The role of the frontal ganglion in locust feeding and moulting related behaviours

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Summary

In the desert locust, *Schistocerca gregaria,* the frontal ganglion (FG) plays a key role in control of foregut movements, and constitutes a source of innervation to the foregut dilator muscles. In this work we studied the generation and characteristics of FG motor outputs in two distinct and fundamental behaviours: feeding and moulting. The FG motor pattern was found to be complex, and strongly dependent on the locust's physiological and behavioural state. Rhythmic activity of the foregut was dependent on the amount of food present in the crop; animals with food in their crop demonstrated higher FG burst frequency than those with empty crop. A very full gut inhibited the FG rhythm altogether. When no feeding-related foregut pattern was observed, the FG motor output was strongly correlated with the locust's ventilation pattern. This ventilation-related rhythm was dominant in pre-moulting locusts. During the moult, synchronization with the ventilation pattern can be transiently switched off, revealing the endogenous (feeding-related) FG pattern. This presumably happens during vigorous air swallowing, and could also be induced experimentally. Our findings suggest that the FG central pattern generator can be modulated to generate a variety of motor outputs under different physiological conditions and behavioural contexts.

Key words: frontal ganglion, central pattern generator, desert locust, *Schistocerca gregaria*, feeding, moulting, ventilation.

Introduction

The insect nervous system has been widely and successfully employed as a model system in the study of the neural basis of behaviour (Hoyle, 1975; Burrows, 1996; Bässler and Büschges, 1998). The desert locust *Schistocerca gregaria* has served as one of the most important insect neurophysiological preparation, offering very well-described nervous as well as neuroendocrine systems (Burrows, 1996). This insect has also served as a leading system for studies of pattern generation and sensory control of motor pattern generation (Wilson, 1961; Wolf and Pearson, 1987). In light of the above it is rather surprising that, to date, very few studies have examined the neural control of foregut peristalsis and the motor patterns associated with foregut activity in the locust.

The locust foregut consists of a pharynx that leads into a short narrow oesophagus. The oesophagus is curved, running dorsally before turning posteriorly to lie beneath the brain. In the prothorax it merges into a muscular crop, which opens into the proventriculus. The muscles of the foregut consist of intrinsic and extrinsic muscles. All dilator muscles are extrinsic, arising from the head walls and tentorium, and attaching to the foregut (Albrecht, 1953). The major source of innervation to the foregut dilator muscles is the frontal ganglion (FG; Aubele and Klemm, 1977; Allum, 1973; Ayali et al., 2002). The FG lies on the dorsal surface of the pharynx, anterior to the brain. A pair of frontal connectives links the FG

with the tritocerebrum, and a recurrent nerve passes backward along the dorsal surface of the pharynx up to the hypocereberal ganglion. Another three pairs of fine nerves arise from the FG to innervate the foregut.

The role of the FG in feeding, growth and development has been the focus of many studies for more than a century (Faivre, 1863; Marchal, 1911). Most of the studies examined the effects of ablating the FG on the subsequent behaviour and development of the insect. Removal of the FG in adult *S. gregaria* resulted in decreased feeding activity (Highnam et al., 1966; Hill et al., 1966). Ganglionectomy in *Locusta migratoria* caused the abolition of crop emptying (Bignell, 1973). Similar results were also reported in Lepidoptera, including adult *Heliothus zea* (Bushman and Nelson, 1990). *Manduca sexta* larvae from which the FG was removed were reported to exhibit slower growth (Bell, 1986) and deficiency in food ingestion (Griss et al., 1991). In adult *M. sexta*, Miles and Booker (1994) found that the FG is essential for the activity of the cibarial pump during feeding, and both necessary and sufficient to produce the motor patterns of the foregut muscles (Miles and Booker, 1994, 1998).

In addition to feeding, in several different insects the foregut and FG play a critical role in at least one other aspect of insect life history: the moult (Bounhiol, 1938; Clarke and Langley, 1963; Penzlin, 1971; Hughes, 1980a; Carlson and O'gara,

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1983; Bell, 1986; Bestman et al., 1997; Miles and Booker, 1998). A moulting insect displays a stereotypical set of behaviours that culminate in the shedding of the old cuticle at ecdysis. There are two stages of ecdysis in which the insect needs to exert pressure on the body wall: during rupture of the old cuticle, and when expanding the new cuticle and wings after emergence (Reynolds, 1980). The principal mechanism locusts employ for exerting this pressure is to fill the gut with fluid or air. Jousset De Bellesme (1877) was the first to show that the pronounced enlargement of freshly emerged dragonflies was accomplished by internal air pressure built up in the digestive tract (summarized by Allum, 1973). Since then, air swallowing during ecdysis has been reported in several insect species (Cottrell, 1962; Carlson and O'gara, 1983; Miles and Booker, 1998; Hughes, 1980d). Hughes (1980d) reported that the success of the imaginal ecdysis of the desert locust depends on inflation of the gut with air.

Bell (1986) suggested that in *M. sexta* the FG plays a role in the ecdysis to the adult stage, or eclosion. The FG was shown to be involved in swallowing air; frontal ganglionectomy abolished air swallowing immediately and thereby caused defects in eclosion and in expansion of the wings. Recent work has revealed that the FG plays a critical role in the successful completion of both larval (Bestman et al., 1997) and adult moults in *M. sexta* (Miles and Booker, 1998). At both stages, the FG controls a foregut motor pattern that is used first to remove moulting fluids from the space between the old and new cuticle prior to ecdysis, and second for air swallowing.

In the accompanying paper (Ayali et al., 2002) we began the characterization of the spontaneous FG motor pattern in an *in vitro* preparation isolated from all descending and sensory inputs. The present study continues this work, and investigates the generation and characteristics of FG motor outputs in the intact locust in two distinct and fundamental behaviours, feeding and moulting.

Materials and methods

Schistocerca gregaria (Forskal) were reared as previously described (Ayali et al., 2002). Adults and fifth instar larvae of both sexes were used. For the feeding-related experiments, locusts were starved for 24 h prior to supplying them with fresh grass. Experimental animals were chosen at different time intervals after the initiation of feeding (10 min, 2 h and 24 h). For the moulting-related experiments, the fifth instar experimental animals were chosen at different and specific stages of the imaginal ecdysis cascade (see Results). Criteria by which these stages were recognized followed Hughes (1980a).

Locusts were briefly anaesthetized in CO_2, and their wings and legs removed. The FG and the nerves leaving it were easily accessible by cutting out a window in the head cuticle (frons), and clearing fat tissue and air sacs as required. Movements of the gut were observed and recorded using a force transducer attached to the oesophagus wall. Extracellular recordings of FG nerves and the activity of a specific foregut dilator

(muscle 37) were made with fine (125–175 µm) insulated silver wire and hook electrodes that were electrically insulated with petroleum jelly. Muscles of the abdominal wall (mostly lateral muscle 176) were recorded in order to monitor the ventilation pattern, using bipolar stainless-steel pin electrodes. Data were recorded using a 4-channel differential AC amplifier (Model 1700 A-M Systems), played back in real time and stored on the computer using an A-D board (Digidata 1320A, Axon instruments) and Axoscope software (Axon instruments).

Locust saline consisted of 147 mmol l^{-1} NaCl, 10 mmol l^{-1} KCl, 4 mmol l^{-1} CaCl$_2$, 3 mmol l^{-1} NaOH, (Frutarom, Haifa, Israel), 10 mmol l^{-1} Hepes (Biological industries, Bet Haemek, Israel), pH 7.2 (Abrams and Pearson, 1982; Penzlin, 1985).

The significance of results was tested using a one-way ANOVA test, followed by Bonferroni test (Instat, GraphPad software inc, San Diego, CA, USA).

Results
The frontal ganglion motor patterns

Fig. 1 shows synchronized rhythmic multi-unit bursts of action potentials recorded from two FG efferent nerves; a frontal connective (FC) and a median pharyngeal nerve (MPN), just after the locust initiated feeding. This rhythmic pattern resembles the output of the FG efferent nerves in the *in vitro* preparation, when totally isolated from all external inputs (Ayali et al., 2002). Considering the muscles that these nerves innervate, the activity recorded shows a rostral-to-caudal phase relation, and the motor pattern generated corresponds to a rostral-to-caudal peristaltic wave of contraction in the foregut, which we have defined as 'feeding-related pattern'. The foregut in our intact preparations was not visible along its entire length and we could only observe rhythmic dilation of its anterior parts as food was passed backwards.

The FG motor output varied greatly between preparations. Rhythmic activity, as above, was not always observable, and when present, displayed variations in cycle period as well as in the phase relations between bursts of action potentials recorded from the different nerves.

Effect of the state of the gut on the FG rhythm

When testing for different physiological states of the animal that would account for the observed variability in the FG motor patterns, we found that differences in cycle period or burst frequency depended on the amount of food present in the gut (Fig. 2). Fig. 2A demonstrates that the FG burst frequency was significantly higher in animals with food present in their crop, compared to those with empty crops (0.30±0.04 Hz *versus* 0.11±0.04 Hz, respectively, N=12). However, in cases where the gut was replete with food throughout its length, no FG bursting activity was recorded. We noted that the slow rhythmic pattern recorded in locusts with an empty gut was similar to the spontaneous intrinsic frequency of totally isolated *in vitro* preparations (0.07±0.03 Hz, N=48) (Ayali et al., 2002). To further confirm the dependence of cycle

frequency on the state of the gut, we artificially manipulated the crop's fullness state. Fig. 2B shows an example of extracellular recording from a FG nerve in a locust with an empty gut, before (Bi), and after (Bii) injecting petroleum jelly into the crop. It clearly shows that filling the crop with petroleum jelly increased the burst frequency (0.36 Hz before *versus* 0.14 Hz after). These results corroborate the reported effect of food and the state of the gut on the FG rhythm burst frequency (Fig. 2A).

Interaction of the foregut and the FG with the ventilation patterns

In our ongoing investigation of the sources of variations in the FG motor patterns we tested for interactions with another known and important central pattern generator in the locust. Simultaneous recordings of the locust ventilation rhythm (monitored by EMG recordings from abdomen wall muscles) and foregut dilation (monitored by a force transducer attached to the oesophagus) revealed that the foregut could be active in synchrony with the ventilation pattern (Fig. 3A), whereas at other times it showed no rhythmic movements (Fig. 3B), or a totally independent motor pattern (Fig. 3C).

We further tested the interaction between the foregut and FG pattern with the ventilation pattern. Fig. 4A shows an example when no independent feeding-related pattern was observed; the FG rhythmic output was strongly coordinated with the ventilation rhythm. Cutting the ventral nerve cord between the pro- and mesothoracic ganglion (where the connectives are relatively long and easy to reach) resulted in uncoupling of the FG and ventilation rhythms. Disconnecting the metathoracic ganglion, which is the site of the ventilation central pattern generator (Bustami and Hustert, 2000) from the FG caused an immediate inhibition of the rhythmic activity (Fig. 4Bi) followed by the emergence of a new independent FG pattern within 15 min (Fig. 4Bii).

Moulting-related FG patterns

At the onset of the moult the fifth instar larval abdomen acts as a ventilatory pump (Hughes, 1980b). Simultaneous extracellular recordings from the abdominal muscles and MPN show that the ventilation pattern recorded at this stage was rapid (0.44±0.04 Hz, *N*=13) and continuous. It was correlated with the FG efferent nerve output (MPN, Fig. 5A). When disconnecting the ventilation central pattern generator (CPG) from the FG (by tightening a pre-implanted ligature on the connectives between the mesothoracic and the prothoracic ganglion) the synchronized activity recorded from the FG was instantly lost (data not present). In order to identify possible neural pathways in which the ventilation CPG interacts with the FG CPG, we consecutively disconnected the FG nerves (Fig. 5). In the control, the FG rhythmic output was strongly
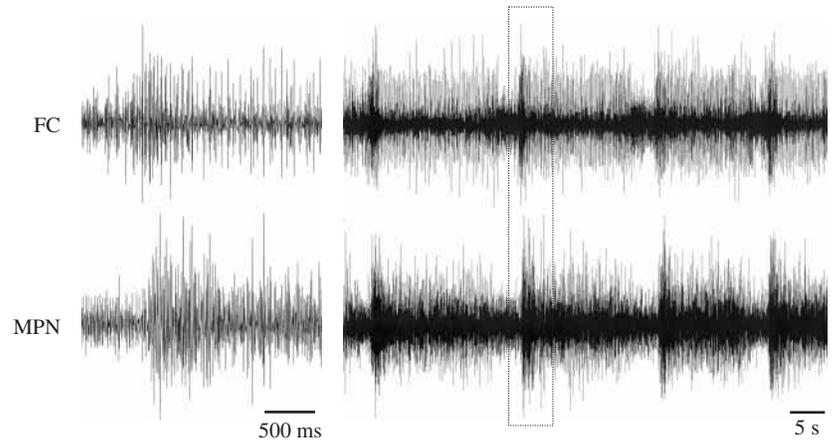

Fig. 1. Simultaneous extracellular recording from two of the frontal ganglion (FG) efferent nerves, frontal connective (FC) and median pharyngeal nerve (MPN), in a fully intact preparation. The boxed areas on the right panels are played (left) at a higher sweep speed to reveal phase relations between different members of the frontal ganglion (FG) central pattern generator.

coordinated with the ventilation rhythm (Fig. 5A). Cutting the recurrent nerve (RN) resulted in the appearance of new rhythmic bursts of action potentials that seemed to be independent of the ventilation-coupled activity (Fig. 5B). Further cutting of the two frontal connectives (practically
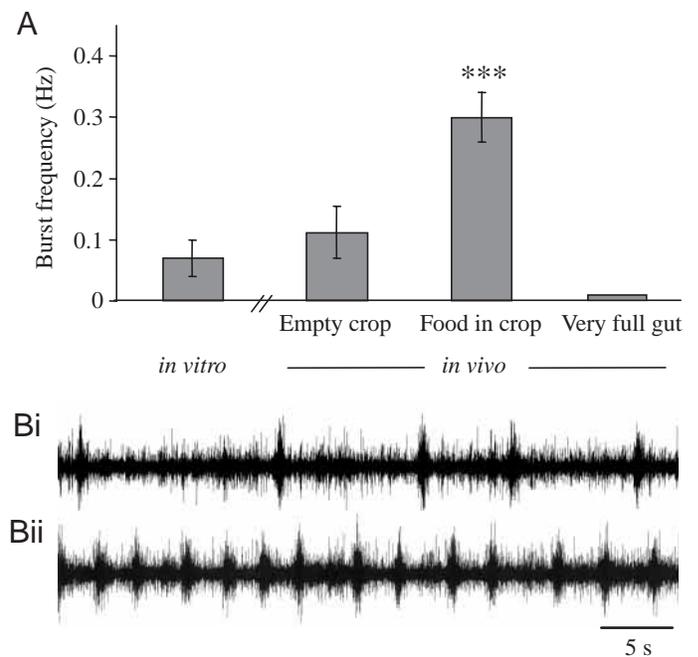

Fig. 2. (A) Differences in burst frequency of the frontal ganglion (FG) rhythmic pattern *in vitro* and *in vivo* reflecting the effect of the amount of food present in the gut. Values are means ± s.d. ***P<0.001. (B) Extracellular recording from an FG nerve before (i) and after (ii) injecting petroleum jelly into the locust's previously empty crop, demonstrating the effect of the state of the gut on the rhythm.
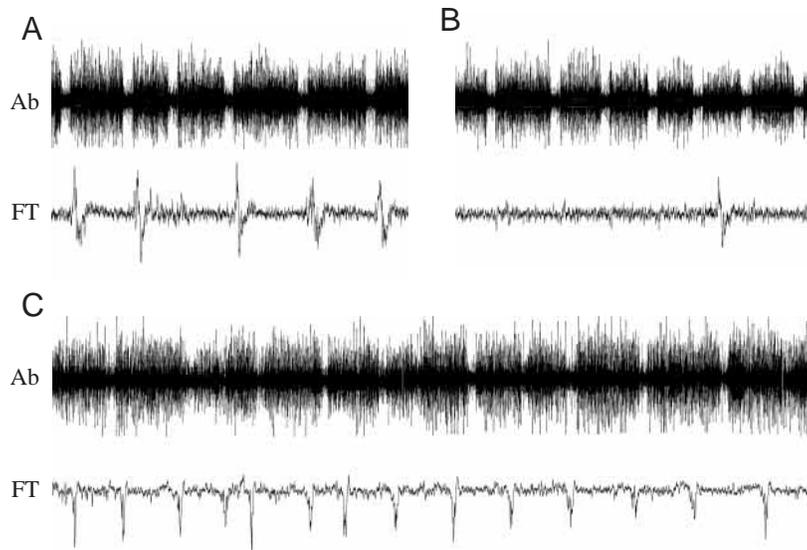
Fig. 3. Recording from an abdomen wall muscle (Ab) and simultaneous output of a force transducer (FT) connected to the foregut wall in a fully intact preparation. The foregut may participate in the ventilation rhythm in almost full synchrony (A). At other times it may show no rhythmic movements (B) (same preparation as in A); or a totally independent motor pattern (C).

isolating the ganglion *in situ*) and subsequent repeated superfusion with saline, caused uncoupling of the two CPGs and emergence of an FG rhythmic pattern that resembled the output of the FG efferent nerves in the *in vitro* preparation (Fig. 5C).

When locusts were collected at a very precise time point,
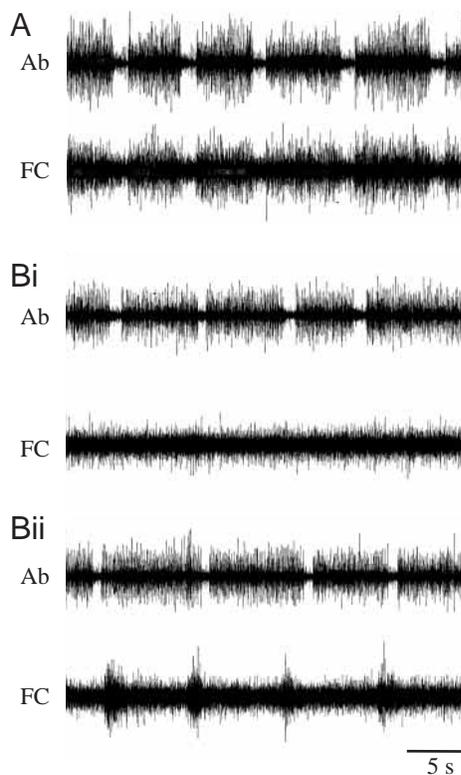
after the animal had found a perch for moulting and moved to an upright position, simultaneous FG and ventilation recordings revealed that the very consistent ventilation-synchronized pattern had changed. The totally synchronized pattern gave rise to alternation between rapid bursts of FG activity (0.74 ± 0.06 Hz, as recorded from muscle 37, N=3) and bouts of ventilation (Fig. 6). At this point the locust has switched to air swallowing behaviour (our observations; Hughes, 1980a). The time window in which air swallowing behaviour is exhibited is very limited, so it was practically impossible to record the nervous activity during this behaviour.

In the different preparations studied (N=19) the ventilation burst frequencies ranged from 0.4 Hz before the onset of air swallowing behaviour, to 0.7 Hz at the time the old cuticle split. As the old cuticle ruptured and the thorax started to emerge, a unique pattern of activity appeared in which the abdomen periodically contracted in long squeeze-like bouts that exerted pressure on the old cuticle (recorded as long periods of tonic, high frequency firing; Fig. 7A). Following the emergence of the pro- and mesothoracic legs and the proceeding of the moult, the described squeezing pattern increased in duration and a variable number of fast ventilatory strokes occurred at the end of each tonic compression (Fig. 7B,C). Fig. 7D summarizes squeeze duration (the duration of the first and longest tonic episode in each cycle) and cycle period during these different behaviours. As in the onset of the moult, the FG pattern closely followed all the changes in the ventilation pattern, from the vigorous abdominal contractions to the later tonic compression pattern with the changes in duration of tonic compression, throughout the expansion phase of the new adult, as described by Hughes (1980c).

Next we wanted to test whether the reason for the transient uncoupling of the FG and ventilation patterns described above is indeed the emergence of the air-swallowing behaviour. In the example shown in Fig. 8A the adult locust has fully emerged, and is occupied in expanding its wings (as in Fig. 7C). At this stage, we punctured the inflated gut by simply inserting a syringe needle through the cuticle and the wall of the crop. As can be seen in Fig. 8B, this caused a marked change in the interaction between the FG and ventilation patterns. The FG rhythm switched from full synchrony between the activity recorded from the different nerves and the

Fig. 4. (A) Simultaneous extracellular recordings from an abdomen wall muscle (Ab) and a frontal connective (FC) in a fully intact preparation, exhibiting full synchrony between the ventilation and the frontal ganglion (FG) patterns. (B) Uncoupling of the ventilation and FG patterns after the thoracic ventral nerve cord has been cut between the pro- and mesothoracic ganglia. The trace shown in Bi, precedes the one shown in Bii, demonstrating an independent FG rhythm after only a few minutes.

ventilation pattern, to a new and different rhythmic pattern. This new pattern resembled the air-swallowing burst frequency ($0.60\pm0.09\,\mathrm{Hz}$ for 10 consecutive bursts, compared to $0.74\pm0.06\,\mathrm{Hz}$, respectively), as well as the described feeding-related behaviour (i.e. a rostral-to-caudal phase relation; Fig. 1), although the latter was much slower. The independent FG rhythm was interrupted at every squeeze-like contraction of the abdomen. The new air-swallowing pattern developed rather progressively and the number of bursts within a bout gradually increased (Fig. 9). The pattern went through fluctuations, probably reflecting fluctuations in air pressure in the punctured gut, as the locust refilled it with air and lost the air again through the punctured crop.

Discussion

The locust foregut is a complex morphological structure that is designed to cope with a diverse diet, consisting of foods of different composition and form. In addition to its role in feeding, the foregut also has a role in air swallowing at different stages of the moult. Control over moulting fluids swallowing during the early stages of the moult has also been suggested (Miles and Booker, 1998). Thus, the motor patterns of the foregut are expected to be multiple and complex, and the FG CPG controlling these motor patterns is expected to generate various motor outputs, depending on the animal's physiological and behavioural state.

In this work we gained a first insight into the role that the multifunctional FG CPG plays in two distinct and fundamental behaviours, feeding and moulting. We have begun to investigate the different rhythmic patterns demonstrated by the FG in these different behavioural contexts.

We have shown that the amount of food present in the gut modulates the frequency of the FG rhythm. In a feeding locust the motor patterns of the foregut work to push food backwards to the crop and empty the crop toward the midgut. In cases when the entire gut seemed to be replete with food, these feeding-related patterns were inhibited altogether and no corresponding rhythmic activity could be recorded from the FG nerves. Volumetric feedback from the gut has been reported elsewhere: in the fly, sensory information mediated *via* stretch receptors from the gut-wall has been shown to be instrumental in the control of feeding (summarized by Möhl, 1972). Simpson (1983) showed in locusts a system in which volumetric feedback from the crop and hindgut interacts in the regulation of meal size. Clarke and Langley (1963) concluded that in *L. migratoria* the FG forms a link in the passage of nervous impulses originating from the stretch receptors of the pharynx and passing *via* the posterior pharyngeal nerve, FG and frontal connectives to the brain. In *M. sexta* the pattern of foregut activity has also been shown to vary with the amount of food present in the foregut and crop
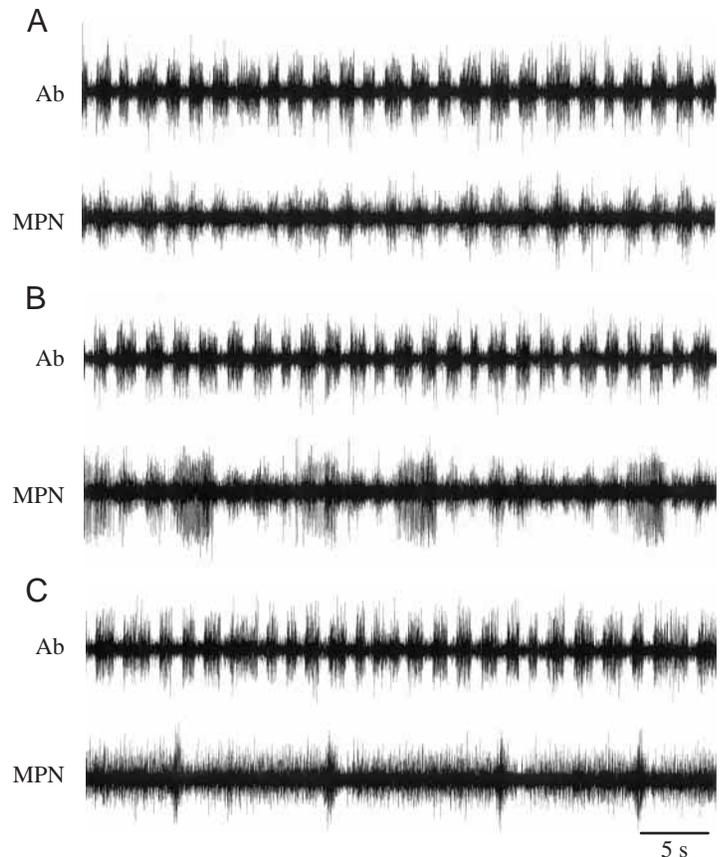

Fig. 5. (A) Simultaneous extracellular recordings from an abdominal wall muscle (Ab) and frontal ganglion (FG) efferent nerve (MPN) of pre-moult fifth instar larvae, showing full synchrony between the ventilation and the FG patterns. (B) New bursting pattern after cutting the recurrent nerve. (C) An independent FG pattern, similar to the *in vitro* preparation, emerges after disconnecting both frontal connectives.

Fig. 6. Alternation between bouts of ventilation rhythm and frontal ganglion (FG) rhythm can be seen during air swallowing in recordings from an abdominal muscle (Ab) and a foregut dilator muscle (37).

(Miles and Booker, 1994). Ascending signals of sense organs (e.g. stretch receptors) could either produce inhibition directly or generate central inhibition (Griss et al., 1991).

FG pattern alteration could also work *via* neuromodulators or humoral factors. Release of humoral factors that have a role
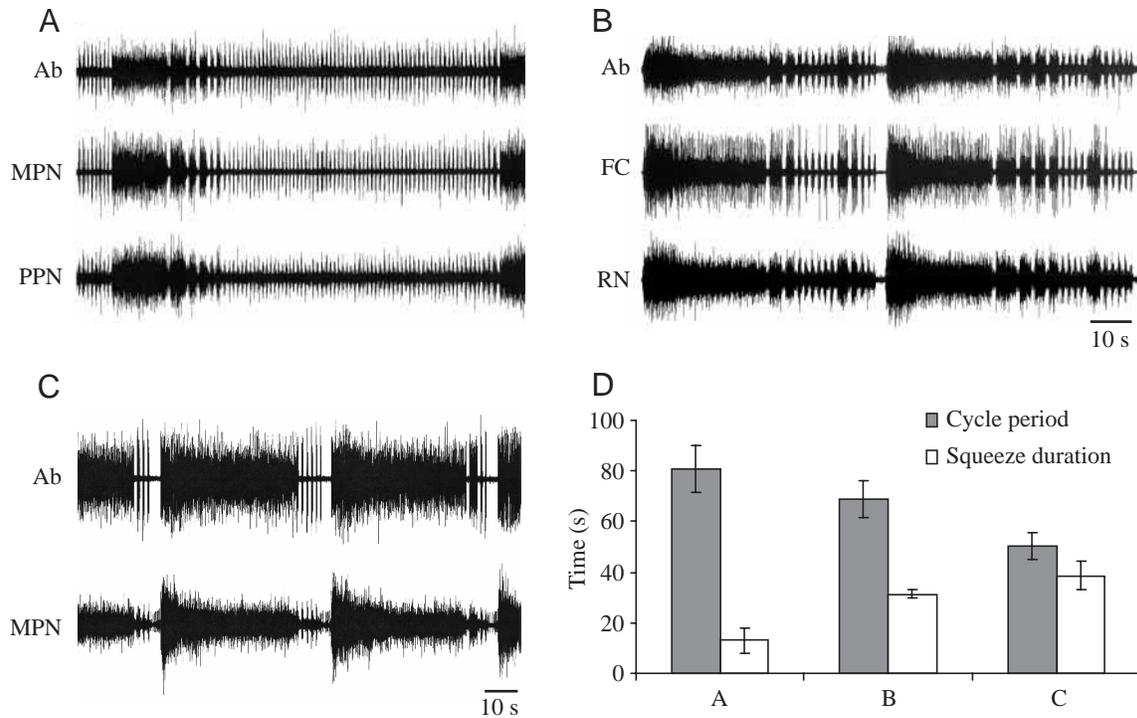
Fig. 7. Simultaneous extracellular recordings from an abdominal wall muscle (Ab) and frontal ganglion (FG) efferent nerves at three different stages of the moult. (A) The old cuticle is split. (B) The head, thorax and pro- and mesothoracic legs emerge. (C) Expansion of the wings. (D) Variation in cycle periods and squeeze duration (first long, high frequency burst in each cycle) in the different moult-related behaviours. The ventilation and the FG patterns are fully synchronized throughout these different stages of the moult. Values are means ± s.D. MPN, median pharyngeal nerve; PPN, posterior pharyngeal nerve; FC, frontal connectives; RN, recurrent nerve.
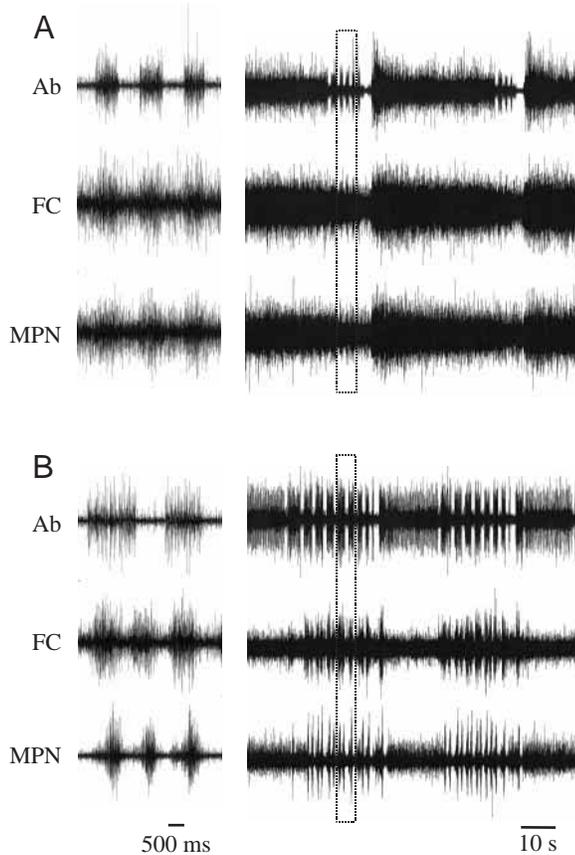
in the cessation of locust feeding and involvement of chemoreceptors of the foregut have already been suggested by Bernays and Chapman (1973). In the adjacent paper we have shown that application of haemolymph (taken from animals with a very full gut or from animals just before the moult) to the FG *in vitro* abolished the rhythm completely. In contrast, haemolymph from feeding locusts had no inhibitory effect. We also showed that the rate of appearance of the FG rhythm in an *in vitro* preparation is dependent on the physiological state of the donor locust, suggesting washout of some modulatory humoral factors. Various neuromodulators have been traced to FG neurons, some of which are known to modulate gut activity (Duve et al., 1995, 1999, 2000; Miyoshi and Endo, 1998; Maestro et al., 1998). These factors could in turn have an effect upon the FG circuits themselves.

When no feeding-related foregut pattern was observed, the FG motor output was strongly correlated with the locust's ventilation pattern. Other workers have showed that in locusts,

Fig. 8. (A) Simultaneous extracellular recordings from an abdominal wall muscle (Ab) and two frontal ganglion (FG) nerves (FC and MPN), showing full synchrony between the ventilation and the FG patterns at the time of wing expansion. (B) Uncoupling of FG and ventilation patterns generated by puncturing a hole in the inflated gut. The FG rhythm resembles feeding/air-swallowing pattern. The boxed areas on the right panels are played (left) at a higher sweep speed.

as in other insects, ventilation interacts with other motor systems (Miller and Mills, 1976; Paripovic et al., 1996; Ramirez, 1998). Our experiments reveal that the full synchrony between the FG and ventilation rhythms can be switched off, which suggests a hierarchical relationship between the ventilation and foregut motor patterns. Gut movements can be recruited to participate in ventilation, probably as a means of helping with haemolymph circulation. Recent work on the neural pathways of cardiac reflexes in lepidopterous insects shows that the heartbeat can be triggered by stimulation of axons in the visceral nerve arising from the FG (Kuwasawa et al., 1999). We still lack evidence for such a direct interaction between the FG and ventilation. We hope to gain more information by focusing on the FG and ventilation CPGs during the moult.

As the moult approaches, the last larval instar locust ceases to feed (approximately 24 h prior to shedding of the old cuticle) (Hughes, 1980a). The abdomen acts as a ventilatory pump, performing characteristic movements that may help to loosen the old cuticle. We have shown that the FG ventilation-CPG interaction is dominant all through the different stages of the moult. The full synchrony between the FG and ventilation rhythms is only momentarily switched off at the specific stage of air swallowing. By filling the gut with air, the larval locust can generate enough internal pressure to split open the old cuticle (Bernays, 1972). As the gut fully inflates, the FG pattern returns to demonstrate synchrony with the ventilation rhythm. This lasts all through the 'expansional motor program' (Hughes, 1980c) that serves to expand the new cuticle into its final form and to expand the wings.

The gut remains inflated until the end of the moult (Hughes, 1980d). Deflating it induces uncoupling between the FG and the ventilation patterns. The locust senses that the gut is loosened and switches its behaviour from full synchronization to a new pattern that correlates to air swallowing activity. Very much like the feeding-related pattern (only faster), the air-swallowing pattern is characterized by a rostral-to-caudal phase delay between bursts of activity recorded on the different FG nerves, which generate a wave of anterior-to-posterior peristalsis in the foregut. Hence, our results support Hughes's (1980d) suggestion that the air-swallowing motor program is regulated by the degree of foregut distension. Its frequency is correlated with the degree of gut inflation, and may be controlled, at least in part, by receptors located on the foregut.

Miles and Booker (1998) reported that in adult *M. sexta*, the FG is activated about 6 h before the adult emerges from the pupal case. The crop initially fills with moulting fluids, then with air. After eclosion, as the moth hangs in a position to expand its wings, the FG is again activated, producing a distinct air-swallowing motor pattern that lasts about 1.5 min.

Fig. 9. Simultaneous extracellular recording from an abdominal wall muscle (Ab) and frontal ganglion nerve (MPN), showing the evolution of the air-swallowing pattern on the MPN after puncturing a hole in the inflated gut. The number of bursts within each bout gradually increases.

During this period, the wings visibly expand. The motor pattern recorded from the FG at air swallowing was similar to that displayed during feeding (Miles and Booker, 1998). As mentioned above, we have also observed many similarities between the FG rhythms recorded during locust feeding and air swallowing.

The elaborate and complex nervous connectivity pattern of the locust stomatogastric nervous system offers many alternative routes between the foregut or the thoracic ventilation CPG to major neuroendocrine centers (e.g. corpora cardiaca) on the one hand, and the central nervous system on the other (Allum, 1973). Thus, at present we do not know the
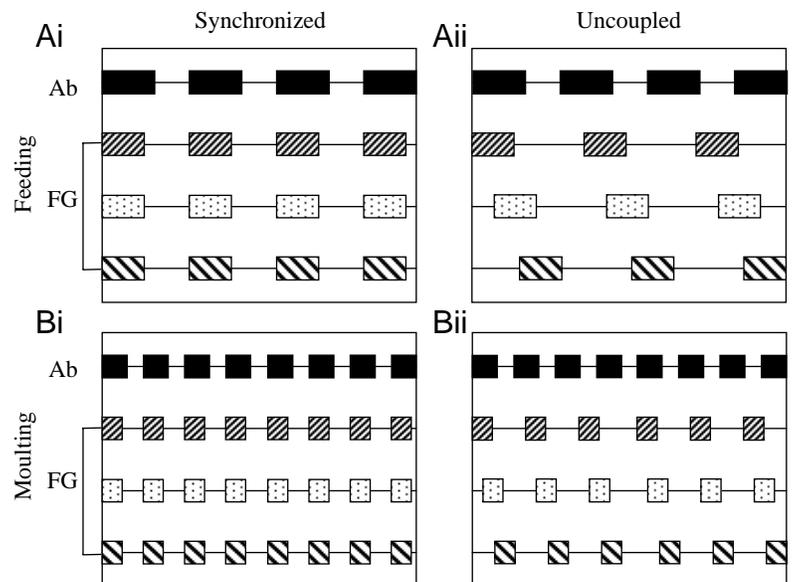

Fig. 10. Schematic illustration of the two activity patterns of the frontal ganglion (FG). The synchronized pattern shows full synchronization of activity recorded on the FG nerves together with the ventilation pattern. The uncoupled patterns show an FG rhythm that is independent of ventilation. See text for details.

sources of the neuromodulators and the routes of modulation of the FG rhythmic motor patterns.

To summarize, the locust FG can generate two major types of motor patterns, which can be defined with relation to the ventilation pattern: the first, synchronized and the other, uncoupled (Fig. 10). In feeding adults or mid-instar larvae the 'feeding related pattern', uncoupled to or independent of the ventilation pattern (Fig. 10Aii), is generated whenever food needs to be passed through the foregut. At other times the synchronized pattern is demonstrated (Fig. 10Ai). In moulting animals, the synchronized pattern is dominant throughout the different stages of the moult (Fig. 10Bi). The uncoupled pattern can transiently take over for specific, brief periods when the animal switches to the air-swallowing behaviour (Fig. 10Bii). Both types of motor patterns can probably be centrally modulated. The uncoupled pattern is volumetrically controlled by the foregut. Interestingly, we were able experimentally to induce a switch from the synchronized pattern to the uncoupled one, but not *vice versa*.

Further identification and characterization of the locust FG central pattern generator network is required in order to conclusively determine whether the two uncoupled patterns (feeding and air swallowing) are comparable, and whether they are generated in a similar way. This work is currently in progress.

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