Several aspects of insect feeding behaviour have been studied intensively. Although present knowledge of the physiology of insect feeding does not allow a detailed description of this type of behaviour in its entirety, attempts have been made to understand food intake as a function of a large set of physiological and external variables such as the size and nutritional quality of the previous meal, endogenous rhythms, food stimuli and the light regime (for a review, see Simpson, 1990). According to these sources, feeding behaviour does not occur randomly in locusts but consists of groups of ‘meals’ that may include short intra-meal gaps. The phases of food intake within each meal are characterized by regular rhythmical action of the mandibular closer muscle. Despite these studies, little information is available on the neuroethological basis of feeding behaviour, especially on the components of the neural pattern generators controlling the mouthparts. In insects, such investigations have been impeded by the inaccessibility of the suboesophageal ganglion. The massive dissection required to gain access to the ganglion usually abolishes all neural activity related to feeding. This problem was partially solved in larvae of the tobacco hornworm Manduca sexta, where cutting the neck connectives disinhibits the chewing motor programme and thus allows electrophysiological studies in isolated suboesophageal ganglia (Rowell and Simpson, 1992). On the basis of this work and that of Griss et al. (1991), some mandibular motoneurones and premotor interneurones of M. sexta were identified and characterised by Rohrbacher (1994a, b).

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**Summary**

Rhythmic activity was recorded from the mandibular motor nerves after treating isolated locust suboesophageal ganglia with the muscarinic agonist pilocarpine. The rhythmic motor pattern consisted of alternating bursts of activity in the antagonistic mandibular opener and closer motoneurones on each side and was synchronised in contralateral homologues. This pattern closely resembled the activity recorded from mandibular muscles in intact feeding locusts. The chewing frequency, however, was approximately three times higher in intact insects than the frequency of the motor pattern recorded from isolated ganglia. Serotonergic neurosecretory cells showed activity synchronous with the pilocarpine-evoked motor pattern. Similarly, rhythmic activity of the motoneurones innervating the two mandibular muscle receptor organs was synchronised with the mandibular motor pattern.

Key words: locust, feeding, pilocarpine, neurosecretion, motor pattern, Locusta migratoria.

**Introduction**

Several aspects of insect feeding behaviour have been studied intensively. Although present knowledge of the physiology of insect feeding does not allow a detailed description of this type of behaviour in its entirety, attempts have been made to understand food intake as a function of a large set of physiological and external variables such as the size and nutritional quality of the previous meal, endogenous rhythms, food stimuli and the light regime (for a review, see Simpson, 1990). According to these sources, feeding behaviour does not occur randomly in locusts but consists of groups of ‘meals’ that may include short intra-meal gaps. The phases of food intake within each meal are characterized by regular rhythmical action of the mandibular closer muscle. Despite these studies, little information is available on the neuroethological basis of feeding behaviour, especially on the components of the neural pattern generators controlling the mouthparts. In insects, such investigations have been impeded by the inaccessibility of the suboesophageal ganglion. The massive dissection required to gain access to the ganglion usually abolishes all neural activity related to feeding. This problem was partially solved in larvae of the tobacco hornworm Manduca sexta, where cutting the neck connectives disinhibits the chewing motor programme and thus allows electrophysiological studies in isolated suboesophageal ganglia (Rowell and Simpson, 1992). On the basis of this work and that of Griss et al. (1991), some mandibular motoneurones and premotor interneurones of M. sexta were identified and characterised by Rohrbacher (1994a, b).

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More general neuroethological work on locust feeding behaviour, similar to the studies in *M. sexta*, has so far been impossible since cutting the neck connectives in locusts does not trigger the chewing motor programme. For this reason, we tried to determine whether this programme could be elicited by application of the muscarinic agonist pilocarpine. This drug is known to evoke motor patterns similar to walking in isolated thoracic ganglia of locusts and stick insects (Ryckebusch and Laurent, 1993; Büschges *et al.* 1995). Here we show that pilocarpine is also capable of reliably eliciting long-lasting rhythmic motor activity in the locust suboesophageal ganglion, and we provide a quantitative analysis of the motor patterns evoked in mandibular motoneurones by pilocarpine, comparing them with the rhythms recorded from the mandibular muscles of intact feeding locusts.

**Materials and methods**

**Dissection and recordings**

Adult locusts, *Locusta migratoria migratorioides* (R. & F.), of either sex were obtained from our own crowded culture. For experiments using isolated ganglia, the insects were taken 1–4 days after imaginal ecysis, since at this age fatty tissue is not yet fully developed, which greatly facilitates dissection. Myogram recordings from mandibular muscles of intact locusts were performed using insects older than 5 days after the imaginal moult to ensure that the cuticle was fully sclerotized.

For *in vitro* recordings, the brain and suboesophageal ganglion (SOG) were isolated from the head and transferred into a Petri dish containing locust saline (Clements and May, 1974). The preparation with intact circumoesophageal connectives was chosen in order to be closer to the *in vivo* situation, where motoneurones located in the tritocerebral lobes of the brain control the muscles of the labrum (Schachtner and Bräunig, 1993), indicating that intersegmental interactions between both head ganglia are likely to exist. To test whether the brain participates in the generation of mandibular motor rhythms, a second set of experiments was carried out with the circumoesophageal connectives cut to determine whether the SOG itself is sufficient for rhythmonogenesis under the influence of pilocarpine. The ganglia were fixed dorsal side uppermost in the dish, and the main tracheae supplying the SOG were teased open at the surface of the saline to provide an adequate oxygen supply. Recordings were made from the main branches of the mandibular nerve containing the motor axons of the mandibular opener and closer muscles (M8, M9), the motor nerves innervating the dorsal and ventral muscle receptor organs (nomenclature according to Snodgrass, 1928; Honomichl, 1978; Bräunig, 1990) and the satellite nerves which contain the axons of serotonergic neurosecretory cells (Bräunig, 1987). Fig. 1 shows a schematic frontal view of the SOG and the major branches of the mandibular nerve. The branches were cut at the sites indicated by arrows and introduced into suction electrodes of appropriate diameter. The concentration of pilocarpine in the bath was increased stepwise by adding defined volumes of concentrated pilocarpine solution until motor rhythms were observed.

For myogram recordings from intact feeding insects, locusts were tethered at the pronotum and placed on a freely rotatable styrofoam ball (diameter 8.5 cm). The tether was constructed so that the locust could turn freely on the ball. Before each recording, the insects were chilled to approximately 5°C using a Peltier cooling aggregate. The cuticle of the head was then punctured at sites of muscle attachment using a fine pin. For differential recordings, stainless-steel wires (diameter 0.03 mm) were inserted into adjacent muscle-fibre bundles and fixed with tissue adhesive (Histoacryl, B. Braun Melsungen AG, Germany). During experiments, locusts were fed on wheat seedlings. In some cases, feeding was encouraged by bumping the wheat blade into a 0.1 mol l⁻¹ sucrose solution or by starving the locust for several days.

**Data analysis**

Electrophysiological data were recorded using a tape recorder (Racal Store 7DS) and digitized off-line using an interface and spike2 software (Cambridge Electronic Design). Spike trains were transformed into burst time series using an internal function of the spike2 program. These time series record both the beginning and end of each burst as discrete events. Since the bursts in the spike trains were clearly separated and almost no activity was present during the pauses, the selection of burst criteria was performed according to a simple principle: from each spike train, the inter-spike interval histogram was constructed, representing an approximation of the probability-density function of the inter-spike intervals. The histogram was always clearly bimodal and thus the interval at the local minimum between the two modes yielded a good burst criterion (Cocatre-Zilgien and Delcomyn, 1992). Statistical analysis of the burst time series generated from spike trains was
performed using the statistical package for the social sciences (SPSS) on a personal computer and by programmes written by the authors in C on a workstation (Silicon Graphics Indigo).

The rhythmicity of the time series was tested by calculating autocorrelation functions. Phase relationships were demonstrated by using autocorrelation functions as references for comparison with cross-correlation functions calculated for pairs of time series. To do this, the burst time series were transformed into square waves that were set to the value 1 between the beginning and end of the bursts and to the value 0 at all other times. Correlation functions were calculated using the algorithm given in Honerkamp (1994). The values of the correlations were normalized to the expected value at zero time lag, thus yielding an estimated cross correlation of 1 for identical square waves and a value of 0 for uncorrelated square waves at time lag 0. According to this normalization procedure, the cross correlation of a square wave and its inverted form would yield an estimated cross correlation of −1. A square wave was accepted as rhythmic when at least the peaks and troughs of the estimate of its autocorrelation function differed from 0 with a probability greater than 95%. The test algorithm used is described in Honerkamp (1994).

The cycle period, burst duration and duty cycle characterizing each burst time series were analysed. Since a chewing cycle consists of an opening and a subsequent closing phase, cycle periods were measured as burst duration plus the duration of the subsequent pause in recordings from mandibular opener nerves and as pause duration plus the duration of the subsequent burst in recordings from the mandibular closer nerves. Duty cycles were calculated by dividing the burst duration by the cycle period. Correlation coefficients were calculated to test whether burst duration depended on the cycle period.

**Results**

**Mandibular motor pattern in vitro**

During in vitro experiments, 41 isolated preparations were investigated. Motor rhythms occurred in 76% of the preparations 5–10 min after the application of pilocarpine. The concentrations of pilocarpine ranged from 10 to 30 μmol·l⁻¹ and the rhythmic activity lasted for at least 1 h. In three control experiments, the neural activity in the mandibular motor nerves was monitored for up to 1 h before the application of pilocarpine. In these experiments, either no motor activity or occasional arrhythmic bouts of motor spikes were observed. Such control experiments were not performed in all preparations because the lifetime of the ganglia is limited. Since the dose of pilocarpine was always increased only to the point at which rhythmicity was established, the data presented here cannot be used to detect dose dependencies of certain parameters.

In seven preparations, the properties of the rhythmic activity of the motoneurones innervating the power muscles were evaluated. The two populations of motoneurones innervating the mandibular closer and opener muscles were alternatingly active in a rhythmic manner. Left- and right-side populations of corresponding motoneurones were strictly synchronised (Fig. 2).

To prove rhythmicity and to demonstrate phase relationships, auto- and cross-correlation functions were calculated from the burst time series generated from the original recordings (Fig. 3). Fig. 3A,B shows the autocorrelation of the ipsilateral mandibular closer motor activity as a reference and the cross correlation with ipsilateral mandibular opener motor activity for comparison. To
prove synchrony of contralateral homologous motoneurone pools, the autocorrelation of the left-side neurones was used as a reference and compared with the cross correlation of left- and right-side motor activity (Fig. 3C, D). The correlation estimates for all peaks and troughs are significantly different from zero \( (P < 0.05) \). The data evaluated in Fig. 3 are from the same recordings as those shown in Fig. 2.

In the recordings referred to above, the experimental preparation consisted of both the brain and the SOG. The brain, however, proved not to be crucial for the generation of the motor rhythms, as no difference was observed between preparations \( (N = 9) \) in which the circumoesophageal connectives were cut after a certain time (Fig. 4 shows the evaluation for a typical preparation). The last 30 cycles before cutting the circumoesophageal connectives were compared with the first 30 cycles after cutting using the \( U \)-test in order to ensure that no short-term changes were induced by the cut. The test was not significant for the comparison of both the cycle period and the duty cycle \( (P > 0.05) \).

To provide further information on the pilocarpine-induced rhythms, several parameters reflecting the distribution of the motor activity within each cycle were investigated (Fig. 5, data evaluated from the same recordings as shown in Fig. 2). These results were also used for comparison with \textit{in vivo} rhythms. Plots of burst duration \textit{versus} cycle period are shown in Fig. 5A–D. In both the left and right mandibular opener and closer motoneurones, a significant correlation between burst duration and cycle period was observed. The great scatter and small correlation coefficient indicate that the variability of the cycle period is mainly due to independent variation in burst and pause durations. Both left and right mandibular closer and opener motoneurone pools burst with approximately the same duty cycle (Fig. 5E). The cycle period histogram for the left mandibular closer motor activity (Fig. 5F) is representative of the distribution of cycle periods in all motoneurone pools investigated since their activity is strictly coupled, as shown in Figs 2 and 3.
To allow a comparison with intact feeding insects, the same kind of analysis was performed with the recordings from intact feeding insects (N=6). Fig. 6 shows recordings from left and right mandibular opener and closer muscles. In these experiments, only two channels were recorded simultaneously and, therefore, the recordings in Fig. 6A, B are from two different locusts.

Estimates of auto- and cross-correlation functions were calculated for burst time series obtained from recordings from intact feeding insects (Fig. 7, the data were evaluated from the recordings shown in Fig. 6) in the same manner as the calculations for the in vitro preparations (Fig. 4). Again, all peaks and troughs were significantly different from zero (P<0.05). The amplitude modulations in the correlation functions are due to subtle frequency modulations in the burst time series that seem to correlate with head movements during feeding. This hypothesis is currently being tested. The fact that the correlation functions calculated from in vivo recordings decline in amplitude faster than in reduced preparations can be explained as follows: as the mandibular motor rhythm is faster in intact insects, the time interval for which the correlation is calculated (here 30 s) contains more cycles in intact insects than in reduced preparations. This enhances the possibility of
disturbances of the rhythm within this interval which cause troughs in the enveloping curve of the correlation function. If such a disturbance occurs early in a time series, the correlation function will decline very rapidly (Fig. 7A); in contrast, a disturbance occurring later in the time series causes only a slow decline. The correlation functions show similar phase relationships in isolated ganglia and intact locusts as well as significant rhythmicity in both situations.

An evaluation of burst duration versus cycle period was also performed using the data originating from intact locusts (Fig. 8, the data are from the recordings shown in Fig. 6). The correlation between burst duration and cycle period is significant; however, as in the isolated ganglia, the great scatter and small correlation coefficient indicate that the variability of the cycle period is mainly due to independently varying burst and pause durations. The median values of the duty cycles do not differ significantly in closer and opener activity. The increased variance in the duty cycle of the opener activity, which can be seen in Fig. 8C, is probably due to the increased noise level in the recordings (see Fig. 6A).

Comparison of in vitro and in vivo preparations

Data from the opener activity of 15 isolated preparations compared with data from five intact locusts showed a significantly longer median cycle period (U-test: \( P < 0.05 \)); in contrast, the null hypothesis that the median duty cycles are

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Fig. 6. Mandibular motor pattern in intact feeding insects (obtained from two different locusts). Myogram recordings from left mandibular closer and opener muscles (A) as well as left and right mandibular closer muscles (B) in intact feeding locusts. Baseline deflections in the pauses between the opener bursts (A, upper trace) are predominantly field potentials generated by other muscles. Most of these potentials are due to the contraction of a maxillary adductor muscle (M10; Snodgrass, 1928) which inserts in close proximity to the mandibular opener muscle (data not shown).

Fig. 7. Phase relationships and rhythmicity of mandibular motor patterns in intact feeding insects illustrated by auto- and cross-correlation functions calculated from 30 s burst time series. (A) Autocorrelation of left mandibular closer motor activity (thin line) and cross correlation of left mandibular closer and opener motor activity (bold line); (B) autocorrelation of left mandibular closer motor activity (thin line) and cross correlation of left and right mandibular closer motor activity (bold line). In B, the auto- and cross correlation are so similar that the bold line hides the thin line over almost the entire range plotted. Therefore, a short section of the bold line has been moved upwards in order to make the thin line visible (arrows). \( \Delta t \), time lag.
equal could not be discarded (U-test; \( P > 0.05 \)) (Fig. 9). This result indicates that \textit{in vivo} and \textit{in vitro} rhythms only differ in their frequency range but not in their qualitative properties. In both intact insects and isolated ganglia, correlations between burst duration and cycle period were significant (Figs 5, 8). Nevertheless, the small correlation coefficient suggests that burst and pause duration tend to vary independently from each other. The variability of \textit{in vitro} rhythms appears to be greater than \textit{in vivo}. This holds for cycle periods as well as for duty cycles. Since it is well known that peripheral sensory feedback can have a considerable impact on centrally generated motor rhythms, we also considered this option as a potential reason for the differences in frequency and variability between \textit{in vitro} and \textit{in vivo} mandibular motor patterns. In the mandibular system, such sensory feedback could be provided by the mandibular muscle receptor organs. These proprioceptors receive motor input from the SOG via motor nerves separate from the motor nerves innervating the power muscles (Bräunig, 1990). If the muscle receptor organs are part of a mechanosensory feedback system with functional relevance for the chewing motor programme, it is to be expected that their efferent control is in some way coupled to the power muscle motor pattern. This hypothesis was tested in isolated preparations.

**Efferent control of mandibular muscle receptor organs**

The motor output to the two muscle receptor organs was
found to be in phase with the activity of the mandibular closer motoneurones in all nine preparations investigated. A typical recording is shown in Fig. 10. Estimates of auto- and cross-correlation functions were calculated from 60 s burst time series in order to demonstrate the rhythmicity and to show phase relationships of these recordings (Fig. 11, data obtained from the recordings shown in Fig. 10). The correlation between burst duration and cycle period was then tested. In all cases, we found significant correlations but, as in the investigations on the motor output to the power muscles, the correlation coefficients were very small \(r=0.63\) to \(r=0.69\); data not shown), indicating that in all cases the variability cannot be attributed to the action of either the closer or the opener phase. Since the muscle receptor organs are inaccessible in intact locusts, it is not possible to compare the motor output in the intact animal with that in vitro.

**Activity of neurosecretory cells**

The three serotonergic satellite neurones located on each side of the SOG can be selectively recorded from the satellite nerve which branches off from the mandibular opener motor nerve (see Fig. 1; Bräunig, 1987). The three units are clearly distinguishable in original recordings from the satellite nerve (Fig. 12). In some preparations, the satellite neurones showed

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**Fig. 10.** Synchrony of efferent control of muscle receptor organs with mandibular closer motor activity. Simultaneous extracellular recordings from both left mandibular closer and muscle receptor organ motoneurones after application of 30 μmol l⁻¹ pilocarpine. The recording of the motor output to the dorsal muscle receptor organ contains only one unit, which is in accordance with the results of cobalt backfills of the motor nerve (P. Bräunig, unpublished results).

**Fig. 11.** Phase relationships and rhythmicity of the efferent control of muscle receptor organs shown by auto- and cross-correlation functions calculated from 60 s burst time series. (A) Autocorrelation of left mandibular closer motor activity (thin line) and cross correlation of left mandibular closer and ventral muscle receptor organ (vmr) motor activity (bold line); (B) autocorrelation of left mandibular closer motor activity (thin line) and cross correlation of left mandibular closer and dorsal muscle receptor organ (dmr) motor activity (bold line). Δ\(t\), time lag.
low-level arrhythmic activity (as described in Bräunig, 1987) before pilocarpine was added to the bath.

Under the influence of pilocarpine, the satellite neurones became synchronously active with the mandibular opener motoneurones ($N=5$) (Fig. 12). As the different satellite units did not spike frequently enough during the opener bursts to generate burst durations with acceptable variances, it was inappropriate to generate satellite burst time series; however, the mean spike frequency was determined for each satellite unit during opener bursts and during pauses separately (Fig. 13, data from the same recording as shown in Fig. 12). For all three units, the spike frequencies during opener bursts and opener pauses differed significantly ($U$-test: $P<0.05$).

Discussion

The aim of the present study was to design a preparation for the analysis of the neural networks controlling feeding behaviour in locusts. Our results clearly demonstrate that bath application of pilocarpine reliably elicits long-lasting neural activity in the mandibular motor system of isolated suboesophageal ganglia. Original recordings as well as statistical analyses show that the evoked activity of both motoneurones and neurosecretory cells consists of rhythmic bursts of action potentials. Opener and closer motor bursts alternate clearly, as observed during feeding bouts of intact locusts. The motor units of the two muscle receptor organs are synchronized with the closer activity, whereas the neurosecretory satellite cells tend to spike predominantly during opener bursts.

The mandibular motor pattern

The pattern generator driving mandibular motor output appears to be restricted to the SOG in its essential parts, as no changes in the activity of the observed neurones were noticed when the circumoesophageal connectives were cut. Although it remains possible that descending neurones from the brain play a role in pattern generation in intact insects, our experiments show that under the influence of pilocarpine the deafferented SOG itself is sufficient to produce motor rhythms that qualitatively resemble those of intact locusts. Thus, descending influences from the brain are either very weak or successfully replaced by the action of pilocarpine in our preparations. The neck connectives were cut in all experiments so that any ascending influences were removed. In contrast, Rowell and Simpson (1992) reported an inhibitory influence from the
thoracic ganglia in *Manduca sexta*. Since, in locusts, spontaneous motor output to the mandibles was not observed after cutting the neck connectives, it is likely that inhibitory influences of thoracic origin – if present at all – are weak and that disinhibition is not sufficient to evoke suprathreshold activity of the pattern generator. Since the SOG consists of three fused segmental ganglia, ascending or descending interactions between segmental pattern generators, provided that more than one such circuit exists within this ganglion, cannot be studied by lesioning as they can in thoracic ganglia. Our experiments, therefore, do not allow comparisons with investigations on intersegmental coupling within the thoracic nerve cord as reported, for example, in Ryckebusch and Laurent (1993, 1994).

The rhythmic motor activities of reduced preparations and intact feeding locusts show great similarities except for an approximately threefold longer cycle period in the isolated preparation. The most likely explanation for this difference is deafferentation. Similar effects are well known from other reduced preparations in both invertebrates and vertebrates (e.g. Bässler, 1986; Grillner and Zangger, 1979; Stevenson and Kutsch, 1987; Wilson, 1961). In these systems, it has been shown that the frequency of oscillations is increased effectively by sensory feedback from proprioceptors responsible for the initiation of a new cycle when the effector has reached a certain position. It is reasonable to assume that similar mechanisms might be at work in the locust mandibular motor system. Potential sources of sensory feedback in the mandibular system include several fields of campaniform sensilla, the two muscle receptor organs and a strand receptor associated with the mandibular ganglion (Thomas, 1966; Seath, 1977; Bräunig, 1990). The response characteristics of these sense organs are not yet known, nor are their influences on opener and closer motor units. Participation of sensory input in the control of mouthpart movement was demonstrated by Seath (1977), who reported that imposed rhythmical movements of one mandible recruited motor units of the contralateral mandible as well as those of the maxillae and labium.

The existence of a synchronized and patterned motor output to the muscle receptor organs in the isolated preparation suggests that these organs may play a role in a sensory feedback system in intact insects. The absence of such feedback in the isolated preparations, however, also shows that this feedback is not necessary for pattern generation. The function of the efferent control of the muscle receptor organs is not known, but its synchrony with the mandibular closer motoneurones supports the following interpretation. While the mandibles are closing, both receptor organs tend to fall slack. This could be prevented by a simultaneous contraction of the receptor muscles, thus providing a constant basic tension of the receptor organs. The morphological analogies between mandibular muscle receptor organs in other insect species and muscle spindles in vertebrate motor systems have given rise to speculations about a possible functional analogy between these organs (Bolender and Honomichl, 1985), but until the response characteristics of the mandibular muscle receptor organs have been elucidated, such an analogy remains hypothetical.

In pilocarpine-induced motor rhythms of isolated thoracic ganglia of stick insects, a strong correlation between burst duration and cycle period was reported for coxal retractor activity, whereas no such correlation was found for coxal protractor activity (Büschges et al. 1995). Thus, the variability in the cycle period is mainly due to the variability in the retractor burst duration, whereas the protractor burst duration remains rather constant. This nicely reflects the walking pattern of intact stick insects, with a variable stance phase and a relatively constant swing phase. Although in our evaluations we also found significant correlations both *in vivo* and *in vitro*, the correlation coefficients are much smaller than those reported in Büschges et al. (1995). Furthermore, we could find no obvious differences in the strength of correlation between mandibular opener and closer muscles as reported for coxal retractor and protractor muscles of the stick insect leg. Thus, in the mandibular pattern, the opener and closer phases seem to have equal and independent variabilities in their burst durations, unlike the stance and swing phases in thoracic rhythms. This was also seen in intact feeding locusts. Thus, it seems reasonable to assume that the mandibular pattern generator does not include central and peripheral mechanisms that affect duty cycle and burst duration as efficiently as in the thoracic pattern generators controlling walking. Since the differences in the variabilities of the swing and stance phase are also visible in deafferented preparations of thoracic ganglia, this may indicate that the thoracic pattern generators include central control mechanisms which cannot be observed in the mandibular system. The lower level of complexity seems reasonable since the mandibles are simple appendages that can only move around a single hinge joint, unlike walking legs which have many joints and segments.

Contralateral interactions show a different organization in the mandibular segment compared with the thoracic segments, both in intact insects and in reduced preparations. In intact feeding locusts, the mandibles are moved in phase with each other (i.e. agonistic contralateral muscles are coactivated) to produce synchronised chewing movements, whereas during walking contralateral legs are moved in antiphase with each other and step alternately. However, in reduced thoracic preparations, the trochanteral levator and the contralateral depressor seem to be strictly coupled, while the converse is not true. The trochanteral levators appear never to be coactive but, nevertheless, they may be active at different intrinsic frequencies, giving rise to a variable ipsi–contralateral phase lag (Ryckebusch and Laurent, 1993, 1994). Our reduced preparations of suboesophageal ganglia do not show such differences in the strength of bilateral coupling. For all four power muscles involved in the chewing movement of the mandibles, the pools of motoneurones act with a fixed phase relationship that is similar to that observed in intact chewing insects. The greater flexibility in the thoracic motor patterns may be because a greater amount of sensory control is required for this system. This also makes sense in a functional context, since independent leg movements are likely to be required for walking on uneven surfaces or across obstacles. In contrast, great flexibility in the coordination of mandible movements during feeding is unlikely to be required;
the strict coupling of left and right pattern generators or even the existence of only a single pattern generator in the mandibular segment could be sufficient.

Does the neural activity in the isolated preparation represent ‘fictive feeding’?

The motor pattern evoked in the isolated preparations by pilocarpine is qualitatively very similar to the natural chewing pattern. As the motor activity recorded from the thoracic ganglia after pilocarpine application was called ‘fictive locomotion’ (Ryckebusch and Laurent, 1993) because of its qualitative similarities to the walking pattern, one might be tempted to call the motor activity in the mandibular nerves ‘fictive feeding’. To be sure, however, further study is needed to demonstrate whether coordinated motor output also occurs in maxillary and labial segments under these conditions. Preliminary experiments addressing this question indicate that, at least in the maxillary segment, pilocarpine indeed causes motor output which is coupled to the mandibular motor rhythm. Another result that also indicates that pilocarpine elicits ‘fictive feeding’ is the activity observed in the neurosecretory satellite neurones (Figs 12, 13). Long-term recordings from the satellite nervous system in intact locusts clearly showed that satellite neurone activity only occurs during feeding bouts and at no other time (Schachtner and Bräunig, 1993). Thus, active satellite neurones appear to be reliable indicators of feeding. We therefore assume that rhythmic activity in the satellite neurones in isolated ganglia after application of pilocarpine could indicate that the ganglion is in a state of ‘fictive feeding’. We are confident that further experiments using the new preparation will not only support this assumption but also enable us to study the neural basis of locust feeding in more detail using intracellular recording techniques.

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