MOTOR PATTERNS IN THE STOMATOGASTRIC GANGLION
OF THE LOBSTER *PANULIRUS ARGUS*

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SUMMARY

1. Activity patterns arising from the thirty cells of the stomatogastric ganglion of *Panulirus argus* are described for both a semi-intact preparation and an isolated one.

2. The thirty or so cells can be divided so far into two functional groupings: the gastric mill group, with at least ten motor elements, and the pyloric group with at least fourteen. There is some, but not extensive, interaction between groups.

3. The main gastric mill activity is arranged in two sets of elements, each of which is composed of reciprocating elements innervating antagonistic muscles. Thus alternation in activity between the single LC and the two LG neurones results in alternate closing and opening of the lateral teeth; alternation between the four GM and single CP units results in alternate protraction and retraction of the medial tooth.

4. The two sets are phased to each other in such a way that they cause gastric mill teeth to operate effectively to masticate food.

5. The main pyloric activity is arranged in a three-part cycle with each of three sets of units active in sequence. Activity in two PD and one AB unit is followed by bursts in IC and LP units followed in turn by activity in up to seven PY units. Activity in a single VD neurone is locked to this cycle in a more complex pattern.

INTRODUCTION

Research on relatively simple networks has proved of value in the study of neuronal interactions and their relation to behaviour as has been well demonstrated in *Aplysia* abdominal ganglion (Kandel & Kupfermann, 1970), *Tritonia* cerebral ganglion (Willows, 1968) and crayfish nervous system (Wiersma, 1967; Kennedy, Selverston & Remler, 1969) to name only a few cases. Even in these systems, however, a full understanding of network functioning is impeded by an inability to record simultaneously the activity of all participating neurones. In systems simple enough for such simultaneous recording, as in crustacean cardiac ganglion (Hagiwara, 1961; Hartline & Cooke, 1969), there is a corresponding loss of complexity and hence ‘interest’ in the behavioural patterns involved. The crustacean stomatogastric ganglion has neither of

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these shortcomings. In this system of some 30 cells it is possible to record and identify, simultaneously, activity from almost all cells. Moreover, these cells control the activity of some 30 muscles to produce a complex co-ordinated sequence of contractions which operate the animal’s stomach. Motoneurone activity patterns for certain of these cells have been described in Homarus (Maynard, 1966) and in the portunid Scylla (Maynard, 1969). Aspects of command fibre input to the ganglion have been reported by Dando & Selverston (1972), and of neuronal interactions among gastric mill cycle units by Mulloney & Selverston (1974a, b) and Selverston & Mulloney (1974). The present work is directed toward the motor output of the ganglion. It describes in detail the sequences of activity both of the muscles in an intact stomach and of the motor neurones in an isolated ganglion, for the spiny lobster Panulirus argus. A summary of some of the results reported herein is given in Maynard (1972).

MATERIALS AND METHODS

Terminology in this paper follows that of Maynard & Dando (1974). Table 1 summarizes the terminology for neurones, the muscles they innervate, and their presumed function, if known. Fig. 1 is a diagram of stomach anatomy showing muscles, their innervation and the chitinous skeletal structures—‘ossicles’—to which the muscles attach. The experiments described were performed during the summer of 1968 at the Bermuda Biological Station, St Georges, Bermuda. Locally obtained lobsters (Panulirus argus) of both sexes weighing 1–2 kg were used. They were maintained in a large tank of running sea water and fed regularly. Two types of preparation were studied, a semi-intact lobster with the stomach exposed for electromyography, and an excised preparation with the ganglion and its associated efferent and afferent nerves dissected free from the stomach.

For EMG work the heart was exposed through a window cut in the dorsal carapace. The anterior aorta was cannulated through the heart and perfused with oxygenated perfusion fluid of the following composition: 872 ml 0.54 M-NaCl; 9 ml 0.44 M-Na₂SO₄;
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Fig. 1. Simplified muscle and neuroanatomy of lobster stomach. This diagram shows a left lateral view of muscles and nerves mentioned in this paper. Skeletal structures ('ossicles') are stippled and selected ones identified by roman numerals. Muscles are divided into four series: cv, cardioventricular; cpv, cardiopyloric valve; gm, gastric mill; p, pyloric. Nerves: Al.n., anterolateral; Am.n., anteromedial; d.Lv.n., dorsal branch of lateral ventricular; Dv.n., dorsal ventricular; Io.n., inferior oesophageal; Iv.n., inferior ventricular; Lv.n., lateral ventricular; Mv.n., medial ventricular; So.n., superior oesophageal; Stg.n., stomatogastric nerve; Stg.g., stomatogastric ganglion; v.Lv.n., ventral branch of lateral ventricular.

Length of stomach around 5 cm for a 1 kg lobster.

28 ml 0.54 M KCl; 69 ml 0.36 M CaCl₂; 22 ml 0.36 M MgCl₂; 1 ml 0.5 M NaOH; 18 ml 0.5 M H₂BO₃. pH was around 7.6. Care was taken not to admit air bubbles into the arteries as these caused blockage. The lateral aspect of the stomach was exposed by using rongeurs to chip out a window in one side of the carapace. This window was extended dorsally to the points of insertion of the extrinsic stomach muscles (muscles inserting on the carapace), but without disturbing these insertions. The mandibular muscle and other tissue overlying the stomach were removed to obtain clear access to all major muscles. The hepatopancreas on one side was carefully removed to obtain EMGs from the pyloric muscles. Care was taken not to expose critical stomach areas to fluids from this organ. EMG recordings were obtained with fine flexible wires insulated except at the tips. An indifferent silver wire electrode was placed, usually on the ventral part of the body wall. It should be noted that this operation severed the posterior stomach nerve on one side, but otherwise potentially left any sensory feedback loops intact.

In the excised preparation the lobsters were bled by a ventral incision at the thoracic-abdominal junction and the stomach was carefully exposed with rongeurs and then removed. When severing the ducts entering the pyloric region from the hepatopancreas, care was taken to keep the hepatopancreatic fluid from making contact with areas containing critical nerve supplies. The excised stomach was slit ventrally and pinned out flat. The anterior aorta was cannulated posteriorly and perfused with
oxygenated saline. Nerves were severed at or near the muscles they innervated and were carefully dissected free from the stomach surface with iridectomy scissors and fine forceps. The dissection usually began at the pyloric end of the stomach by freeing branches of the ventral lateral-ventricular nerve (vLv.n.), then the dorsal Lv (dLv.n.) and the common Lv (Lv.n.) up to the dorsal ventricular nerve (Dv.n.). The process was then repeated for the other side. The dorsal ventricular nerve was usually left attached to the wall of the anterior aorta, as was the ganglion. The medial ventricular nerves (Mv.n.) and anterolateral nerves (Al.n.) were similarly dissected up to their entrance points to the anterior aorta. The stomatogastric nerve (Stg.n.) was freed far enough anterior to the ganglion to enable placement of stimulating and recording electrodes. Sometimes it was freed to include its branch points into the inferior and superior oesophageal nerves (Io.n.; So.n.), and inferior ventricular nerve (Iv.n.).

The dissection took as long as 6 h and resulted in an isolated stomatogastric system including almost all of the major and sub-major branches of the system, though one could not count on getting all branches out successfully every time. The dissected preparation, with perfusion still operative, was transferred to a transparent-bottom dish containing perfusion fluid and a layer of mineral oil. Selected nerve branches were drawn up into the mineral oil on pairs of silver-wire hook electrodes for conventional bipolar extracellular recording. Amplified activity was recorded on a 7-channel Ampex FR-1300 tape recorder at 7½ in/sec FM for later playback and photography. Temperature was not rigorously controlled, but was around 23 °C.

RESULTS

The data can be introduced in the context of the function of the stomatogastric system in feeding, digestion and assimilation. There are no detailed studies of digestive physiology for this particular decapod, so we will refer to work on similar crustaceans to supplement our own observations. Many decapods only partially masticate food with their external mouthparts. Patwardhan (1935) and Reddy (1935) relate this to the animals' need to return to a safe haven as soon as possible after securing food. Food passes through a short oesophagus in the form of strips and other relatively large pieces and enters the large sac-like cardiac stomach (so called from vertebrate convention, the heart actually being posterior to the stomach in the lobster). Food in the cardiac stomach is probably subjected to digestive juices (Yonge, 1924) and to the action of the gastric mill, a set of toothed articulated, chitinous ossicles located posterodorsally. Opening posteroventrally from the mill is the pyloric stomach where food is probably further broken down by digestive fluid and plate-like ossicles, and sorted by sieve-like plates of hairs. Food ready for absorption is directed into either the midgut or hepatopancreas, probably according to size (Yonge, 1924; Reddy, 1935).

For purposes of this paper the neuromuscular activity of the stomach will be grouped into (A) gastric mill and (B) pyloric cycles since the rhythms of these subsystems are largely (though not completely) independent of each other. Also, for simplicity, muscles will be referred to by the designations given to their motor neurones. Table 1 lists the neurones and corresponding muscles of the stomatogastric system. A more detailed anatomy will be found in Maynard & Dando (1974).
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Fig. 2. Diagrams of gastric mill action. Operation of the lateral teeth (top two; ventral view) under control of the LC and LG neurones, and of the medial tooth (bottom two; lateral view) under control of GM and CP neurones. Bars indicate activity in muscles which are correspondingly heavily stippled in the diagrams above them. Tooth movements indicated by arrows. Skeletal structures (ossicles; teeth; carapace) non-stippled.

A. Gastric mill cycle activity

1. Intact stomach

The most conspicuous activity in cardiac stomach came from muscles operating the gastric mill. The mill consists of a pair of serrated ‘lateral teeth’ with a prominent enlargement on the anterior end of each, and a single ‘medial tooth’ located above and between the lateral teeth. Operation of the gastric mill is not completely worked out, but a simplified diagram (Fig. 2) shows the attachment and action of the mill’s musculature. Simultaneous EMGs from four principal gastric-mill-cycle muscles are shown in Fig. 3A, and a diagram of the activity sequences in all major muscles is shown in Fig. 4.

**LC neurone.** Typical gastric mill cycles began with contraction of the bilaterally paired muscles innervated by the LC neurone. Such contraction acting through a pivot arrangement between ossicles V and XIV causes the lateral teeth to come together (possibly to hold food between them; Fig. 2, top left). EMGs from the LC muscle showed large, regularly spaced potentials which began at a lower frequency, reached a peak of 15–25 Hz, then declined in frequency and abruptly halted. They typically showed an initial slight increase in amplitude. Total burst time was usually 2–4 sec. Deviations from this pattern occurred and tonic activity was sometimes seen in the absence of gastric mill cycling. LC potentials were large enough to be recorded from several places on the stomach.

**GM neurones.** Part way through the LC burst the extrinsic muscles innervated by the four GM neurones began their activity. Contraction of these muscles brings the medial tooth down and forward (perhaps grinding food clamped in the lateral teeth; Fig. 2, bottom left). The action of these muscles may aid clamping of the lateral teeth by way of a coupling between ossicles II and V, and between V and VI via IV. EMGs from GM units were less regular than those seen in the LC, probably in part reflecting the larger number of units (4) driving the GM muscles.
Fig. 3. Gastric mill cycle.

A. Simultaneous EMGs from the four major muscles involved in gastric mill operation (semi-intact preparation). Note the alternation between LC and LG activity and that between GM and CP activity. Note also that GM activity commences part way through the LC burst. Bottom record is a faster film speed of the middle part of the top record. Time calibration 1 sec.

B. Extracellular records from nerves carrying certain gastric mill cycle axons. Bottom record is an expansion of the middle of the top record. A period of stimulation to the stomatogastric nerve at 10/sec is indicated by the bar. Note the spontaneous activity in the GM, LG and AM units, and its inhibition by stimulation in the latter two groups; immediate post-stimulation rebounds occur in LC, GP, GM and AM units. A delayed rebound in the two LG units does not commence until the GP rebound is over. Time calibration 1 sec.

**LG neurones.** After termination of the LC burst, but usually within the GM burst, the paired muscles innervated by the two LG neurones contracted. This apparently 'resets' the lateral teeth, which are pulled laterally, posteriorly and perhaps dorsally (Fig. 2, top right). Again the EMG was typically irregular in 'spike' amplitude.

**CP neurone.** Muscles controlled by the CP neurone effect resetting the medial tooth, to complete the gastric mill cycle (Fig. 2, bottom right). CP activity occurred during LG activity, usually after cessation of GM activity. The CP burst started abruptly, reached a peak of 25–30 Hz, then ended abruptly. Muscle potentials tended to be larger at lower frequencies. CP activity often overlapped with the beginning of LC activity.
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GP neurone. Another unit, the GP, innervating a sheet of muscle just posterior to the gastric mill, was active during the period of LC activity, although there was not always exact coincidence of the bursts. The function of this muscle is not known, but conceivably it might push food into the mill or tighten the mill (Yonge, 1924).

Reliable activity in the muscle innervated by the AM neurone was not obtained in these experiments.

Thus the typical gastric mill rhythm consisted of activity in two groups of neurones, LC-LG and GM-CP. Each group was composed of reciprocating sub-units controlling mutually antagonistic muscles. Activity periods in antagonists tended to be mutually exclusive, but not entirely so. Activity in each unit occupied roughly half of the 5- to 7-sec cycle duration. Phasing was not so strict for lateral teeth vs. medial tooth units. Delays between the beginning of the LC burst and the beginning of the GM burst ranged from 0 to 0.3 of the cycle duration, with intermediate values being usual for an active stomach. Other evidence for looseness of coupling between the two groups was the occurrence of cycling in one group with little or no cycling in the other. At times of inactivity in the stomach, a tonic discharge was often observed in one of the muscle sets. In particular, cases of tonic firing in just the LC or just the LG units were seen.

2. Excised ganglion

In the isolated preparation rhythmic activity was rarely seen in gastric units. In two experiments one or two cycles of activity in LG units were observed following electrical stimulation of the stomatogastric nerve. In the remainder of the experiments the LG units were often spontaneously active but showed no rhythmicity. Their activity could be inhibited by antidromic stimulation of the nerve containing the LC axon. Other gastric units were generally quiet. As a rule certain gastric units (LG, GM, LC, AM, see Fig. 3 B) were initially somewhat excited during stimulation, but with stronger stimulation especially, this was short-lived and gave way to quiescence or suppression of at least two groups of units (LG, GM). At moderate voltages all units except the LGs rebounded when the stimulation was halted, firing in a prolonged after-discharge. GM units tended to fire in clusters. GM rebound was delayed by a second or more at high voltages, while that of LC, GP and CP tended to be immediate. The LG units were inhibited for several seconds following cessation of stimulation (during rebounds in other units) then resumed their spontaneous discharge (see Fig. 3 B).

B. Pyloric cycle units

Both in the intact stomach EMGs and in the excised preparations following ‘priming’ by electrical stimulation of the stomatogastric nerve, sequences of unit activity in the pyloric cycle were quite similar, and hence they will be described together (Fig. 5 A and 5 B, bottom record). Functions of muscles of the pyloric region are less well understood (see ‘Discussion’), and the suggestions made here must be viewed as tentative. A ‘basic’ pyloric cycle consists of three phases, termed PD, LP and PY, after the principal units active in each.

PD-time neurones. The muscles innervated by the two PD cells are extrinsic, and insert on several ossicles, on which they appear to pull in opposite directions. To some
it has seemed possible that this action opens entrances to the pyloric region of the stomach, hence the name 'pyloric dilator' for these units. PD muscle potentials showed a marked decrease in amplitude with time into the burst. This would seem to be only partly due to a reduction in overlap of potentials as the two PD units fire more out of phase. Within the burst, the frequency of PD impulses started at a low value and reached a peak just before the burst's often abrupt termination. Frequencies were usually very closely parallel between the two PD units (less than 5% difference). The apparently single 'AB' neurone (for 'anterior burster'), whose axon leaves the ganglion via the stomatogastric nerve for an unknown destination, was also active at PD time.

**LP-time neurones.** Following the abrupt termination of the PD burst there was a distinct pause, some 100–200 msec long, followed by a burst of activity in the single LP ('lateral pyloric') unit. The muscle innervated by this unit spans the distance between the insertions of the two major PD-innervated muscles, hence its contraction seems to antagonize the action of those muscles. The IC cell ('inferior cardiac') was also an LP-time neurone. However, it usually fired fewer impulses per burst and at a lower frequency than did the LP. If stomatogastric nerve stimulation was needed to activate the IC unit, it required stronger stimulation to reach threshold than did the LP cell. Most of its activity closely paralleled the LP unit, so it appeared much like an LP unit with a lower excitability. The muscle operated by this cell is located just anterior to the pyloric region, but its function in the stomach is unknown.
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A. EMG-Pyloric muscles

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<th>VD</th>
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B. Excised preparation-pyloric units

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Stomatogastric nerve stimulation

Fig. 5. Pyloric cycle activity.
A. Simultaneous EMGs from the muscles involved in pyloric activity (semi-intact preparation). The basic cycle consists of a PD-LP-PY sequence. Note the gap between PD and LP activity, and the overlap between the end of LP and beginning of PY activity. VD activity commences part way through the PY phase and overlaps slightly (less than was typical) the PD phase. IC activity is approximately coincident with LP.

B. Simultaneous extracellular nerve records from the same units and the same preparation as A following isolation of the ganglion (the three records are contiguous). Note the similarity in pattern to A following priming stimulation (bottom record). Top record shows spontaneous cycling before stimulation. System excitability is sufficiently low that only the basic-cycle units, PD-LP-PY, are active. Stimulation of the stomatogastric nerve at 10/sec (middle record) inhibits the LP and PY units, drives the VD 2:1, and excites the PD units and the burst rate. Note the gaps in the PD bursts synchronized to the stimulus artifacts. PD units are the only cyclically active units in this instance (AB not monitored though). Following cessation of stimulation (bottom record) the burst rate is increased above the spontaneous level and VD and IC units are active then. Time calibration 1 sec (both A and B.).

PY-time neurones. A burst of activity in the PY neurones followed LP time, sometimes starting before activity of the LP unit had halted. Frequently the final impulses of the LP burst were associated with gaps in the PY burst. At least seven distinct PY units have been seen, based on impulse shape, amplitude and firing pattern. The stronger a priming stimulation to the stomatogastric nerve, the greater the number of PY units activated. No relation between impulse amplitude and threshold was
observed (this should be examined in more detail since there may be a tendency in some units, but not others, to fire in clusters (Fig. 5)). The PY neurones innervate a variety of muscles posterior to the entrance to the pyloric region. Not all units were found in all nerve branches, though this could be a result of selective injury. The appearance presented by the pyloric stomach during the LP–PY phases was of a peristaltic wave of contraction propagating posteriorly, but its significance is unclear. Contents of the ampulla (under muscle p 9) could be seen to move during this phase.

VD-neurone. The last neurone of the pyloric cycle group, the VD unit ('ventricular dilator'), innervates an extrinsic muscle which inserts anterior to the pyloric region entrance. Its function is also unknown and its behaviour was a bit unusual. Its activity usually began part way through the PY burst (or in the absence of a PY burst, well ahead of the PD burst) and terminated at the end of the PD burst or slightly later. With moderate activation, however, it frequently developed a substantial hiatus or gap in its firing pattern during the latter part of the PD burst (Fig. 7, top). With weak activation (e.g. when firing spontaneously) it often showed little or no sign of such a gap, and in fact more or less paralleled the PD-cell activity (Fig. 7, bottom right). The period of activity after the hiatus was usually limited to from zero to three impulses only, corresponding approximately to the gap between the PD and LP bursts. In the semi-intact preparation, the activity of the VD muscle also sometimes exhibited this hiatus during the PD burst, making it contract in 'double time'. In the excised preparation, threshold for activation of the VD unit was usually high, though cases of spontaneous activity were seen.

Effects of priming stimulation

In the semi-intact preparation the pyloric cycle was usually fairly active spontaneously, cycling at the rate of around 1 Hz. Producing the same cycling rate in excised preparations usually required moderate-intensity stimulation of the stomatogastric nerve (twice threshold voltage at 10/sec for several sec). Following cessation of stimulation, cycle rate and number of impulses per burst decreased more rapidly at first, over the next 30 sec (Fig. 5 B). Typically, PD cells were easiest to activate by stimulation, followed by LP, and then PY cells. During stimulation of the stomatogastric nerve at moderate rates (5–10 Hz), firing in PD and PY cells usually alternated (LP and IC were inhibited), but their bursts were partitioned into subbursts in synchrony with each stimulus (Fig. 5 B, middle record). This partitioning may reflect a sequence of excitation and inhibition which follows each stimulus. Consistent with this is the observation that PD and VD cells, especially, can fire impulses 1:1 with the stimulus during the 'silent' phase of their cycle (PY units active) (Fig. 5 B, middle record).

Departures from the basic cycle pattern

Departures from the basic PD–LP–PY alternation were common and seemed to reflect differences in unit excitability. The PD cells were capable of burst activity without activity in any of the other pyloric sequence units, even, in one case, in an intact stomach. Such isolated bursting was never observed in LP or PY units and only in one case was alternation between LP and PYs with little PD activity observed (AB unit not monitored, however). Alternation between PDs and LP without PYs was seen,
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Fig. 6. Sequences of pyloric cycle unit activity. Upper diagram indicates the muscles (stippled) and corresponding units which are active at each phase of the pyloric activity cycle. Diagram below shows the relative phasing of these activities to each other.

VD patterns

Fig. 7. VD-unit activity. Activity of VD unit (PD and IC for comparison) immediately following a stimulus train applied to stomatogastric nerve (30/s; last three stimulus artifacts at beginning of record). As excitation from the stimulation wanes, the hiatus in VD firing during the PD burst fills in (lower record). Note the decrease in unit firing frequency and bursting rate as excitation wanes.
Fig. 8. 'Wiring diagram' of basic pyloric cycle units. All connexions between units of different kinds are inhibitory. PD units inhibit both LP and PY units; LP inhibits PDs and weakly inhibits PYs; PYs inhibit only LP. PDs are assumed to have an endogenous oscillatory activity capability.

particularly in states of low excitation. Alternation between PDs and PYs without LP was often seen immediately following stomatogastric nerve stimulation. This could be due to continued LP inhibition beyond stimulus-off time. Slow waning of inhibition may explain a progressive increase in LP or IC impulses per burst often seen for the first few bursts following stimulus-off (Fig. 5B). Sometimes following stimulus-off the PY burst would come before or in the middle of the LP burst (LP shuts off in this case). Gaps in any of the bursts were often associated with single impulses in certain other units (PD gaps with LP impulses, LP gaps with PY impulses, and PY gaps with PD impulses).

Antidromic stimulation

Antidromic stimulation of certain axons had marked effects on specific units. Stimulation of the nerve containing the PD axons inhibited activity of the LP unit, and stimulation of the nerve containing the LP axon inhibited the PD units. Stimulation of the Mv.n. elicited impulses in the VD axon which would not always spread into the contralateral axon of that unit, even though orthodromic impulses occurred synchronously in both. This was reminiscent of the 'truncation' phenomenon described by Hartline (1967) in cardiac ganglion, and must be regarded as further evidence that antidromic impulses are not necessarily equivalent to orthodromic ones in their properties and effects (see also Mulloney & Selverston, 1972).

DISCUSSION

Function of stomatogastric muscles

The hypothetical view of gastric mill function presented above wherein the lateral teeth clamp food, the medial tooth rasps down and forward over the food, followed by a sequenced reversal of these actions, is at best a simplified one. The muscles controlling these four phases can have more complex actions than described. The durations of the activity periods may vary and certain cycles may even operate alone, as in the cases where alternation between GM and CP units (operating the medial tooth) occurred without LC-LG (lateral teeth) cycling. Also, the relative phasing of the activity periods may vary quite a bit, at least in the semi-intact animal, with the consequent possibility that actions and functions may vary as well.

Several early authors noted in various decapods the protraction of the medial tooth by contraction of muscles presumably homologous to the GM-innervated ones of
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Panulirus (Huxley, 1880 in the crayfish Astacus; Yonge, 1924 in the lobster Nephrops; Patwardhan, 1935 in the crab Paratelphusa). They describe a coupling of the lateral teeth to this action such that the three teeth meet in the middle to crush food. Coupling is also present in Panulirus but the contribution of the LC-driven muscle is quite significant in closing the lateral teeth, and this action can occur independently of any activity in GM-driven muscles. In both the lobster Homarus and the crayfish Procambarus, the articulation of ossicles and arrangement of muscles associated with the lateral teeth would permit a separate clamping action similar to that seen in Panulirus (Hartline, unpublished observations). Whether such indeed happens as part of the normal gastric mill activity has not been determined. Mention of such action is largely missing from the literature. Patwardhan (1935) notes a contribution from LC homologues, to which in Paratelphusa he ascribes a minor role, that of raising the lateral teeth slightly. Only recently have Dando, Chanussot & Nagy (1974) given a description similar to ours (including LC action) of the functioning of the gastric mill in Cancer.

The pyloric region of the stomach contains several distinct channels for passage of food particles, and complex arrays of setae which act as filters, admitting fine particles to the pyloric region and the finest particles to the hepatopancreas (Yonge, 1924). The three-phase co-ordinated activity of the pyloric muscles must have some function in moving food through the region. However, no study that we have encountered gives a description of the specific action of these muscles, nor have we examined it carefully in this study.

Comparison with patterns in other decapods

Pyloric cycle

Prior to our work, physiological studies had been carried out on the motoneurone activity of the stomatogastric ganglion of two other decapods, the American lobster, Homarus americanus (Maynard, 1966) and the Australian mud crab, Scylla serrata (Maynard, 1967, 1969). In both cases the patterns studied were part of the pyloric cycle group. In Homarus a tripartite cycle was described involving activity in two ‘I’ neurones, followed by activity in one ‘a’ neurone, followed in turn by one ‘m’ neurone. These neurones innervate muscles which are homologous to those innervated by the PD, IC and VD neurones, respectively, in Panulirus (Maynard, unpublished observations). It is apparent that the phase relationships in this cycle are about the same as in Panulirus, though a double-time VD burst was not mentioned for Homarus. The Homarus PD cells are capable of firing bursts without activity in the VD or IC cells, which was frequently the case in Panulirus as well, but it is not known whether this occurred in the absence of activity in other relevant neurones (the homologues of the LP and PY). It is of more interest that the VD and IC neurones of Homarus were observed to fire alternating bursts in the absence of recorded activity in the PD cells. This situation was never seen in Panulirus, where the PD cells invariably participated in all rhythmic bursting of the pyloric-cycle cells of more than transitory duration. More recently, Morris & Maynard (1970) recorded pyloric cycle activity in intact Homarus, finding the same basic sequence of PD, LP and PY units as described here.

Of the Brachyura, a tripartite cycle of two ‘A’, one ‘B’ and about five ‘s’ neurones was described by Maynard (1967, 1969) in Scylla. These neurones all have axons
running in the lateral ventricular nerve (Lv.n.) and presumably would be homologous to PD, LP and PY neurones of *Panulirus*. Their activity as far as it was studied, resembles that obtained from both extracellular and intracellular records in *Panulirus*. In *Cancer*, Dando et al. (1974) report a PD–LP–PY cycle in an intact preparation. In this animal there are four PD-time neurones present in the posterior nerves, the smaller two of which show certain variability in phasing of their activity to those presumably homologous to the *Panulirus* PD cells.

**Gastric mill cycle**

In *Cancer* Powers (1973) described alternation between GM and CP groups in intact animals. No consistent relation of LC activity to this cycle was determined. Dando et al. (1974) observed a similar alternation, with activity in several units, including the presumed LC unit, occurring after CP activity. In *Panulirus interruptus*, Mulloney & Selverston (1974b) describe three patterns of gastric-mill activity in isolated stomatogastric ganglia. They find the same basic alternation among antagonistic neurones operating a given set of teeth, but the relative phasing of the two sets is somewhat different. Their 'high pattern B' activity is most similar to the patterns we observed, though their GM–CP (DG) phasing is more retarded. The difference in central and sensory input between the two preparations may contribute to this disparity in results.

**Origins of rhythms**

The pyloric rhythm was usually present spontaneously in the isolated ganglion, or could readily be primed into cyclic activity lasting long after the cessation of a stimulation period. Thus this cycle seems to be produced by the ganglion itself. It is not so clear from these particular studies that the gastric rhythm is intrinsic in the ganglion, since it was never obtained in full in an isolated preparation. In one intact preparation, however, the stomatogastric nerve was cut during gastric mill cycling, and the muscles underwent a couple of cycles before the rhythm disappeared. In this case, however, sensory feedback to the ganglion could still have been present. Recently Mulloney & Selverston (1974) and Hartline (unpublished) have obtained gastric mill rhythms in isolated *P. interruptus* ganglia, though not reliably, so it appears that this rhythm too can under some circumstances be generated intrinsically.

Next, there is the question of whether the rhythmicity is inherent in one special group of cells or whether it is a 'network property' dependent on interactions among many different cells. The best perspective on this comes from intracellular studies (see Maynard, 1972), but simply from extracellular records it can be said that the pyloric rhythm can exist without the participation of VD, IC, PY and even LP units, suggesting that the PD/AB units themselves, or in combination perhaps with non-motor units, are capable of producing the pyloric rhythm. This is supported by intracellular observations of oscillatory slow potentials in PD cells.

**Sequence generation**

Again, the more illuminating work on this aspect comes from the intracellular recordings (see Maynard, 1972). Fig. 8 shows a 'wiring diagram' of the main pyloric sequence units derived from those studies. The patterns described above are quite
consistent with this wiring scheme. The PD cells are assumed to be primary oscillators, or to be driven by such; when they fire, they inhibit both LP and PY cells. The LP cell is the first to recover from the inhibition; following a short pause it gives a rebound discharge, holding the PD cells off and delaying the PY rebound through weak inhibitory connexions. When the PY cells recover from the PD inhibition and overcome the weak LP inhibition they fire a burst which shuts off the LP cell, thereby releasing the PD cells and allowing them to start a new cycle. This connectivity diagram is consistent with the observed effects of antidromic stimulation described above. A peculiar aspect of pyloric activity is the development of a gap in VD activity during the latter part of the PD burst at high activation levels. Since the AB neurone, which inhibits the VD (Maynard, 1972), was usually not monitored, we cannot assess the possibility that activity level in this cell was the variable entity, though in one preparation, at least, presence of AB burst activity was not invariably sufficient to cause the gap.

For the gastric mill units, activity patterns and antidromic stimulation experiments suggest that units innervating antagonistic muscles are coupled inhibitorily to each other. Intracellular work (Maynard, 1972; Mulloney & Selverston, 1974a, b; Selverston & Mulloney, 1974; Hartline, unpublished observations) has borne this out but it has also shown the connectivity to be quite complex. Neither the significance of this connectivity nor the way in which it leads to the observed output is fully understood as yet.

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