a microphone placed under the animal. With longer flight sequences muscle potentials could be used to trigger a stroboscope (see Wilson and Weis-Fogh 1962) and, in this way, the recruitment of the muscles during the wing cycle could be determined.

Muscle recordings. Motor output was monitored by recording the electrical muscle activity (EMG). Locust flight movements are induced by the alternating activity of wing depressor and elevator muscles (Wilson and Weis-Fogh 1962). Since muscles of each set are almost synchronous the basic flight motor pattern can be described by recording from a single pair of antagonistic muscles (Stevenson and Kutsch 1987; Pearson and Wolf 1987). For *Carausius morosus* Marquardt (1940) has described the muscles of the thorax and their innervation. Based on topographical observations (points of insertion, innervation pattern, etc.) Marquardt was able to associate nearly all muscles of *Carausius* with their 'homologues' in locusts (Snodgrass 1929). Among the pterothoracic muscles we concentrated on two pairs present in all examined Phasmida. For a standardization of the muscle systems we adopted the nomenclature of Snodgrass (1929) for locusts: M90, M119 (first remotor coxae) and M99, M129 (subalar muscle) of the meso- and metathorax, respectively.

For muscle recordings stainless steel wires (insulated to the tip) were inserted through the cuticle. Due to differences in muscle thickness electrode diameter had to be adapted (30 µm for small, 40 µm for large animals) and depth of insertion had to be precisely controlled (from 0.3 mm for both segmental subalar muscles of *Carausius* to 2.5 mm for the metathoracic remotor coxae of *Extatosoma* females). Electrodes were inserted through the pleural wall (by puncturing the cuticle with a minute needle); in the wingless *Carausius* the Remotor coxae electrodes were inserted from the tergum where the point of origin could be identified externally. To increase the probability of good recordings, in both segments two electrodes were inserted into each muscle (for technical convenience only the left side was considered). The location of electrodes was routinely checked post-mortem by the Prussian blue method (Bentley and Kutsch 1966). An earthed reference electrode was implanted into the abdominal haemocoel. The electrodes were secured to the cuticle with a resin-beeswax mixture. Their free ends were soldered to a multi-channel board connected to a conventional electrophysiological set-up (pre-amplifier, storage oscilloscope), including a 4-channel tape recorder (Racal 4 FM) for subsequent analysis of data. Since occurrence of flight motor output varied for the examined species the number of studied animals per group was different. It ranged from 4 in *Sipyloidea* to 73 in *Carausius.*

Results

Short description of tested Phasmida

The males of the species *Phyllium, Acrophylla* and *Extatosoma,* as well as the parthenogenetic female *Sipyloidea* (see Fig. 1, *Sy* ♀) possess a pair of small forewings (elytra) covering the bases of the large hindwings (alae), which at rest extend to the abdominal tip. The female of *Acrophylla* represents the only case among the chosen species in which both sexes appear to be similar with respect to wing morphology, though the female's body is much heavier and the wings much larger than in males. The female of *Extatosoma* is large (heaviest species of all), she possesses only vestigial wing pairs, scale-contoured. The female of *Phyllium* is rather flat. Large leaflike forewings cover the body, her hindwings are almost completely reduced. Finally, the parthenogenetic female of *Carausius* lacks wings.

The following abbreviations will be used throughout: *Ac* ♂, *Ac* ♀ *Acrophylla wuelfingi* male, female; *Ex* ♂, *Ex* ♀ *Extatosoma tiaratum* male, female; *Ph* ♂, *Ph* ♀ *Phyllium bioculatum* male, female; *Sy* ♀ *Sipyloidea sipylus* female; *Ca* ♀ *Carausius morosus* female.

General flight ability

There is no information available of flight performance in nature concerning the chosen species. Therefore, a general test for flight ability was carried out by throwing them into air, and observing their flight path. Trials were performed in a large illuminated hall and also outside in the sun. *Ac* ♂, *Ex* ♂, *Ph* ♂, and *Sy* ♀ possess large hindwings. When thrown into air they opened their wings and used them for active flight, resulting in horizontal flight or even a short ascent. *Ph* ♂ can take off from the surface either spontaneously or when chased, and will circle around for some time. *Ac* ♀ opened her large hindwings, but they vibrated only slightly, decelerating her fall down to the floor. After launching *Ex* ♀ dropped to ground, during descent a slight opening of the vestigial wings was observed. For *Ph* ♀ a slight tilting of the rigid forewings is seen. This behaviour, in connection with her body shape, resulted in a gliding towards the ground. All species spread their long legs and this was occasionally also seen in the wingless *Carausius.* This typical posture will be termed 'flight position'.

The flight ability of the 4 active fliers was also tested when tethered in the warm wind stream. The duration of continuous wing movements was measured for 5 animals per group, each tested 5 times at 2 min intervals. When flight exceeded the limit of 3 min, wind was stopped which resulted in cessation of wing movements (only a

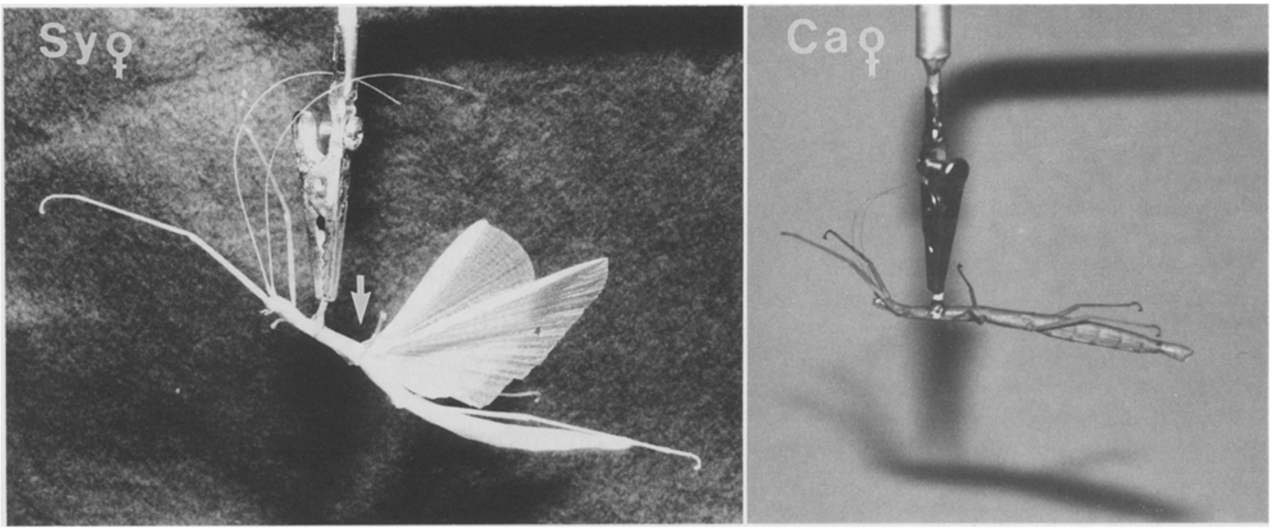

Fig. 1. Position of tethered *Sy* ♀ (active flier) and *Ca* ♀ (non-winged) in the windstream. Typical features of this posture (termed 'flight position') observed in both instances are: raised and extended legs, stretched abdomen. The opened forewings in *Sy* ♀ are barely visible at the posterior end of the mesotergum (arrow)

Table 1. Tests of several flight parameters of examined Phasmida species

Species	Free flight[a]	Duration of active flight[b] (s)			Wing-beat frequency[c] (Hz)		Terminology
		Mean (±SD)	Min	Max	Mean (±SD)	*n*	
Ph ♂	excellent	142 (58)	19	>180	13.4 (2.2)	5	active fliers
Ac ♂	good	10.4 (7.1)	3	31	9.3 (1.0)	8	
Ex ♂	good	6.0 (8.9)	<1	43	11.7 (1.3)	5[d]	
Sy ♀	good	4.8 (3.8)	<1	12	12.0 (1.4)	4	
Ac ♀	glide				9.8 (1.0)	4	winged non-fliers
Ph ♀	glide				10.0 (2.1)	6	
Ex ♀	none				8.6 (1.8)	7	
Ca ♀	none				10.9 (1.9)	14	non-winged

[a] General flight ability, tested by launching animals into air. [b] Duration of active flight, tethered in the wind stream; see text. [c] Wing-beat frequency, based on analysis of rhythmic motor output, *n* number of different animals. [d] For *Ex* ♂ wing-beat frequency has been calculated on microphonic recordings only

few flights continued for a further couple of seconds). Table 1 summarizes the results, including the range of flight duration and the mean. *Ph* ♂ had exceedingly long flights, usually reaching the upper conditional limit of 3 min. Counting such programmed interruptions as 180 s flights, for *Ph* ♂ a mean flight duration of 142 s was calculated (statistical differences of the means compared to any of the other groups, $P < 0.001$). For *Sy* ♀, *Ac* ♂, and *Ex* ♂ no statistically significant difference between the means is apparent ($P > 0.01$, unpaired *t*-tests). Therefore, while *Ph* ♂ can be designated as an excellent flier, the other 3 species comprise a more homogeneous group of active fliers that exhibit flights of short duration.

Flight motor pattern

Due to the morphology of the wings and flight ability we have grouped the animals into 3 classes (see Table 1): 1) active fliers: *Ph* ♂, *Ac* ♂, *Ex* ♂, *Sy* ♀; 2) winged non-fliers, with developed or reduced wings: *Ac* ♀, *Ph* ♀, *Ex* ♀; 3) non-winged: *Ca* ♀. For these 3 classes the flight motor pattern was analyzed by recording the electrical activity of pterothoracic muscles which appear to be equivalent to the flight muscles in locusts (e.g. Wilson and Weis-Fogh 1962).

Active fliers. Muscle electrode implantation did not impair the normal flight performance. The active fliers readily took the typical flight position (see Fig. 1, *Sy* ♀): stretching of all legs, the forelegs about 45° with respect to the longitudinal axis, the middle legs perpendicular to the body length axis, the hindlegs nearly 30° pointing caudally. The elytra were turned sideways, thereby allowing the alae unhindered movements. Vibrations of the forewings could be observed. The abdomen is stretched or slightly tilted upwards.

EMGs clearly reveal the regular activation of the

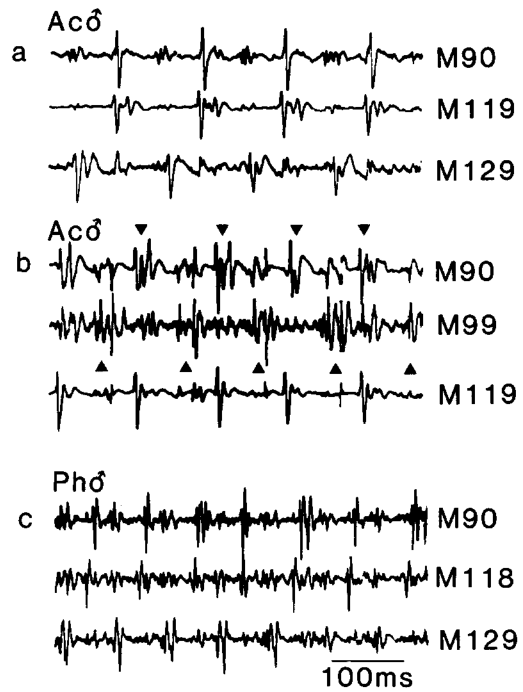

Fig. 2a–c. Flight motor output of active fliers. **a, b** Motor pattern of *Ac* ♂ demonstrating the antagonistic activation of the chosen muscle pair in the hindwings (elevator-depressor; M119–M129) and forewings (elevator-depressor; M90–M99); additionally, the activity of serial homologues (M90–M119) is seen. Due to some cross-talk the bursts generated by the specific muscles are indicated (triangles). **c** Motor pattern of *Ph* ♂, showing the recruitment of another metathoracic elevator (M118) in relation to the commonly recorded depressor (M129); additionally, the activity of a mesothoracic elevator (M90) is seen

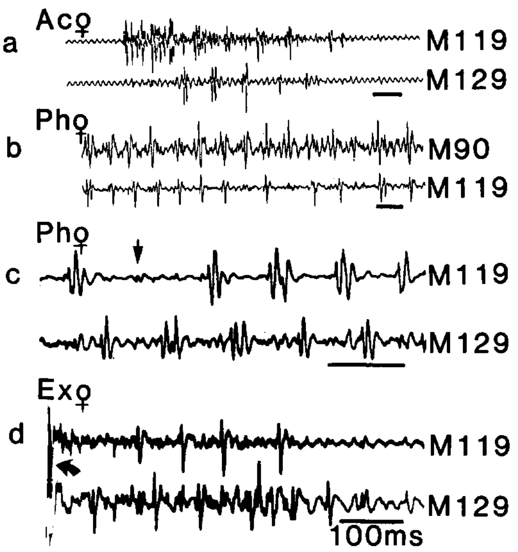

Fig. 3a–d. Flight motor output of winged non-fliers. **a** Muscle activity in *Ac* ♀ demonstrating the initial elevator (M119) burst at the beginning of flight followed by a short sequence (5 cycles) with antagonistic activation of the metathoracic muscle pair. **b** Flight sequence in *Ph* ♀ demonstrating the regular activation of serial homologous elevators of both segments (M90–M119). **c** Antagonistic activation of the metathoracic muscle pair in *Ph* ♀. Arrow indicates the apparent failure of this motor unit's activity during one cycle. **d** Short antagonistic sequence of the metathoracic muscle pair in *Ex* ♀, initiated by wind and a stroke to the holder system (curved arrow)

chosen muscle pairs (Fig. 2). Typically, there were one or two discharges per motor unit. Due to an analysis of the EMGs (potential amplitude and form) at least 2 motor units are expected for M129, while there are at least 3 motor units for M119 (in accordance to 3 fast motoneurones in *Carausius* retractor coxae; Graham and Wendler 1981). The two muscles are recruited antagonistically. Stroboscopic illumination (see Materials and methods) demonstrated an excitation of M129 near the upper wing position, while M119 was activated when the lowest wing position was reached. This not only confirms the neurogenic principle of muscle activation in Phasmida flight (cf. Pringle 1981), but also indicates that both muscles act as depressor and elevator of the wings, respectively, in accordance to their homologues in locust flight (cf. Wilson and Weis-Fogh 1962; Stevenson and Kutsch 1987).

Serially homologous muscles of both wing pairs were activated with the same frequency and almost in synchrony (for further analysis, see below) (Fig. 2a, b). This was best seen for the elevator pair M90–M119, and, occasionally, for the depressor pair (M99–M129), too.

As typical for locust (Stevenson and Kutsch 1987), flight started with an activation of the elevator muscles indicating raising of the closed wings. Very often activity stopped transiently before regular activity of both antagonists commenced. Occasionally, other pterothoracic muscles were encountered. They were observed to be recruited as known for their locust homologues; as an example, see the metathoracic promotor coxae (M118) (Fig. 2c) which serves as an elevator in locust flight.

Winged non-fliers. Within this group 3 species have been studied with rather different wing morphology exhibiting gliding or no flight ability (see Table 1). For *Ac* ♀ short flight sequences could be elicited correlated with raising of both wing pairs and weak flapping of the alae. Despite the irregular appearance of wing movements, muscle recordings revealed an antagonistic activation pattern (Fig. 3a). Typically, performance started with the contraction of the elevator (M119); both segments operated with the same frequency, and serial homologues were in near synchrony. These results could also be demonstrated for *Ph* ♀ (Fig. 3b). Then the broad flat forewings were tilted and vibrated. It was of special interest to detect antagonistic activation of the muscles of vestigial hindwings (Fig. 3c) which are rigidly embedded in the surrounding cuticle. For *Ph* ♀ regular flight activity of more than 5 s duration have been encountered. For *Ex* ♀ such a performance never lasted longer than 1 s. For this species flight position could usually be released only by additional mechanical stimuli, such as stroking to the holder system (Fig. 3d) or supplementary wind puffs to the body. With these stimuli, the legs were often briefly raised and vibrated together with the two wing pairs (scales). The examined hindwing muscles were excited antagonistically (Fig. 3d). Both segments operated at the

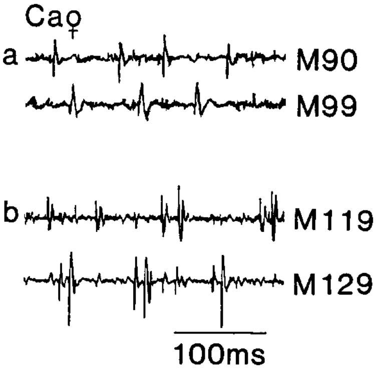

Fig. 4a, b. Flight motor output of the wingless *Ca* ♀. **a** Antagonistic activation of the mesothoracic muscle pair. **b** Antagonistic activation of the metathoracic muscle pair

same frequency, though the brevity of activity and the small size of the forewing subalar (M99) prohibited further investigation of mesothoracic muscle activity.

Adoption of flight position was not always correlated with the typical flight motor activity. Often irregular motor patterns were produced, ranging from: 1) tonic activation of only one muscle of the pair; 2) tonic activation of one muscle interspersed with pauses during which the antagonist was recruited; 3) tonic activation of both muscles with no clear antagonistic pattern. Occasionally, tonic and rhythmic sequences followed each other, even when different segments were considered. These results are similar to previous studies of locust larvae in the wind stream (Kutsch 1971, 1985).

Non-winged. Finally, we have tested the non-winged *Ca* ♀. For this species it became very difficult to elicit a response to the wind stimulus. Usually, *Ca* ♀ adopted the typical position of thanatosis (see Materials and methods). Light touching or wind stimuli did not induce any movements or clear muscle activation. However, muscle activity could often be elicited by a simultaneous removing of tarsal contact and stroking the holder system. If these strong stimuli were combined with the wind stimulus then the legs were sometimes transiently spread out. This posture was similar to that shown by active fliers in the wind stream (see Fig. 1, *Ca* ♀). Mostly, EMGs showed a very unspecific tonic muscle excitation, comparable to the irregular patterns as mentioned for winged non-fliers. Occasionally, however, transient rhythmic sequences (shorter than 1 s) of muscle activity were detected. Then, antagonistic muscle activation might occur in both segments (Fig. 4). Compared to active fliers it should be noted that the intervals between successive spikes of a muscle can change instantaneously. Serial homologues on one side can be recruited at the same average frequency, though the coordination between the segments might vary. Nevertheless, it is quite clear that this pattern exhibited typical features of the flight motor

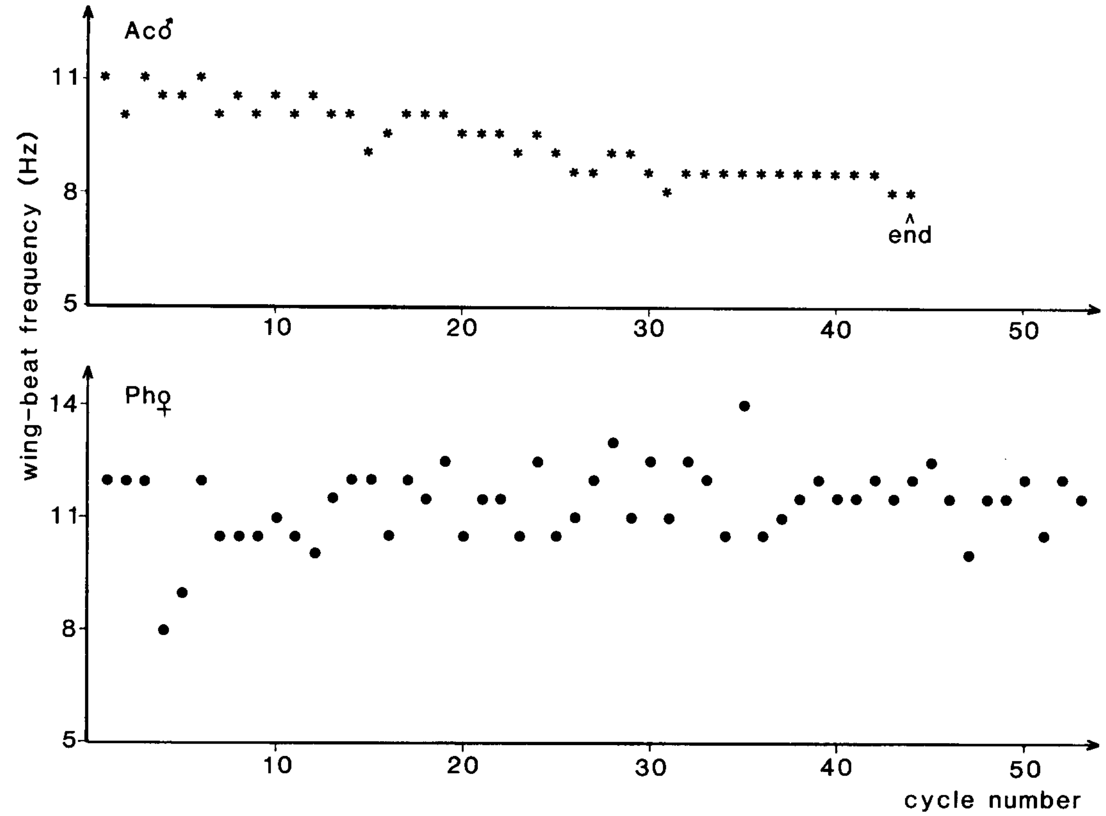

Fig. 5. Sequential frequency histogram of an active flier (*Ac* ♂) and a winged non-flier (*Ph* ♀) from start onwards. For the active flier regular (muscle potential) intervals occur and a slow decrease of wing-beat frequency is seen from start to end. For a winged non-flier the duration of successive intervals is more variable; no general frequency change during the flight sequence is apparent (this flight continued in a similar fashion for another 29 cycles)

pattern, even though it is not as perfect as for winged active-flying species.

Analysis of the flight motor pattern

In the following section some more information is given with respect to parameters describing the flight motor pattern as exemplified for locusts (cf. Wilson and Weis-Fogh 1962; Stevenson and Kutsch 1987; Kutsch and Stevenson 1988).

Output frequency. For *Locusta* a slight increase in wing-beat frequency occurs after the beginning of flight (Weis-Fogh 1956; Gewecke and Kutsch 1979; Kutsch and Stevenson 1984) followed by a slow decline to a cruising flight frequency. This overall pattern was, in general, observed in active flying Phasmida (Fig. 5, *Ac* ♂). The initial increase in wing-beat frequencies was not so distinct, but a slow decrease during continuous flight was observed, correlated with rather regular intervals of successive muscle activations. For winged non-fliers, such as *Ph* ♀, a gradual frequency change was not apparent throughout a flight sequence. When individual cycles were examined, considerable fluctuations of cycle time were evident (Fig. 5, *Ph* ♀). Changes of intervals were most pronounced in the short sequences of the non-winged *Ca* ♀.

For a further comparison of output frequency we examined regular intervals, for each animal comprising a period of at least one second during midflight (for non-fliers occasionally also shorter flight sequences had to be evaluated) (see Table 1). The best flier (*Ph* ♂) clearly produced the highest mean wing-beat frequency (approx. 13.5 Hz), while the lowest wing-beat frequency (approx. 8.5 Hz) was seen in *Ex* ♀, the winged animal with the weakest flight performance (*Ex* ♀). Output frequency in the non-winged *Ca* ♀ was found between both extremes.

Phase relationship of the antagonistic muscle pair. In locusts the phase of the elevator within the depressor cycle remains more or less constant independent of variations in cycle time (Waldron 1967; Stevenson and Kutsch 1987; Pearson and Wolf 1989). For long sequences of active flying Phasmida a linear correlation between cycle length and depressor-elevator interval could also be demonstrated, resulting in an almost constant phase (Fig. 6a). This relationship was also valid for winged non-fliers (Fig. 6b). Due to the short sequences of antagonistic activity we did not consider this phase for the non-winged *Carausius*. For the phase of the elevator within the depressor cycle the following values were calculated (mean ± S.D.): active fliers: 0.5 ± 0.03; winged non-fliers 0.47 ± 0.08. There was no statistical difference between both groups indicating that, on average, this phase relationship was independent of flight performance.

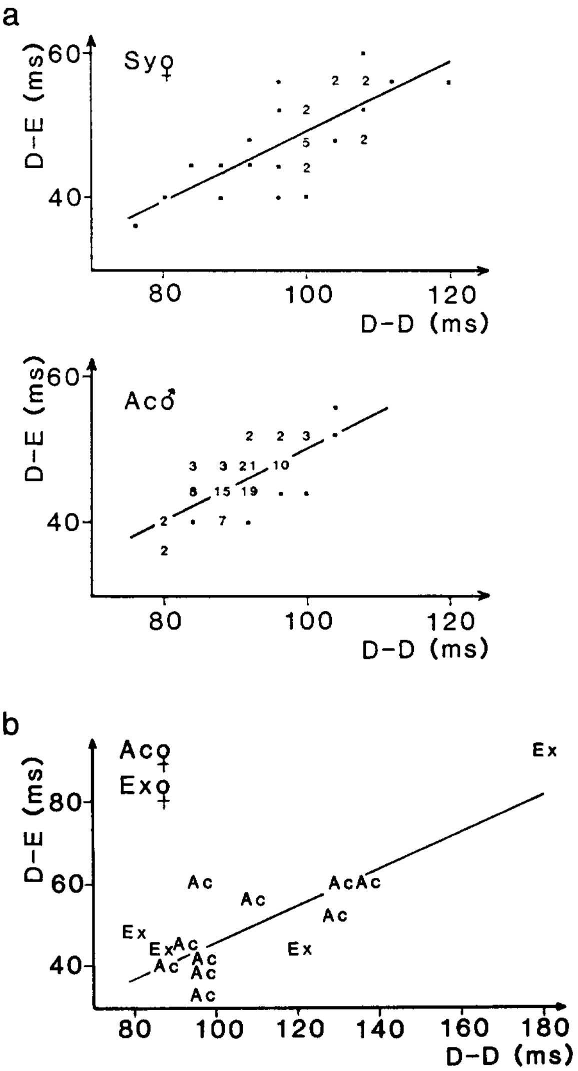

Fig. 6a, b. Correlation of depressor-elevator latency (D–E) with cycle length (D–D) in active fliers (**a**) and winged non-fliers (**b**). While in **a** a single long flight performance for each species (*Sy* ♀, *Ac* ♂) has been analyzed, in **b** (*Ac* ♀, *Ex* ♀) several short sequences have been pooled. Linear regression analysis reveals a positive correlation of both parameters in all instances

Latency of serial homologues. As mentioned above, in Phasmida homologous muscles of both pterothoracic segments were activated at the same frequency. With respect to the recruitment of serial homologous muscles for an active flier the hindwing muscle tended to lead its counterpart by about 5 ms with only a small variation around the mean (e.g. Fig. 2a). In a winged non-flier, however, there was a broad distribution around 0 ms indicating a more general synchrony of both serial homologues (e.g. Fig. 3b). This variation in activation of serial homologues was also obvious in the wingless *Carausius*.

Muscle activity during struggling

The examined muscles are also attached to the coxa, and in locusts can be recruited in both, flight and walking (Wilson 1962; cf. also Ramirez and Pearson 1988). We thus tested motor activity during leg movements in order to be certain (especially in non-flying Phasmida) that the

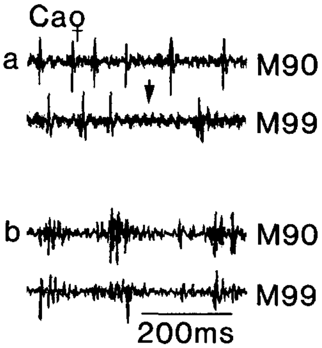

Fig. 7a, b. Comparison of motor output during flight position (**a**) with output during leg struggling (**b**); forewing muscle pair of the same individual (*Ca* ♀). **a** muscles are activated antagonistically (arrow points to an apparent failure of M99), **b** synergistic muscle activation combined with a lower frequency

above described pattern represents a motor output typical for (active or fictive) wing movements. Various stimuli (such as touching the legs or pricking the abdomen) can lead to leg struggling. During such sequences muscle bursts could reach frequencies of up to 6 Hz. Under these conditions no specific co-ordination of middle and hindlegs was apparent. No specific phase of serial homologous muscles was predominant such as seen during coordinated walking (Delcomyn 1987). During such struggling movements bursts occurred whereby both muscles of the chosen pair were recruited synergistically (Fig. 7b). Therefore, not only the overall output frequency but also the phase relation of the specific muscles was quite distinctive and different for both patterns (cf. Fig. 7a, b). Their recruitment for both motor patterns (flight programme vs. leg movement) was such as postulated by the model of muscle bifunctionality (Wilson 1962; Ramirez and Pearson 1988).

Discussion

Previously several criteria have been listed to describe the basic flight motor output in mature locusts (see Introduction). The present study indicates that these parameters can also be demonstrated for the motor output in Phasmida correlated with flight posture, irrespective of the configuration of the wings and flight ability. Even the phase value of specific muscles coincides quite well with that calculated for flying intact locusts (Waldron 1967; Stevenson and Kutsch 1987). There are, however, some differences between species. Active fliers produce rather regular and long series of muscle activity and the time relation of hindwing to forewing serial homologues is very rigid. Non-fliers can also show such a pattern. But these are less likely to generate such activity, and, when produced, only for a short period. For this group it appears that the duration of successive intervals may vary more and the timing of fore- and hindwing homologues is not as perfect as in active fliers. It has been shown that proprioceptive feedback not only strengthens the precision of successive intervals (Kutsch 1974) but also the co-ordination among the four wings (Wendler 1974).

It is assumed that in non-fliers sensory input from the wings is reduced or changed either due to reduction of the wings or restrictions of their excursions. This might result in greater variability of the flight motor output in this group. Differences and irregularities of sensory inflow and its central integration might also explain the appearance of irregular motor patterns as well as differences in duration (Reye and Pearson 1988).

It becomes apparent that a flight motor pattern can be elicited independent of the periphery. Reduction of wings to immobile vestiges in the flightless grasshopper *Barytettix* is correlated with the absence of primary flight muscles, even though the relevant motoneurones are similar to those of *Schistocerca* (Arbas 1983). This resulted in the notion that "insect motoneurones are not dependent upon trophic influences from their targets for survival and maintenance of their differentiated phenotype" (Arbas and Tolbert 1986). The present results extend our knowledge insofar, as not only the neural structure *per se* but also their basic functional circuitry (at least in connection to the studied motor programme) is independent of the periphery, substantiating other studies with flight of insects and birds (Provine 1983; Provine et al. 1984; Robertson and Olberg 1988).

According to fossil records the Pterygota appeared during the Devonian period (approx. 380 mill. years ago; Hennig 1961), from which the Protorthoptera parted off during the upper Carboniferous period (approx. 300 mill, years ago; Sharov 1971). Phasmatodea and Orthoptera have been separated since the middle of the Permian period (approx. 250 mill. years ago) (Hennig 1961; Sharov 1971). Although it cannot be proven, it might be assumed that the flight motor pattern in the present locusts is basically similar to that of their common ancestors. This pattern should have evolved during a period of about 100 mill. years. With respect to the separation of the Phasmatodea and their phylogenetic trend to reduce their wing system it is interesting to speculate that apparently 250 mill. years of evolution did not result in a considerable change in basic features of this motor output. A similar conclusion is drawn for the evolution in birds. Though spanning a much shorter time scale, it is shown that neither domestication nor longer-lasting evolutionary changes towards flightlessness in fowls led to a loss of the central pattern generator for flight (Provine et al. 1984; Provine 1984).

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