

MOVEMENTS AND MOTOR PATTERNS OF THE BUCCAL MASS OF *PLEUROBRANCHAEA* DURING FEEDING, REGURGITATION AND REJECTION

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SUMMARY

Feeding, regurgitation, and rejection in the marine gastropod *Pleurobranchaea* all involve similar but not identical rhythmic movements of buccal mass structures such as the radula, jaws and lips. The part of the motor pattern which produces rhythmic radula movement, as recorded in the major external muscles of the buccal mass of behaving semi-intact preparations, was similar during the three different types of behaviour, suggesting that they share a common motor-pattern generator. Other parts of the motor pattern were only obviously different during the vomiting phase of regurgitation. Differences in the function and motor patterns of feeding and rejection are presumably accounted for by differences in the activity of muscles which could not be recorded from in this study (e.g. jaw muscles). A general conclusion is that buccal rhythms in gastropods cannot automatically be assumed to underlie feeding, and this is particularly true for dissected preparations which do not execute a clear behavioural response. It would be necessary either to record motor activity that is unique for a given behaviour, or to employ preparations which execute unambiguous behavioural responses.

INTRODUCTION

Animals often use similar movements of the same parts of the body to perform different types of behaviour. For example, drying, swimming, jumping, and defensive kicking in the locust all involve similar rhythmic movements of the legs and are expressed by similar motor pattern activity (Heitler & Burrows, 1977; Pflüger & Burrows, 1978*a, b*). In such cases it is usually assumed that the different types of behaviour involve a common motor-pattern generator (MPG).

The present study compares the kinematics and motor patterns in the marine gastropod *Pleurobranchaea* during feeding, regurgitation and rejection, which involve similar but not identical rhythmic movements of buccal mass structures such as the radula, jaws and lips. Natural stimuli were presented to behaviourally active semi-intact preparations in order to record the motor patterns during the complete and un-

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ambiguous execution of each of the three behavioural responses. In contrast, in most previous gastropod studies spontaneous radula movements have been assumed to underlie feeding, and all buccal rhythms have been thought to represent a 'basic feeding motor programme'. The present study indicates that new strategies are necessary for dealing with the different functions involving the gastropod buccal mass.

Parts of this study have been reported previously (McClellan, 1978).

METHODS

Experiments were performed on the marine gastropod *Pleurobranchaea californica* (Fig. 1A), supplied by Pacific Bio-Marine Co., Venice, California or Sea Life Supply, Sand City, California. Animals weighing 100–500 g were housed in separate 8.0 l tanks and maintained at 12–15 °C by circulating artificial sea water.

Behavioural studies

Observations were made on freely moving animals or on animals suspended in their tanks by small hooks placed superficially through the dorsal mantle. In the latter case the mouth region (Fig. 1B) could be observed in detail.

1. *Feeding.* Application of either homogenized or sliced squid mantle to the anterior chemoreceptive areas, such as the oral veil or lips (Fig. 1), induced feeding responses (Davis & Mpitsos, 1971; Lee & Liegeois, 1974). The swallowing phase of feeding was examined either following the ingestion of a long strip of squid mantle or following the injection of squid homogenate directly into the buccal cavity (Fig. 1).

2. *Regurgitation.* This behaviour was elicited by applying fresh homogenized squid to the oral veil and 'tricking' the animal into partially ingesting a polyethylene tube, through which 1–2 ml of either rotten squid homogenate or a dilute soap solution (10% Ivory Liquid in sea water) was injected into the buccal cavity. The latter stimulus was most often used because it could be consistently prepared.

3. *Rejection.* Application of fresh squid homogenate to the oral veil was also used to 'trick' animals into first ingesting an indigestible object, such as a narrow strip of rubber tubing. Subsequent removal of the food substance resulted in rejection of the object.

Conventional semi-intact preparation

This preparation was employed to record the motor patterns during 'swallowing' (feeding behaviour) and regurgitation (McClellan, 1978, 1980). A small dorsal flap of mantle overlying the buccal mass was removed, and the animal immobilized in the recording dish. The buccal mass was held at its rest position (Fig. 1B) by two insect pins. The distal end of the oesophagus (not shown in Fig. 1) was cannulated with a rigidly held piece of glass tubing through which either squid homogenate or soap solution was injected. All major ganglia, connectives and nerves were left intact.

The 'swallowing' response, elicited by injection of squid homogenate into the cannulated oesophagus, is assumed to be part of the feeding behaviour and will be distinguished from unambiguous feeding in which squid mantle is both ingested and swallowed (see below). The vomiting of material during the regurgitation behaviour is clear, but less powerful than in intact animals.

The position of the radula within the buccal mass was monitored by recording the movements of the mechanically coupled radular sac (Fig. 1 D, E) with a displacement transducer (McClellan, 1982*b*). In some preparations the movements of the lips and jaws were revealed by pinning the buccal mass in a forward position so that the proboscis was partially extended (Fig. 1 C, D).

Modified semi-intact preparation

The conventional semi-intact preparation above was limited because rejection and the entire feeding behaviour could not be elicited. The results from this preparation were verified and extended with the suspended preparation (Gillette, Kovac & Davis, 1978) and the modified semi-intact preparation (developed with C. Cohan & G. Mpitsos; see McClellan, 1980), both of which execute complete and unambiguous feeding, regurgitation and rejection responses. Only the modified semi-intact preparation will be discussed here.

MgCl₂ equal to 5% of body volume was first injected into the buccal cavity. After 20–30 min a dorsal flap of mantle overlying the buccal mass was removed and the animal immobilized in the recording dish. In contrast to the conventional semi-intact preparation, the oesophagus was left intact to allow swallowing, and the buccal mass was left free to move forwards or backwards. Recordings could easily be made from most muscles and nerves. The modified semi-intact preparation is more complete and less traumatized than the conventional semi-intact preparation, and therefore displays a greater part of the animal's behavioural repertoire.

Neurophysiology

All motor activity was recorded from preparations which were maintained at 12–15 °C in artificial sea water with 1% dextrose added. Electromyograms (EMGs) and extracellular nerve activity were recorded with flexible polyethylene suction electrodes which were drawn to a fine tip (100–300 μm) in a small flame. Potentials were amplified by high-gain differential amplifiers (McClellan, 1981). A special purpose two-channel audio monitor (McClellan & Cohan, 1978) was used to listen to the general pattern of alternating motor activity.

All neurophysiological data was stored on magnetic tape with an eight-channel FM tape recorder (Model A; H. R. Vetter Co), and was later photographed from an eight-channel oscilloscope with a Nihon Kohden oscillographic camera.

Statistics

Results are expressed as mean ± S.E.

RESULTS

Behavioural descriptions

Feeding

Feeding in *Pleurobranchaea*, a carnivore, consists of three sequential phases: (1) an appetitive phase; (2) a consummatory phase, which includes a bite-strike response followed by ingestion; and (3) a swallowing phase (Davis & Mpitsos, 1971).

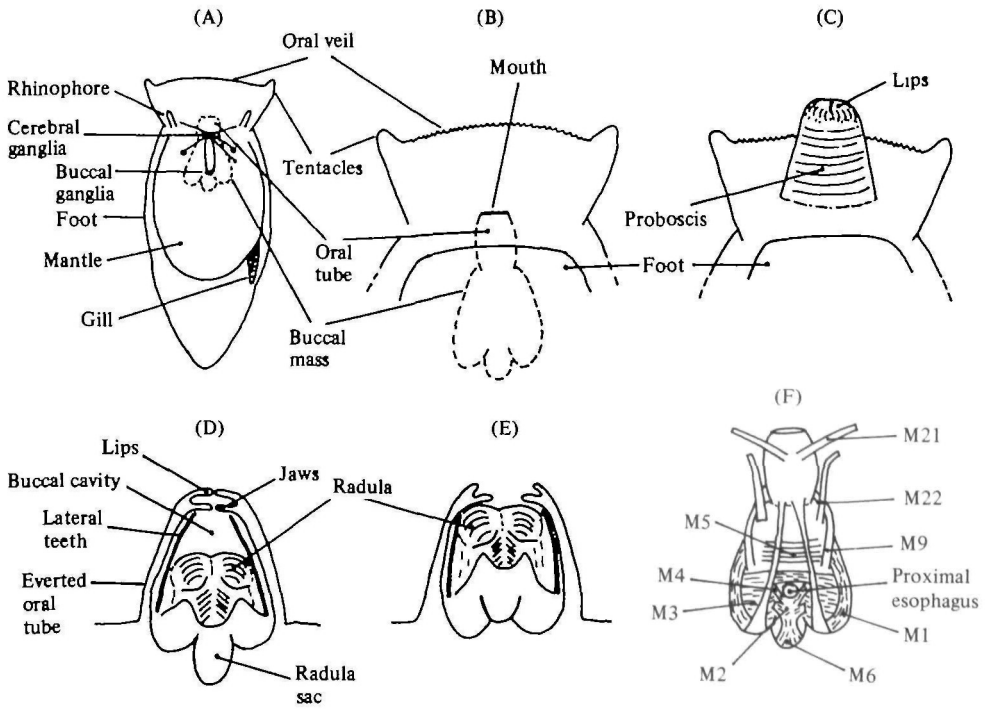


Fig. 1. Position and structures of the buccal mass in *Pleurobranchaea*. (A) Dorsal view. Intact quiescent animal illustrating the relevant external structures and the internal buccal mass and oral tube (dotted). The nervous system lies just dorsal to, and innervates, the buccal mass and oral tube (adapted from Davis & Mpitsos, 1971; Lee & Liegeois, 1974). (B) Ventral view. The oral tube is attached anteriorly to the mouth opening and posteriorly to the buccal mass. (C) Ventral view of proboscis extension. The buccal mass is partially extended anteriorly through the mouth opening and becomes surrounded by the everted oral tube. The anterior region of the oral tube becomes the lips. This posture is displayed to varying degrees during feeding, regurgitation and rejection. (D, E) Highly simplified dorsal view of a horizontal section through the buccal mass during ingestion, exposing the lips, jaws, lateral teeth and radula. The radula sac is mechanically coupled to the radula. (D) Maximum radula retraction and initial protraction are accompanied by jaw closing. The lips may be weakly parted during this phase. (E) Maximum radula protraction and initial retraction are accompanied by jaw opening and forward thrusting of the proboscis. See text for discussion of radula, jaw and lip movements during regurgitation and rejection. (F) Organization of intrinsic and extrinsic muscles associated with the buccal mass as observed in a semi-intact preparation (adapted from Davis & Mpitsos, 1971).

The feeding behaviour will be described here to point out the similarities and differences with the other behaviour discussed later.

1. *Appetitive phase*. Presentation of food to a quiescent animal initiates the appetitive phase of feeding or simply the 'extension' response (Davis, Mpitsos & Pinneo, 1974). The proboscis, which consists of the buccal mass surrounded by an everted oral tube (Lee & Liegeois, 1974), is extended beyond the mouth opening (Fig. 1 B, C).

2. *Consummatory phase*. The appetitive phase is quickly followed by the bite-strike response (Davis, Mpitsos & Pinneo, 1974) when the food substance is of adequate concentration. The buccal mass is rapidly thrust forward within the oral tube, while the jaws open and the lips part (Fig. 1 E). Almost simultaneously the radula is rapidly moved forward (protraction) in the buccal cavity beyond the tips of the jaws. The

initially separated halves of the radula, which are lined with fine teeth, close and grip the food.

Ingestion of the captured food is then accomplished by coordinated rhythmic movements of the radula and jaws while the proboscis remains extended. The jaws remain open as the radula moves backwards (retraction), which allows the food to be pulled into the buccal cavity. As the radula releases the food and moves forward (protraction), the jaws close and prevent the food from being pushed out of the buccal cavity. Near the extreme of radula protraction the jaws open and allow the radula to grip the food and begin another ingestion cycle. Lip parting is rather weak during ingestion but is in phase with radula retraction.

3. *Swallowing phase.* Following ingestion, the proboscis is gradually withdrawn as the food is swallowed. Rhythmic radula movement transfers the food from the buccal cavity to the oesophagus, whereupon oesophageal peristalsis carries the food to the gut. During swallowing the jaws generally remain closed while the lips part weakly in phase with radula retraction.

Regurgitation sequence

Regurgitation typically lasted 30–90 min with the stimuli used in this study and consisted of two phases which alternated: (1) the vomiting phase – a relatively short bout of active regurgitation during which noxious material was expelled from the buccal cavity (McClellan, 1978); and (2) the writhing phase – a relatively long period during which animals did not expel material but writhed in response to visceral distress. Both phases of the regurgitation sequence involved proboscis extension and rhythmic movements of the radula, jaws and lips that were similar but not identical to those during feeding (McClellan, 1980).

1. *Vomiting phase.* These bouts lasted 46.1 ± 6.9 s ($n = 32$, 6 animals), and occurred at irregular intervals during the regurgitation sequence. The number of bouts was quite variable.

Noxious material was first transferred from the gut and oesophagus to the buccal cavity. Contraction of body-wall and gut muscles presumably increased the pressure within the visceral cavities and helped to force material out of the gut. Tonic shortening of the oesophagus, which enlarged the oesophageal lumen, also facilitated the transfer of material from the gut to the buccal cavity. Reverse peristalsis of the oesophagus was not observed.

Once in the buccal cavity, noxious material was expelled by rhythmic radula movement. The rhythmic protraction–retraction movements of the radula in the buccal cavity were somewhat analogous to the action of a piston within a cylinder, with the consequences of these movements dependent in part on the phasing of jaw opening. The jaws were closed during the early stages of forward radula movement (protraction), presumably to increase the pressure in the buccal cavity. In the late stages of radula protraction the jaws opened and allowed noxious material to be forcibly expelled 1–3 cm from the extended proboscis. During this part of vomiting, the phasing of jaw and radula movements was similar to that during the ingestive phase of feeding (see above). However, in contrast to ingestion, in the early stages of backward (retraction) movement of the radula the jaws closed during vomiting,

presumably to prevent expelled material from being sucked back into the buccal cavity. During vomiting, radula movements occurred with a short cycle time of 6.9 ± 1.0 s ($n = 39$, 6 animals) and with an amplitude greater than that during ingestion.

There were additional differences between the feeding behaviour and the vomiting phase of the regurgitation sequence. During feeding, lip movements were generally weak and cyclic, and the oral veil could be partially extended. During vomiting, the lips were tonically separated and the oral veil was clearly withdrawn, presumably to provide a clear path for the expelled material. The shape of the radula was probably also different during feeding (i.e. to grip food) and vomiting (i.e. to push material out of the buccal cavity) but could not be clearly observed.

2. *Writhing phase.* The proboscis was extended but less than during vomiting, and the radula moved rhythmically back and forth within the buccal mass (cycle time = 12.8 ± 0.5 s, $n = 224$, 6 animals). Rhythmic parting of the lips occurred in phase with radula retraction, while cyclic opening of the jaws occurred less frequently during the protraction-retraction transition of the radula movements. Finally, peristalsis of the oesophagus was often observed. The writhing phase is thus similar in appearance to an exaggerated version of the swallowing phase of feeding.

Rejection

The single-phase rejection behaviour was different from vomiting (regurgitation sequence) and involved the ejection of indigestible objects, such as rubber tubing, from the buccal cavity (McClellan, 1980). The objects must, of course, first be ingested (see Methods) and the movements during this response could be directly compared to the subsequent rejection process.

Rejection occurred while the proboscis was extended and was achieved by rhythmic movements of the radula and jaws. The phasing of these movements was different from that during ingestion and vomiting. (The jaws often remain closed during swallowing and the writhing phase). During rejection, the jaws were open or at least not actively closed during forward (protraction) movement of the radula to allow the object to be expelled. As the radula moved backwards (retraction), the jaws closed and held the partially rejected object in place. The phasing of radula and jaw movements during rejection was, therefore, opposite to that during ingestion.

Comparison of motor activity patterns

The conventional semi-intact preparation was used to record the motor activity during the 'swallowing' phase of feeding and during regurgitation. The modified semi-intact preparation was used to study activity during complete feeding, rejection and regurgitation (see Methods). A summary of all motor activity appears in Fig. 8.

Conventional semi-intact preparation

1. *Common parts of the motor patterns:* M_1 , M_2 , M_3 , M_4 , M_6 . Rhythmic forward and backward movements of the radula were mediated in part by two sets of antagonistic muscles that are intrinsic to the buccal mass: the dorsal radula retractor group

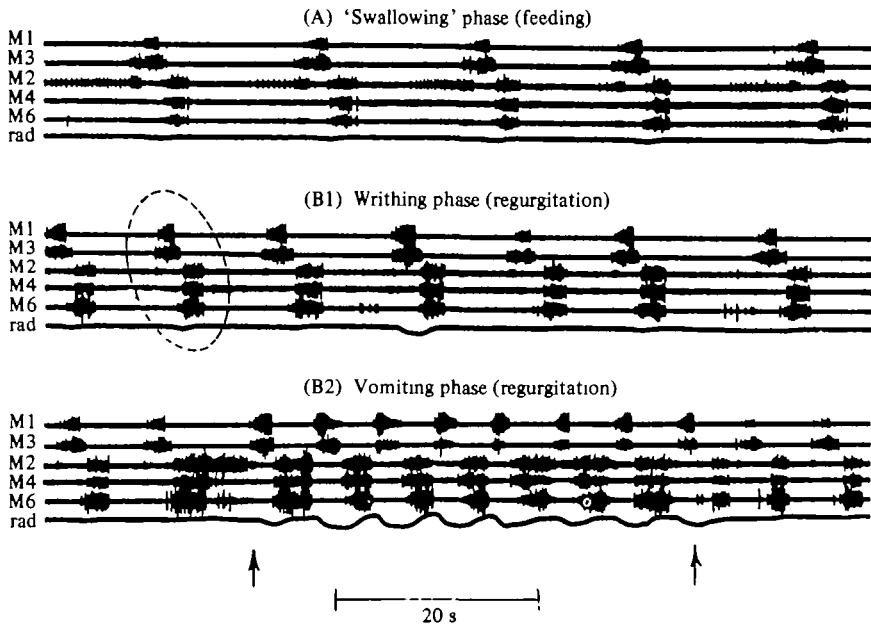


Fig. 2. Motor activity recorded from the intrinsic buccal muscles of a conventional semi-intact preparation during (A) the 'swallowing' phase of feeding, and (B1) the writhing phase and (B2) vomiting phase (between arrows) of regurgitation. Upward deflection of radula trace (rad) designates radula protraction, which is controlled by M2, M4 and M6. M1 and M3 produce radula retraction. The basic retraction-protraction cycle (B1, dotted circle) is common to all the patterns except for moderate changes in the burst envelopes of radula protractor activity. Differences in the average cycle times (T) of the three rhythms are evident. 'Swallowing' is a slow rhythm ($T = 15.63 \pm 0.9$ s, $n = 16$), the writhing phase is a medium-frequency rhythm ($T = 12.0 \pm 1.2$ s, $n = 27$), and the vomiting phase is a fast rhythm ($T = 5.94 \pm 0.7$ s, $n = 11$).

(M1, M3) and the dorsal radula protractor group (M2, M4, M6) (Fig. 1 F and Davis & Mpitsos, 1971). Ventral and internal muscles of the buccal mass also contributed to the movements of the radula and mechanically coupled radula sac (Fig. 1 D, E) but were less accessible.

The major radula retractor and protractor muscles were active in a similar, alternating pattern during the 'swallowing' phase of feeding (Fig. 2 A) as well as during the writhing and vomiting phases of the regurgitation sequence (Fig. 2 B1, B2). During a bout of vomiting, however, the amplitude and duration of one or more radula protractor bursts (Fig. 2 B2, between arrows) was generally greater than during 'swallowing' or the writhing phase. As in intact animals, relatively long periods of writhing motor activity were periodically interrupted by relatively short bouts of vomiting motor activity.

Motor activity consisted of biphasic cycles (dotted circle in Fig. 2 B1), with a retraction-protraction sequence followed by a variable period of inactivity dependent on the cycle repetition rate. Double bursts in some protractor muscles were observed on rare occasions (Fig. 2 A), thus creating a three-phase cycle, but the first protraction burst was weak and may be nonfunctional.

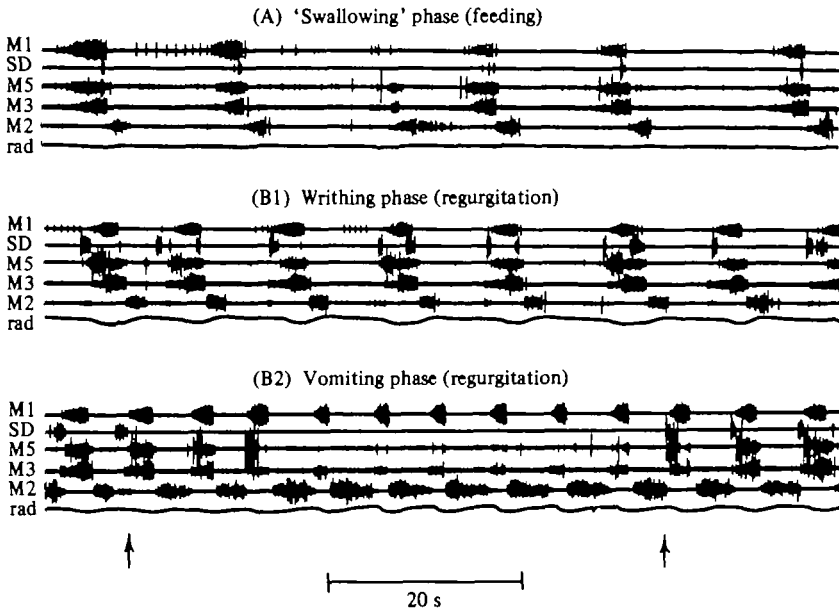


Fig. 3. Motor activity in the salivary duct (SD) and buccal muscle five (M_5) in a conventional semi-intact preparation during (A) the 'swallowing' phase of feeding, and (B1) the writhing phase and (B2) vomiting phase (between arrows) of regurgitation. The interval during SD inactivity is generally taken as a convenient measure for the duration of a bout of vomiting. Notice that M_5 also becomes inactive during these bouts, while the burst envelope of M_3 is only partially decreased. Upward deflexion of radula trace (rad) designates protraction.

2. Different parts of the motor patterns

(a) *The salivary duct (SD) and buccal muscle five (M_5)*. The salivary duct system is innervated by the salivary nerve, which exits from the buccal ganglia (Thompson & Slinn, 1959; see fig. 7 in McClellan, 1982a). Saliva is carried by peristalsis through the posterior duct to a bulbous enlargement, which will be referred to as the SD. Contraction of the muscular SD then forces stored saliva through the anterior branch of the duct and into the buccal cavity.

Buccal muscle five (M_5) is the dorsal part of a circular muscle that is intrinsic to the buccal mass (Davis & Mpitsos, 1971; Fig. 1 F here). This muscle is said to strengthen the bite during feeding (Davis & Mpitsos, 1971).

The SD and M_5 were active during each cycle of both the 'swallowing' phase of feeding (Fig. 3 A) and the writhing phase of regurgitation (Fig. 3 B1). The SD bursts were variable but generally occurred either at the onset of radula protraction activity or just prior to radula retractor activity. In contrast, the M_5 burst always occurred in phase with radula retractor activity.

During the vomiting phase of the regurgitation sequence (Fig. 3 B2, between arrows), SD bursts were totally absent, and M_5 bursts were either totally absent or markedly reduced. The period of SD inactivity is therefore used as a convenient measure for the duration of a bout of vomiting in all figures (i.e. between arrows). The occasional absence of one or two SD bursts during other motor patterns (e.g. Fig. 3 A) does not signify vomiting but only lability of this motor pattern component.

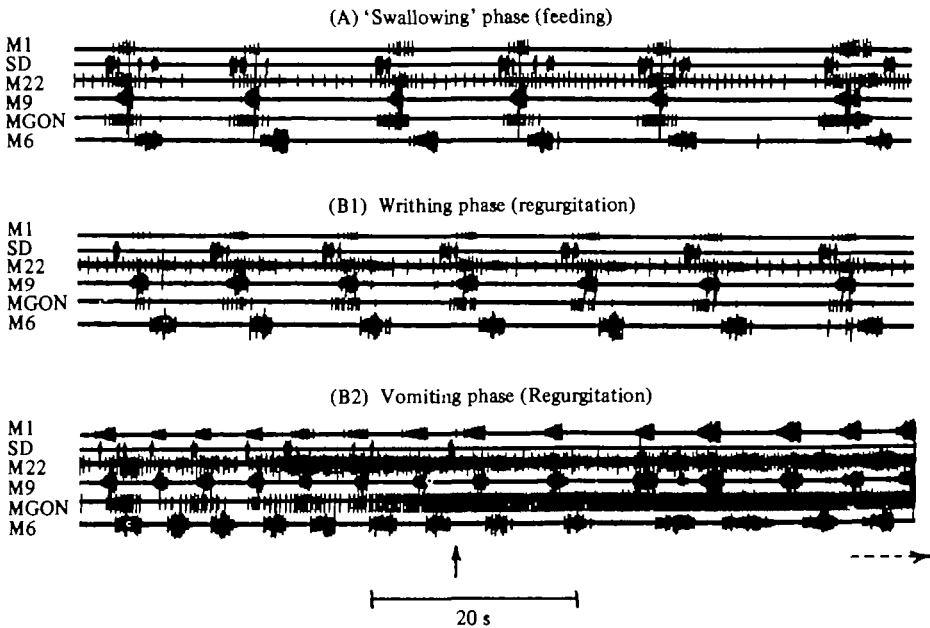


Fig. 4. Neural activity in the medial gastro-oesophageal nerve (MGON) taken from a conventional semi-intact preparation during (A) the 'swallowing' phase of feeding, and (B1) the writhing phase and (B2) the vomiting phase (between arrows) of regurgitation. Phasic and tonic activity in the MGON accompanies peristalsis and shortening of the oesophagus, respectively.

during weak cycles. The previously proposed function of M5 (Davis & Mpitsos, 1971) is thrown into question here because this muscle was found to be active when biting was not occurring and inactive during periods of obvious jaw closing (e.g. Fig. 3 B2).

(b) *Oesophageal nerve (MGON)*. The medial gastro-oesophageal nerve (MGON) exits from the stomatogastric ganglia (Davis, Siegler & Mpitsos, 1973) and innervates the medial and distal oesophagus (see fig. 7 in McClellan, 1982a). During the 'swallowing' phase of feeding and the writhing phase of the regurgitation sequence, bursts in the MGON were in phase with radula retraction activity (Fig. 4 A, 4 B1). These bursts preceded the initiation of peristaltic waves in the proximal segment of the oesophagus during both of the above responses (also see *Behavioural descriptions*).

During the vomiting phase of the regurgitation sequence, when the oesophagus tonically shortens, the activity in MGON switched from phasic bursts (above) to tonic, high-frequency firing (Fig. 4 B2, between arrows).

(c) *Lateral strap muscle (M9)*. Several strap muscles run along the lateral aspect of the buccal mass (Davis & Mpitsos, 1971). One of these strap muscles, M9, causes parting of the lips (C. Cohan, unpublished). Parting of the lips and bursts in M9 occurred during radula retraction activity of 'swallowing' and the writhing phase (Fig. 5 A, 5 B1). The greater intensity of lip parting during the writhing phase was often reflected in the intensity of M9 bursts.

During the vomiting phase of the regurgitation sequence, when the lips were tonically parted, the level of activity in M9 increased and often became tonic during the initial part of the bout (Fig. 5 B2, between arrows).

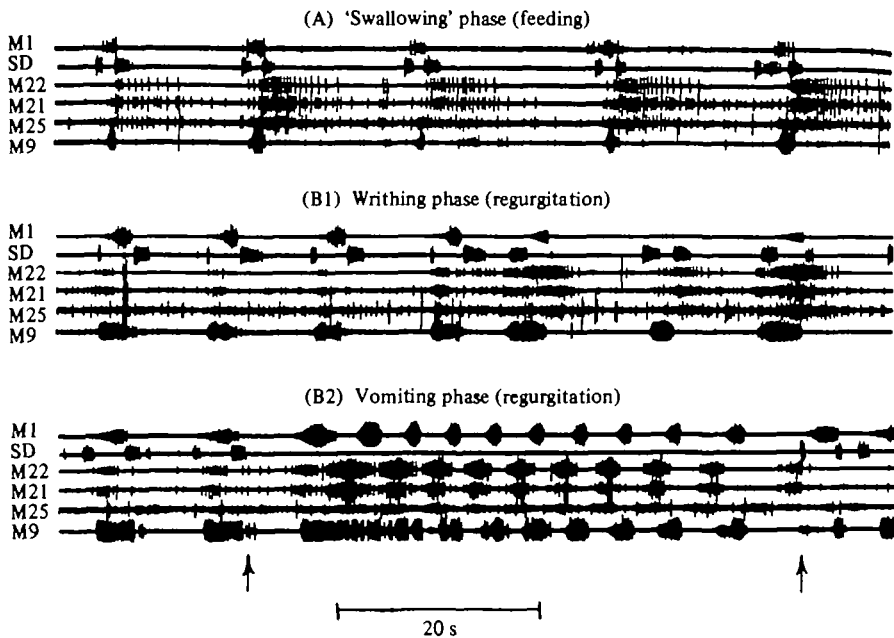


Fig. 5. Motor activity recorded in anterior strap muscles (M22 and M21) and lateral strap muscle (M9) in a conventional semi-intact preparation during (A) the 'swallowing' phase of feeding, and (B1) the writhing phase and (B2) vomiting phase (between arrows) of regurgitation. During the transition to vomiting, there is a phase shift in anterior muscle activity and an increase in M9 activity.

(d) *Anterior strap muscles (M22 and M21)*. Two strap muscles, M22 and M21, originate from the anterior body wall and insert, respectively, on the anterior buccal mass and oral tube (Fig. 1F; Lee & Liegeois, 1974). These muscles produce three types of actions: withdrawal of the oral veil and anterior body wall; movement of the proboscis to a partially extended position; and directional side-to-side movements of the proboscis (Lee & Liegeois, 1974).

Bursts in these muscles were approximately in phase with radula retraction movements during the 'swallowing' phase of feeding and the writhing phase of regurgitation (Fig. 5A, 5B1). In some preparations, the major parts of the bursts in these muscles lagged radula retraction activity during 'swallowing' and slightly led radula retraction activity during the writhing phase. These differences, however, were not consistent. Contraction of M22 and M21 during these responses may account in part for the rhythmic and very weak withdrawal of the oral veil.

During the transition from the writhing phase to vomiting, the oral veil became tonically withdrawn, and proboscis extension often increased as a result, in part, of an increase in M22 and M21 activity (Fig. 5B2, between arrows). During vomiting, the activity in these muscles was either switched in phase and occurred during the end of radula protractor bursts or was tonic. However, an increase in muscle activity seemed to be the main change.

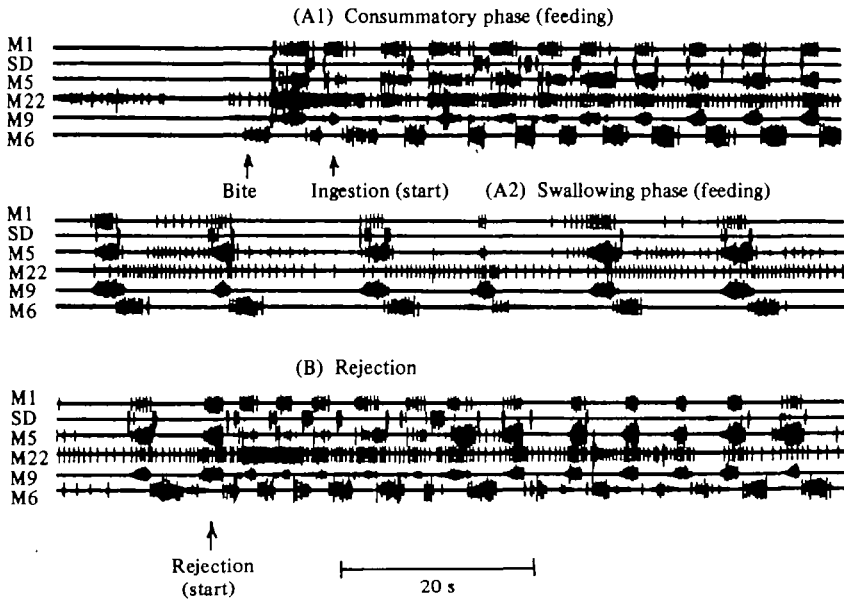


Fig. 6. Motor activity recorded from muscles in a modified semi-intact preparation during (A₁) biting and ingestion of squid mantle followed by (A₂) swallowing of the food. (B) Motor activity recorded during rejection after the animal had been 'tricked' into ingesting a strip of rubber tubing.

Modified semi-intact preparation

During complete and unambiguous feeding, regurgitation and rejection (Figs. 6, 7; see Methods), the major external muscles of the buccal mass which produce rhythmic radula movement were active in a similar pattern (Fig. 8, solid blocks; only M₁ and M₆ are shown in Figs. 6, 7).

1. *Feeding (ingestion and swallowing)*. Presentation of squid mantle resulted in proboscis extension, which was mediated in part by a burst in M₂₂, followed by a clear bite response (Fig. 6A₁). The food was ingested (Fig. 6A₁) and then swallowed (Fig. 6A₂). The high level of activity in M₂₂ during ingestion maintained the proboscis in an extended position. During a bite, when the lips were widely separated, there was a strong burst in M₉. The activity in M₉ was weak during the initial cycles of ingestion, possibly to allow antagonistic lip-closing muscles to aid in holding partially ingested food. The swallowing motor pattern verified the previous results from the conventional semi-intact preparation.

2. *Rejection*. As in intact animals, this preparation could be 'tricked' into partially ingesting non-digestible objects, such as rubber tubing (see Methods). The object was then rejected from the buccal cavity (Fig. 6B). The SD and M₅ were both active during rejection, but the M₅ burst was slightly weaker during the initial cycles. A relatively high level of activity in M₂₂ helped maintain the proboscis in an extended position. The activity in M₉ was weak during the initial cycles of rejection, and this may have allowed lip-closing muscles to aid in holding partially rejected objects.

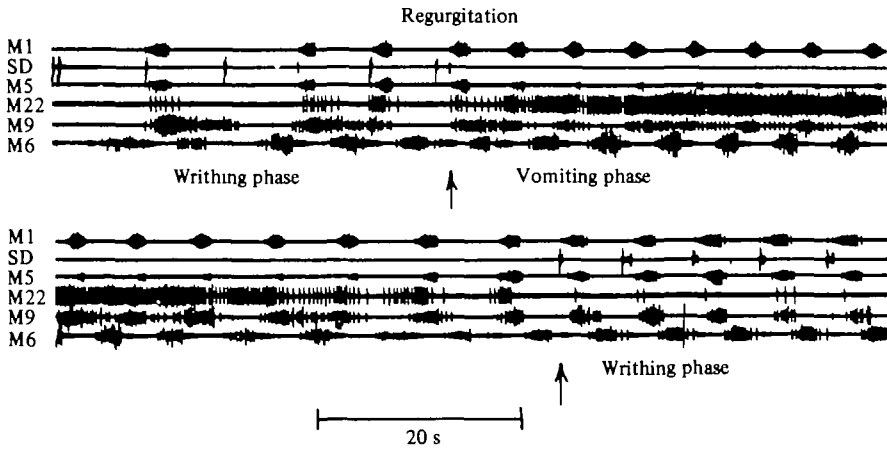


Fig. 7. Two continuous records illustrating the motor activity recorded in a modified semi-intact preparation during the regurgitation behaviour. Bouts of vomiting (between arrows) periodically interrupt the writhing phase (beginning and end of continuous record).

3. *Regurgitation (vomiting and writhing)*. The motor patterns recorded during regurgitation verified those obtained from the conventional semi-intact preparation. The intensity of vomiting was stronger in the modified semi-intact preparation and approached that observed in intact animals.

DISCUSSION

Authenticity of regurgitation and rejection

Regurgitation has been studied in several invertebrate animals (e.g. *Hydra*, Gardner, 1972; bees, Chapman, 1969; Prosser & Brown, 1965), and presumably is employed by *Pleurobranchaea* to expel rotten food. Rejection has received less attention in other animals, but could be employed by *Pleurobranchaea* and other gastropods (Bovbjerg, 1968; Kupfermann, 1974; Audesirk & Audesirk, 1979) to expel unpalatable objects such as pebbles or indigestible animal parts that have been ingested together with food.

Reflexive versus volitional action patterns

Regurgitation (i.e. vomiting), and rejection are 'all-or-nothing' responses which are released automatically, much like a programmed reflex, in response to noxious and indigestible material in the buccal cavity, respectively. This is to be expected because these stimuli threaten the survival of the animal and must be expelled relatively quickly regardless of the animal's motivation. In contrast, feeding in *Pleurobranchaea* can be variable and is clearly dependent on motivation (Lee & Palovcik, 1976; Davis *et al.* 1977) and associative factors (Mpitsos, Collins & McClellan, 1978).

First, the above information provides a plausible explanation as to why vomiting can be elicited in reduced semi-intact or even isolated preparations (McClellan, 1979, 1980, 1982*a*), while complete and unambiguous feeding can only be elicited in more intact preparations (cf. Figs. 6, 7). In fact, presentation of food to dissected prepara-

ctions occasionally elicits vomiting instead of feeding (McClellan, 1980). Second, the above behavioural differences are partly accounted for by known differences in neural organization. That is, the all-or-nothing nature of vomiting is thought to result from positive feedback between higher-order neurones and the motor-pattern generator (MPG), while variability of feeding is suggested to result from a heterogeneous group of higher-order neurones which can activate the motor network over a more continuous range (A. D. McClellan, in preparation).

Structure of the motor patterns

In *Pleurobranchaea*, motor activity during feeding, regurgitation and rejection consists of biphasic cycles which begin with radula retraction (Fig. 8). Presumed feeding motor activity in other gastropods begins with radula protraction and is biphasic in *Helisoma* (Kater & Rowell, 1973), triphasic in *Tritonia* (Bulloch & Dorsett, 1979) and quadriphasic in *Lymnaea* (Rose & Benjamin, 1979). The significance of these species differences is unknown.

Behavioural identification of motor patterns

It is common practice in neurobiology to assume that the motor activity recorded from dissected preparations underlies or is the 'neural correlate' of a behaviour displayed in the intact animal. However, the motor patterns which underlie different behavioural responses may have several features in common (see below).

In previous gastropod studies, the behavioural function of feeding has been assigned to the muscle activity associated with rhythmic radula movement, particularly spontaneous radula movement (Davis & Mpitsos, 1971; Berry, 1972; Kater & Rowell, 1973; Bulloch & Dorsett, 1979; Rose & Benjamin, 1979). These preparations have no stimulus to operate upon, and the patterns have not been shown to underlie feeding rather than some other response, such as rejection.

Differences between the motor patterns underlying different behavioural activities should first be found in relatively intact preparations which display complete and unambiguous responses (e.g. modified semi-intact preparation). The differences can then be used in assigning a behavioural function to a given pattern in more dissected preparations in which the mechanical consequences of the pattern cannot be observed. Accordingly, the strategy in the present study was to record motor activity elicited by natural stimuli from behaviourally responsive preparations. It is now clear that *Pleurobranchaea* displays several behavioural responses which involve similar but not identical rhythmic movements of buccal structures and which are expressed in part by similar motor patterns. These results have shown that the previously assumed feeding rhythm in the isolated nervous system of *Pleurobranchaea* underlies vomiting (McClellan, 1979, 1980, 1982a).

The sub-pattern generating rhythmic movements of the radula was found to be common to feeding, regurgitation and rejection (solid blocks, Fig. 8). This pattern can therefore no longer be termed a 'basic feeding motor programme', nor can other responses be said to result from modifications of this basic motor programme. It would be interesting to know whether this sub-pattern was present during other

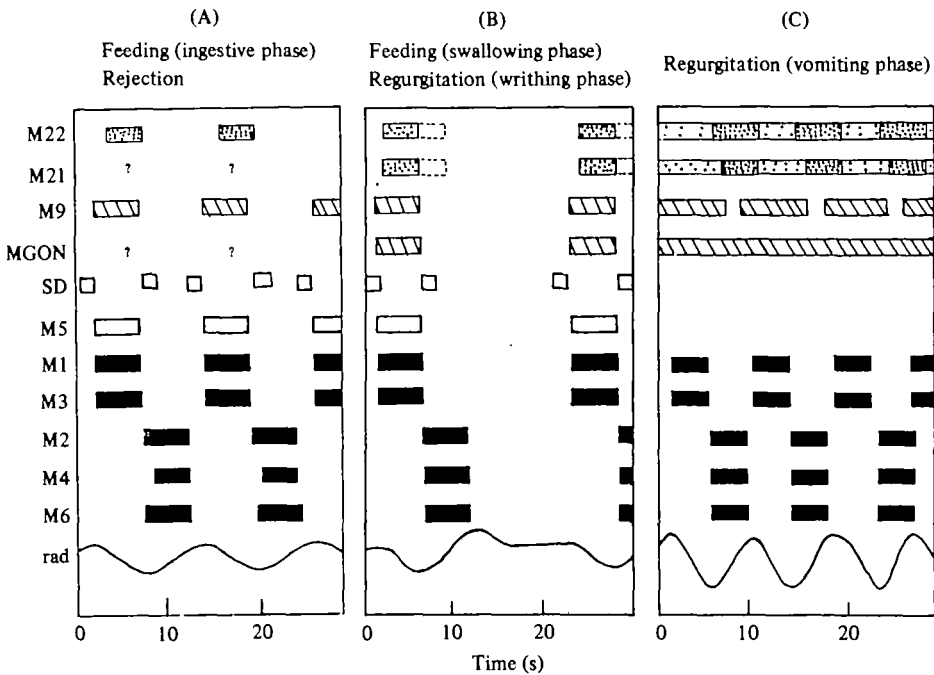


Fig. 8. Schematic summary illustrating the phasing of motor activity during feeding (ingestion and swallowing phases), regurgitation (writhing and vomiting phases), and rejection. The motor patterns recorded (A) during ingestion and rejection and (B) during the swallowing phase and the writhing phase are rather similar, except for differences in cycle time and minor unreliable differences in motor activity. The functional differences of these responses are presumably accounted for by the activity in muscles not recorded in this study. During the transition from the writhing phase to the vomiting phase of regurgitation (C), components of the motor pattern either become inactive (clear blocks), become tonically active (hatched blocks), or switch phase (stippled blocks). During all the behavioural responses, the muscles which produce rhythmic radula movement are active in a similar pattern (solid blocks). The variability of M22 and M21 activity during swallowing is indicated by the dotted extension of the bursts.

functions of the buccal mass. For example, defensive biting (Davis & Mpitsos, 1971) and gill grooming (G. Mpitsos, personal communication) also involve rhythmic movements of buccal structures, such as the radula, jaws and lips (see A. D. McClellan, in preparation).

Other components of the motor patterns (stippled, hatched, clear blocks; Fig. 8) indicate that certain features, such as SD inactivity, occur only during vomiting, and thus can be used to identify vomiting motor activity even when the preparation is dissected to the extent that it can no longer execute this response (McClellan, 1979, 1980, 1982a).

In contrast to the above, the parts of the motor activity recorded here during feeding (ingestion and swallowing), the writhing phase of the regurgitation sequence, and rejection are rather similar (Fig. 8), except for rhythm frequency differences. The behavioural identities of these patterns are none the less clear because the functions of the accompanying responses can be observed directly (cf. Figs. 6, 7). In dissected preparations, it will therefore be necessary to identify and record from other muscles

In order to distinguish between feeding and rejection motor activity as well as between ingestion and swallowing motor activity. Behavioural observations (see Results) suggest that the muscles which control the jaws and the shape of the radula are active in different ways during ingestion and rejection. (The jaws often remain closed during swallowing and the writhing phase.) Unfortunately, jaw muscles are at present unidentified, and inner radula muscles are difficult to record from in dissected, behaviourally active preparations. Unique differences in the pattern of leg muscle activity have been shown for ingestion, rejection and walking in *Limulus* (Wyse & Dwyer, 1973).

The swallowing phase of feeding and the writhing phase of the regurgitation sequence are similar in both appearance and motor activity, except for differences in intensity. It is, in fact, possible that the writhing phase also represents swallowing, but in response to noxious stimuli instead of food. If this is true, there should be no major differences in the motor patterns during these two responses.

Organization of the motor pattern generator

Feeding, regurgitation and rejection are expressed in part by similar motor activity (solid blocks, Fig. 8). It is therefore logical to assume that these responses are controlled at least partly by a single motor-pattern generator (MPG) network (McClellan, 1979, 1980). Several MPG models have been proposed for generating relatively fixed patterns (reviewed by Kristan, 1980). In *Pleurobranchaea* the MPG network could include separate oscillators which control the rhythmic movements of different buccal structures and which are coupled together in different combinations to produce the motor patterns underlying several responses. Alternatively, the MPG could consist of a single, flexible oscillator whose output depends on operating conditions within the network. In either case, the operation of the MPG would be determined by higher-order neurones, such as 'command' neurones, and sensory inputs. These possibilities are discussed in more detail elsewhere (A. D. McClellan, in preparation).

In other animals, single MPG networks have been proposed to generate the motor patterns underlying different behavioural responses which involve similar movements: warm-up and flight in the locust (Kammer, 1968); walking, righting and grooming in the cockroach (Sherman, Novotny & Camhi, 1977; Reingold & Camhi, 1977); flight and courtship movements of the wings in insects (Elsner, 1974; Ewing, 1977); forward and backward swimming in fish (Grillner & Kashin, 1976); various song patterns in the cricket (Bentley, 1977); ecdysis in the cricket (Carlson, 1977*a, b*); and different behavioural activities involving the legs in the locust (Pfluger & Burrows, 1978*a, b*), the lobster (Ayers & Davis, 1977; Ayers & Clarac, 1978), and the cat (Grillner, 1973; Edgerton *et al.* 1976; Berkinblit *et al.* 1978). The strategy of generating several responses with a single MPG network conserves neural elements and is presumably common in the organization of nervous systems.

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