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Pharyngeal movements during feeding sequences in *Navanax inermis*: a cinematographic analysis

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Summary. Pharyngeal movements during feeding in *Navanax inermis* were filmed and correlated with known neural activity controlling the pharynx. Seven distinct components of feeding were identified. Occurrence of a component was in some cases fixed, in that once initiated the act went to completion, and in other cases reflex, in that tonic stimulus control was needed for the act to be maintained. As few as 2 or as many as 7 different motor acts could occur in a feeding sequence. The specific acts which make up a sequence were dependent upon the nature of the prey stimuli that elicited feeding: qualitatively as well as quantitatively different feeding sequences were elicited by prey of differing sizes or by prey which was withdrawn from *Navanax* at different stages in a movement. The data indicate that the sequence of pharyngeal movements is not preprogrammed, but rather the sequence is appropriate to a specific type of prey. Flexibility in fitting a feeding sequence to the prey that elicits the sequence is achieved by combining in different ways a limited number of specific, fairly stereotyped motor acts.

Introduction

Feeding in gastropods has been intensively studied, to gain insight into neural mechanisms which may generate and modify a complex motor act (for review, see Kandel 1976, 1979; Kohn 1983). A number of studies have focused upon the opisthobranch *Navanax inermis*, because of its remarkably fast and dramatic mode of feeding. Ingestion of prey is produced by rapid pharyngeal expansion, pulling prey into the pharyngeal cavity (Murray 1971; Spira and Bennett 1972; Woollacott 1974; Spira et al. 1980). Neural control of feeding may also be easier to study in this animal than in some other gastropods. The pharynx is composed primarily of 3 orthogonal muscle groups, and neurons producing contraction of muscles of each orientation have been found (Woollacott 1974; Cappell et al. 1979, 1980; Spira et al. 1980; Zimering et al. 1981). By contrast, gastropods which feed via a radular mechanism require the coordination of a large number of muscles oriented in many directions (for review, see Kandel 1979).

Much is already known about the neural circuitry underlying feeding movements. Sensory neurons respond to touch of specific regions of the pharynx (Spray et al. 1980a), synapse upon one another (Spray et al. 1980b), and onto motoneurons producing expansion (Spray et al. 1980b; Spira et al. 1980). Motoneurons responsible for general and localized expansion (Spira et al. 1980) and constriction (Cappell et al. 1979, 1980; Zimering 1981) of the pharynx have also been identified. Motoneurons to radial musculature that produces expansion are electrotonically coupled to one another (Levitan et al. 1970; Spira and Bennett 1972), presumably synchronizing activity of action of motoneurons and contributing to speed and synchrony of expansion (Spira and Bennett 1972; Spira et al. 1980). Coupling between radial motoneurons can be reduced by inhibitory synaptic inputs produced by specific stimuli, thus allowing motoneurons to function independently (Spira and Bennett 1972; Spira et al. 1980). Synaptic interactions between expansion motoneurons, as well as from expansion to circumferential motoneurons, have also been described (Levitan et al. 1970; Spira and Bennett 1972; Spira et al. 1976, 1980). Circumferential motoneurons are also coupled to one another, and the coupling can be functionally reversed by synaptic inputs via inhibitory interneurons (Spira et al. 1976).

In spite of the wealth of data on control of pharyngeal musculature, there is relatively little behavioral information on the role of the pharynx during feeding. Most behavioral studies of *Navanax* have been concerned with trail-following (Blair and Seapy 1972; Paine 1963; Murray 1971) and other aspects of food-finding behavior (Susswein et al. 1982). Pharyngeal movements during feeding were observed by Murray (1971), who divided feeding into 3 stages, elicited by activation of 3 separate populations of receptors: (1) trail following, leading to contact of the *Navanax* with the prey; (2) protraction of the pharynx, leading to contact of the prey with the pharyngeal lips; (3) pharyngeal expansion, causing prey to enter the pharynx. There is also an additional phase of feeding, (4) peristalsis, which pushes prey out of the pharynx and into the esophagus (Bennett 1974; Woollacott 1974; Cappell et al. 1980; Zimering et al. 1981). It is difficult to relate a particular piece of neural circuitry with a specific aspect of behavior. The studies reported in this paper attempt to provide a more complete behavioral framework for neural studies on control of the pharynx during feeding.

The work reported in this paper attempts to provide a bridge between behavioral studies of feeding performed upon a whole animal, and neural studies performed upon severely dissected preparations. The feeding sequence observed in intact *Navanax* is divided into a number of distinct components and the stimulus conditions required for the occurrence of a component of movement are examined. Criterion for selection of a movement as a distinct component of feeding is that independent control is exerted over the occurrence or intensity of the movement. A particular point of emphasis in the study was to observe whether a given component of feeding will go to completion when stimuli initiating the movement are withdrawn, or whether stimuli must be tonically maintained for a movement to proceed.

A preliminary report of some of these findings has appeared (Susswein et al. 1979).

Methods

Experiments were performed upon *Navanax inermis* purchased from Pacific Biomarine (Venice, California, USA) which were maintained individually in perforated plastic or plastic mesh cages immersed in recirculating seawater at a temperature of 16–17 °C and adjusted to a specific gravity of 1.025. The holding tank was filled with artificial seawater (Instant Ocean) in New York, and locally drawn Mediterranean seawater in Ramat-Gan. The stimuli that elicited feeding were either whole specimens of *Bulla gouldiana* or *Hermissenda crassicornis* (Pacific Biomarine), or pieces of *Bulla* meat held at the tip of a hemostat. During filming, animals were removed from the holding tanks, and were hand-held in a seawater-filled tub. Water in the tub was exchanged every 10–15 min. Because of outline of the pharynx is more readily observed through the lightly pigmented ventral skin than through the more darkly pigmented dorsal skin, in most cases animals were held ventral side up.

16 mm films were made with a Bolex H16 reflex movie camera. Speed of filming in different sequences varied from 16 frames /s to 64 frames/s. Films were edited and were then analyzed with an NAC Dynamic Frame model DF-16B variable speed motion analysis projector. The frame counter of the projector was used to time movements. Frames within a sequence were then marked, and enlargements made from them. Drawings illustrating various movements were traced from the enlargement, or were traced directly from the projected image. When the pharynx was visible, the relative width of the pharynx at different stages of feeding was measured directly from the projected image. In some cases, the absolute size of the lips or pharnx was estimated by reference to the width of the thumb of the experimenter holding the animal.

Results are based upon over 200 filmed sequences of feeding. Each sequence was observed at least 10 times and some sequences were observed closer to 100 times.

In some feeding sequences, food was removed at various stages of the sequence, to determine to what extent later portions of the sequences are dependent upon maintained presence of stimuli. We often failed to remove food precisely between specific components of feeding, nevertheless, the large number of sequences observed allowed us to film at least some sequences in which food was removed precisely between one component and another.

Results

Figure 1 shows a labelled diagram of the parts of *Navanax* which are discussed below, and are involved in feeding.

Figure 2 shows a freely-moving *Navanax* approach and engulf a *Bulla* prey. The tentacles (Fig. 1), which bear chemoreceptors that help to localize prey (Murray 1971), are protracted during approach toward prey. Contact with prey initiates pharyngeal expansion (Fig. 2C–E), followed by prey ingestion (Fig. 2D–F). In the sequence shown, time from prey contact (Fig. 2B) to when the entire prey was within the pharynx (Fig. 2f) was 1.56 s.

In order to observe the events occurring during prey capture more clearly, it was necessary to create conditions in which the encounter between *Navanax* and its prey was under experimental control. This was accomplished by hand-holding both the *Navanax* and its prey, and bringing the two together for part or all of a feeding sequence. Hand-holding *Navanax* upside-down has little or no effect upon feeding movements (Susswein and Bennett 1979). Under these conditions, 3 stages of feeding could be discerned. Each stage was made up of one or more motor acts. We have termed these stages: (1) protraction and flaring; (2) prey seizure; (3) expansion and retraction.

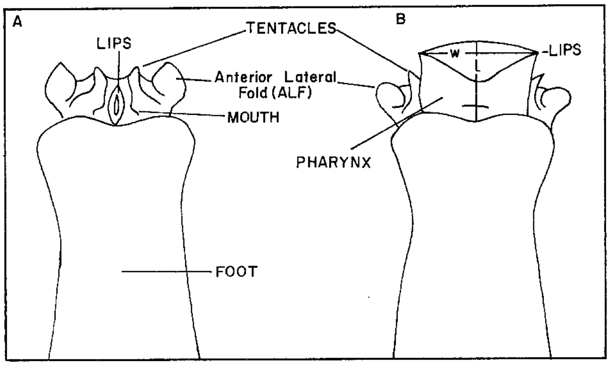

Fig. 1 A, B. Anatomy of all parts of *Navanax* discussed in the text. Drawing is from the ventral aspect. **A** Head and mouth when the pharynx is retracted. The tentacles and anterior lateral folds are sensory structures on either side of the mouth. The lips are anterior extensions of the pharynx, and exit the mouth during feeding movements. **B** Appearance when the pharynx is expanded. Lines labelled W and L show the locations where pharyngeal width and exposed length were measured (see below, Figs. 7, 8)

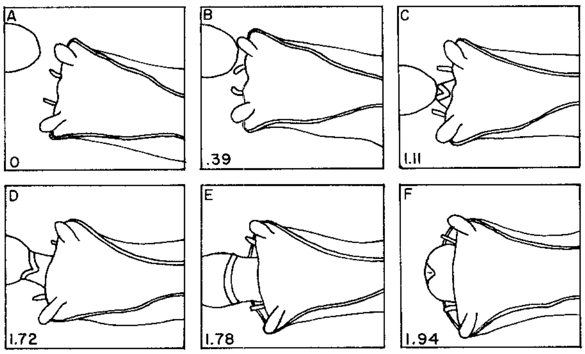

Fig. 2 A–F. Drawing traced from film, showing a freely-moving *Navanax* approach and engulf prey. Numbers represent seconds following the first frame shown

Protraction and flaring

Externally observable movements of the pharynx begin with protraction (Fig. 3). During protraction the mouth opens, and the pharyngeal lips, an anterior specialized region of the pharynx, protract out of the mouth. Protraction is accompanied by a second motor act, flaring of the anterior pharynx and lips, which is in part due to expansion of the anterior pharynx immediately behind the lips (Fig. 3).

The stimulus initiating protraction is touch of food to the tentacles (Murray 1971). Withdrawal of *Navanax* from the food following initiation of protraction does not immediately arrest this movement: protraction continues (Fig. 3). Neurophysiological studies will be required to determine the extent to which continued activity after prey removal is similar to that occurring in presence of prey.

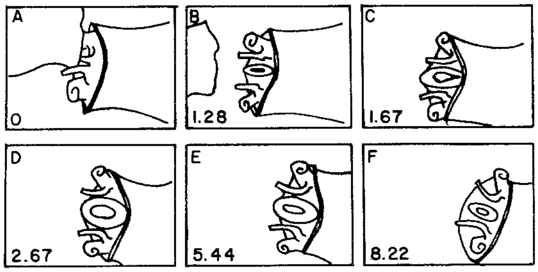

Fig. 3 A–F. Outline drawing traced from film of protraction and retraction of the pharynx. **A** The stimulus for protraction is touch of prey (*Bulla*) to the tentacles, and anterior lateral fold. **B–D** The lips and anterior pharynx protract out of the mouth. The lips emerge from the mouth flared. **D–E** Protraction is maintained. **E–F** Retraction of the pharynx back into the mouth occurs. Numbers represent seconds following the first frame shown

Protraction is a relatively slow movement. In Fig. 3, 2.67 s ensued between the stimulus eliciting protraction until maximal protraction occurred. The sequences illustrated in Figs. 2 and 3 occurred under conditions that were probably close to optimal, and so protraction was likely to be occurring at close to its fastest speed for the ambient temperature. Protraction is an order of magnitude slower than movements associated with prey seizure or expansion (see below).

Prey seizure

Prey seizure consists of two movements (Fig. 4); (1) the snap, a rapid closing shut of the flared lips onto or around the prey; (2) the strike, in which the pharynx moves rapidly forward and thrusts onto the prey. The strike and the snap occur more or less synchronously and therefore will be treated together.

If prey is withdrawn after protraction is initiated but before the start of prey seizure, the feeding sequence does not proceed: protraction is maintained for a period of about 3 s (Fig. 3D–E), and is then followed by retraction instead of by prey seizure (Fig. 3E–F). This indicates that prey seizure is not an automatic consequence of protraction, but requires a new external stimulus. The stimulus for initiating prey seizure is touch of food to the lips (Murray 1971). If prey seizure does not occur, an alternate movement, retraction, restores the pharynx to the rest position.

The strike and snap are together wholly sufficient to capture small prey or a small piece of meat (Fig. 5). For larger pieces of prey, these movements appear to function to seal the lips against the prey, so that suction produced by subsequent expansion can be efficiently applied, and will lead to successful prey capture.

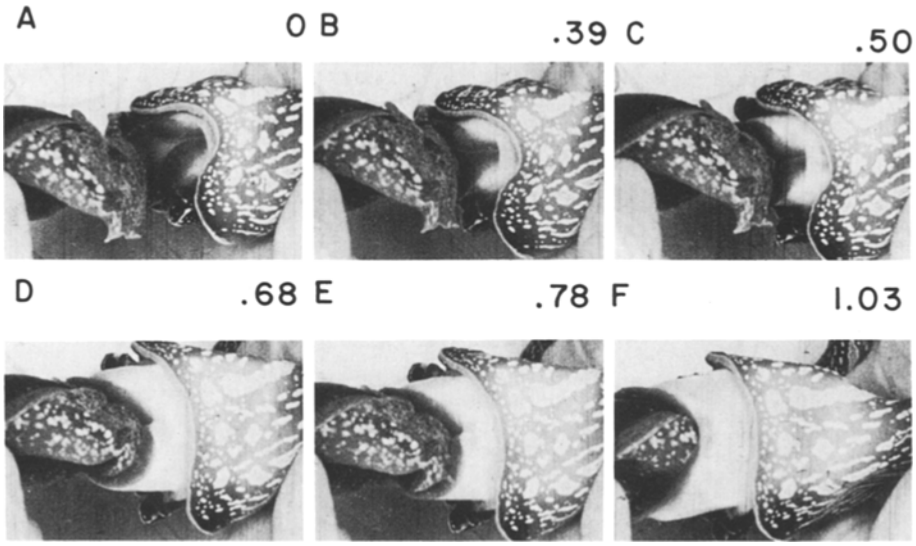

Fig. 4A–F. Prey seizure, followed by pharyngeal expansion. **A** Prey seizure is initiated by touch of prey to the lips; **B** Snap and strike have occurred. The prey is in contact with the anterior pharynx; **C–F** Expansion of the pharynx, pulling prey into the interior of the pharynx. In this sequence, retraction of the pharynx (not shown) did not occur, until much after maximal expansion; in other sequences, such as that shown in Fig. 7, expansion and retraction occurred simultaneously. Numbers in each frame represent seconds following the first frame

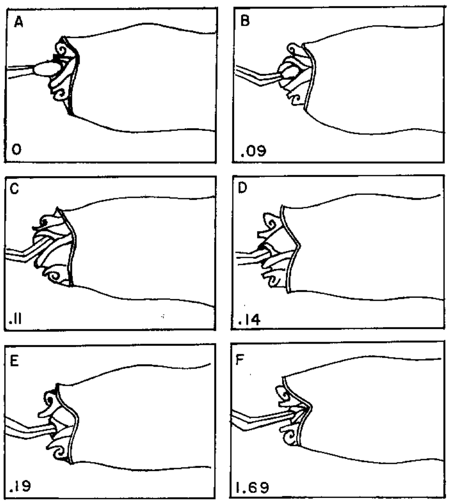

Fig. 5A–F. Outline drawing traced from film of snap and strike that are sufficient to capture small prey. **A** The stimulus for prey seizure is food touched to the lips. **B–C** Strike brings the entire prey into the interior of the pharynx. **D–E** Snap traps the prey inside the pharynx. **F** Retraction of the pharynx and prey occurs slowly, with no clearly evident subsequent expansion. Numbers in each frame represent milliseconds following the first frame shown

The strike and the snap are independently controlled movements, though closely coordinated. Thus, in some sequences, the strike precedes the snap, while in other sequences the order was reversed. Also, the strike was somewhat variable in intensity from sequence to sequence, while the snap seemed to be relatively constant in form.

In many cases, lip closure during the snap did not eliminate the intrapharyngeal hollow formed by expansion of the anterior pharynx during flaring, rather, the snap occurred anterior to the hollow, leaving the anterior pharynx expanded. This was particularly clear when small prey were captured, and when prey was missed.

Time for prey seizure was measured in 30 cases. Onset and termination of strike and snap were readily recognized, since these are dramatic movements, and even at filming speeds of 64 frames/s the pharynx is noticeably changed frame to frame during prey seizure. The onset of prey seizure was defined by the first frame in which a sudden outward movement of the pharynx occurred, or in which the lips began to close. Termination of prey seizure occurred when the pharynx was no longer rapidly moving outward, or when the lips were no longer in the process of closing. Mean time for prey seizure to occur took 0.38 s $\pm$ 0.20(SD).

The width of the pharynx was measured during 51 prey seizure sequences. The percent change in width during prey seizure is shown in Fig. 6. The figure shows that in prey seizure movements which miss prey, a small (less than 5%) increase in pharyngeal diameter is observed. In dissected preparations in which a window was cut through the body wall, permitting direct visibility of the anterior pharynx, a small increase in the width of the anterior pharynx can be directly observed during prey seizure (Susswein et al., in preparation). By contrast, in movements in which prey enters the pharynx, there is substantial increase in pharyngeal diameter (Fig. 6). This probably represents the start of the next phase of feeding, expansion, which is triggered by entry of prey into the anterior pharynx (see below), and often immediately follows prey seizure without a clear break between the 2 phases of feeding. The data in Fig. 6 indicate that the diameter of the pharynx during even successful prey seizure movements is much smaller than dur-

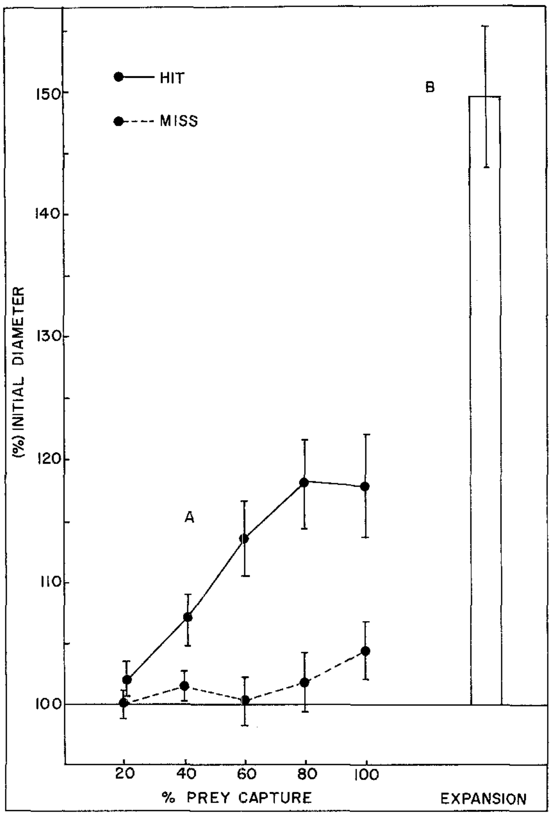

Fig. 6. **A** Percent change in width of the pharynx as a function of time following initiation of prey seizure. For this figure each of 51 prey seizure movements (21 misses, 30 hits) was divided into 5 equal portions, and the width of the pharynx was measured during each fifth, as well as just before the start of prey seizure. The pharyngeal width was normalized to the initial width by expressing all subsequent measurements as percentages of the initial width. The data indicate that the pharyngeal width increases both when *Navanax* miss and hit the prey, but the increase in width is much greater when prey is hit. **B** Width of the pharynx during maximal expansion in 10 animals, expressed as a percentage of pharyngeal width just before prey seizure. Width of the pharynx is much larger during expansion than during prey seizure. Standard errors are shown in both **A** and **B**

ing later phases of feeding: Figure 6B shows that at the maximal expansion the pharynx is much wider than during prey seizure. These data indicate that radial muscles producing an increase in pharyngeal volume are maximally activated in later phases of feeding when prey has already entered the pharynx.

Prey seizure is usually followed by retraction of the pharynx. If prey has been missed, retraction represents a return to rest conditions in preparation for a further feeding attempt. If prey has been captured, retraction may serve an additional function, in that prey lodged in the pharynx is pulled into the interior of the animal along with the pharynx. Once the pharynx and prey are inside the animal, body wall or other extrapharyngeal muscles may work along with the pharynx in propelling food further into the gut.

Expansion and contraction

Expansion is characterized by a large, dramatic increase in pharyngeal diameter (Fig. 4). Initiation of expansion occurs following onset of prey seizure, but prey seizure may still be in progress at the start of expansion. Expansion usually continues well after prey seizure is over. Pharyngeal retraction may occur while expansion is still in progress (Fig. 7), or after expansion has already occurred (Fig. 4). Occurrence of expansion and retraction with relation to prey seizure is illustrated in Fig. 7.

Expansion is clearly differentiated as a stage of feeding separate from prey seizure, since under certain circumstances prey seizure is not followed by expansion (Fig. 5). In most cases when prey was missed, expansion did not occur. In 4 of 12 filmed sequences in which small pieces of food were captured by animals, no expansion subsequent to prey seizure was observed (Fig. 5). Even when large prey was presented to *Navanax*, in many cases no expansion occurred; however, if expansion was absent, pharyngeal contraction often occurred instead. Contraction consists of a reduction of pharyngeal volume, which pushes oversize prey out of the pharynx (Fig. 8). In addition to occurring immediately after prey capture as an alternative to expansion, contraction can also occur after expansion, if expansion is insufficient to pull prey into the pharynx. Contraction may function to expel prey, or to prepare the pharynx for further expansion movements.

Even though expansion is not an automatic consequence of prey seizure, prey seizure or associated events seem to be a necessary precondition for expansion to occur; in experiments in which prey was placed directly into the pharynx with no preceding prey seizure movement, expansion did not occur.

Stimulation of the external lips does not seem to be an essential component for triggering expansion, even though in most cases when expansion occurs some part of the oversize prey remained outside of the pharynx stimulating the lips. In at least some instances, expansion occurred when prey was wholly within the pharynx due to the preceding prey seizure movements.

Stimulation of a local region of the pharynx by prey does not produce expansion limited to the region stimulated; expansion of pharyngeal areas

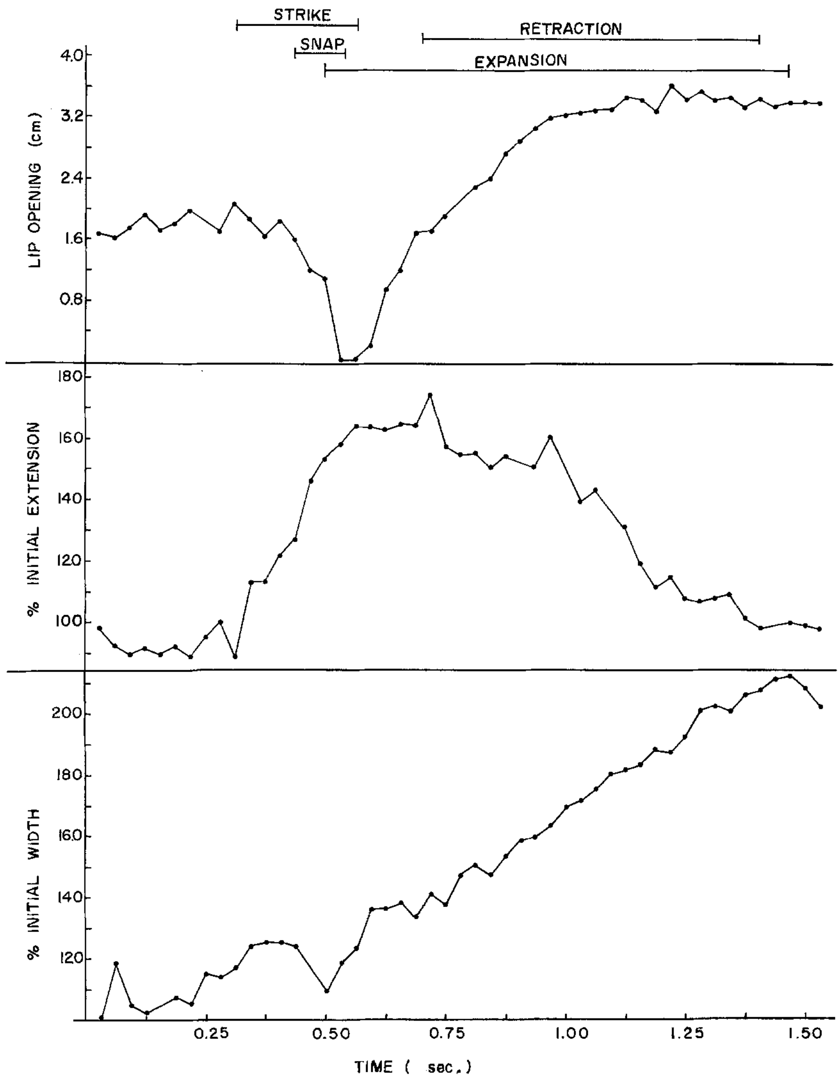

Fig. 7. Prey seizure and subsequent expansion in a single feeding sequence, graphically represented by measurements of various parameters of the pharynx. Three parameters were measured: pharyngeal width, expressed as a percent of the width in the first frame (percent initial width); length of the pharynx that extends out of the mouth, expressed as the percent extension seen in the first frame (percent initial extension); lip opening, estimated from the size of the thumb of the experimenter holding the animal (see Methods). Points at which measurements were made are illustrated in Fig. 1. The strike is characterized by a dramatic increase in length of the pharynx that is extended. During the snap, the lips close sharply. Strike and snap occur together. Expansion produces a gradual increase in pharyngeal width, coupled with an increased lip opening as prey enters the pharynx. Retraction is reflected by a decrease in the extension of the pharynx, as the pharynx is pulled back into the body of the *Navanax*. The sequence shown was filmed at 64 frames/s. Each point is the mean of measurements made upon 2 successive frames

distant from the stimulus also occurs. The specific site where expansion is triggered seems to be the anterior pharynx. Figure 9 shows a sequence in which the prey animal never reached further than the anterior pharynx, while most of the expansion occurred posterior to the prey.

Time course of observable expansion is highly variable. In the sequences shown in Figs. 1, 7 and 9, the initial stage of expansion took from 0.25 s to over 0.9 s. The data suggest that expansion is generally 50–100% slower than the strike and the snap movements that occur during prey seizure.

Some expansion movements are very slow, occurring in a time course of seconds. An expansion movement was observed that took over 6 s. It is not clear whether slow and fast expansion represent qualitatively different acts triggered by different stimulus conditions, or whether the same trigger elicits quantitatively longer or shorter acts due to differing prey resistances.

Variations in intensity and sequencing

Protraction and flaring. Intensity of these movements is to some extent variable. Partially satiated animals perform slower, smaller protractions than do hungry animals (Susswein and Bennett 1979). Flaring is partially under stimulus control, since when food is withdrawn after triggering the movement, extent of flaring is less than in presence of food. Stimuli controlling extent of flaring could be contact of food to either the lips or tentacles.

Prey seizure. In order to determine whether prey seizure is varied by the size of the eliciting prey, or by whether or not the *Navanax* succeeds in capturing the prey, movements were observed that were elicited by small and large pieces of prey, that were successfully captured, or that were pulled back before ingestion was completed. Prey seizure consisting or strike and snap was found to occur

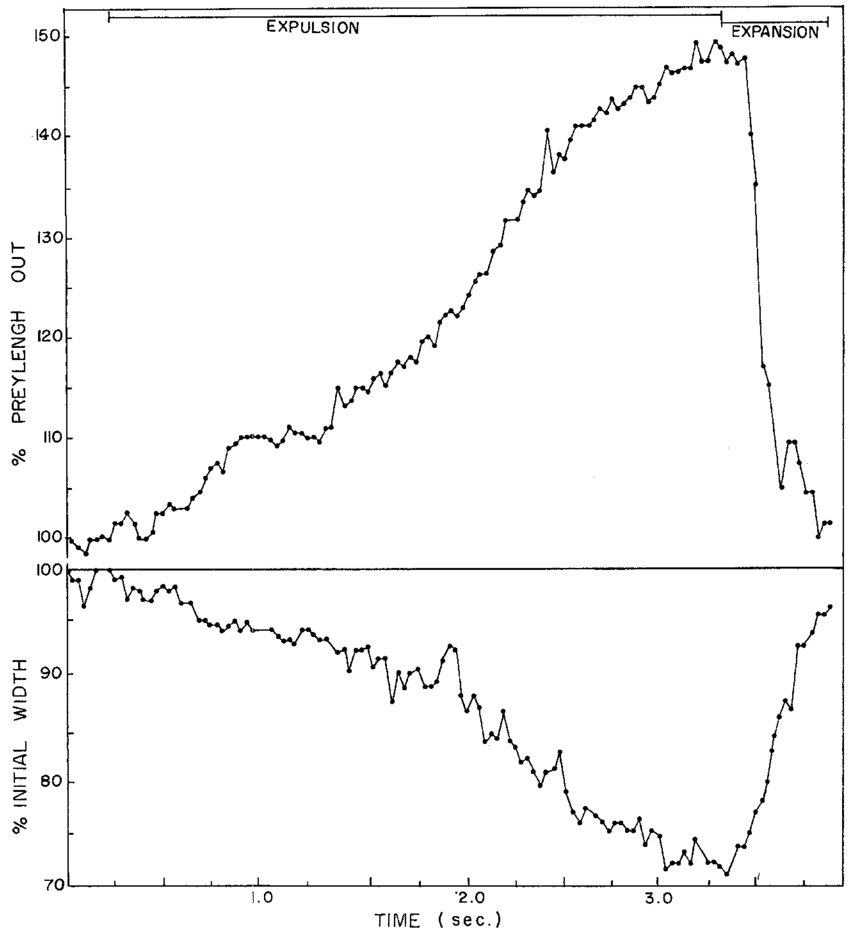

Fig. 8. Contraction leading to prey expulsion, and subsequent expansion in a single sequence, graphically represented by measurements of pharyngeal width (expressed as a percentage of that in the initial frame), and length of prey (a large *Bulla*) that is outside of the pharynx (expressed as a percentage of that in the initial frame). Prior to the constriction shown in the figure, prey seizure and expansion occurred. Contraction is characterized by a decrease in pharyngeal width, which forces prey out of the pharynx. Time course is over 3 s. Subsequent to contraction, expansion occurs. Width increases, again pulling prey into the pharynx. The sequence graphed was filmed at 64 frames/s. Each point represents the mean of measurements made upon 2 successive frames

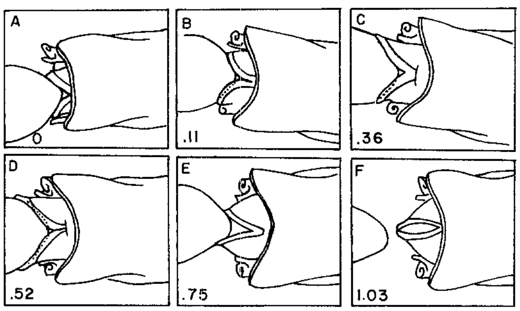

Fig. 9A–F. Outline drawing of expansion of the pharynx triggered by prey that was in contact only with the anterior pharynx, without subsequent prey entry. **A–C** Prey capture, and entry of prey into the anterior pharynx. **C–F** Expansion of the pharynx, even though the stimulus triggering the expansion is withdrawn. Dotted line shows the extent of penetration of the prey (a large *Bulla*) into the pharynx. Numbers in each frame represent seconds following the first frame

in all conditions, with no systematic difference in time for the movements to occur. Effects on speed of prey seizure due to differences in motivational state (Susswein and Bennett 1979) are likely to be more significant than are differences due to the type of prey.

Expansion and contraction. Time of occurrence of these movements is quite variable. Expansion can occur while prey seizure is still in progress (Fig. 6), immediately following prey seizure (Fig. 7), or after a lag of a few seconds. A lag between prey seizure and expansion was observed with both small and large prey. With large prey, a late expansion was often an additional expansion occurring after the initial expansion failed to bring the entire prey into the pharynx. Often, but not always, a contraction movement separated the 2 phases of expansion (Fig. 8). Expansion is at least to some extent a triggered movement. In the sequence shown in Fig. 9, expansion continued following withdrawal of *Bulla* prey; we cannot eliminate the possibility that maintained sensory information may modulate the intensity of expansion, since muscle tension and negative pressure were not measured.

Discussion

Feeding is composed of a number of specific acts, produced by the integrated activity of muscle

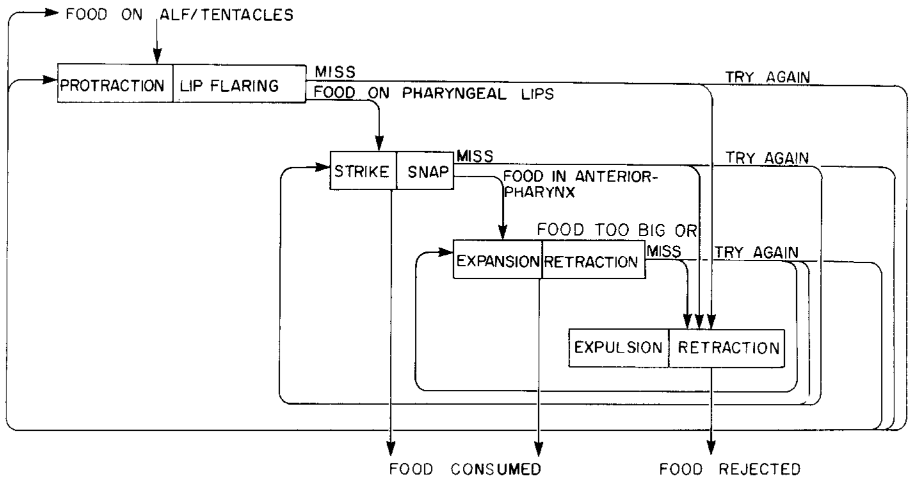

Fig. 10. Flow diagram showing the sequence of motor acts which can occur in a feeding movement. See text for explanation

groups which are under the control of a variable number of interneurons and motoneurons. To understand feeding in terms of the action of individual cells, it is useful to divide the behavior into distinct components, and to clarify their nature.

In the present paper, the feeding sequence of *Navanax* was divided into a number of individual acts.

1. *Protraction.* This movement is initiated by touch of food to the tentacles.

2. *Lip flaring.* This movement occurs simultaneously with protraction. The stimulus is touch of food to either the tentacles, to the lips, or perhaps to both.

3. *Prey seizure: strike.* This movement is initiated by contact of food to the lips.

4. *Prey seizure: snap.* This movement in most cases is simultaneous with prey capture, but in some cases is independent.

5. *Retraction.* This movement has a number of functions, and may not be the same movement in all cases. If proper conditions for prey seizure are not present, retraction occurs as an alternative to prey seizure. If prey seizure movements occur, retraction follows both successful and unsuccessful prey seizure. The stimulus requirements and the nature of retraction have not been explored, but likely stimuli may be protraction itself, or feedback from proprioceptors in protractor muscles.

6. *Expansion.* The movement is initiated by food in the pharynx, probably in the anterior pharynx. Because the movement generally occurs with larger prey, the activity of stretch receptors may be an essential component for triggering the movement. Additional factors are also needed before expansion is triggered, since the movement will not occur, unless it is preceded by prey seizure. The movement has a variable time course, and may not be the same movement in all cases.

7. *Contraction.* This movement can be an alternative to expansion, or can occur subsequent to expansion. It may represent rejection of the prey, or preparation for a new attempt at ingestion through expansion. The movement has to date been observed in intact animals only with oversize food, suggesting that a component of the stimulus for rejection may be stretch of the pharynx, perhaps of a magnitude larger than that needed to induce expansion. Contraction sometimes was initiated by gentle pull of the prey out of the pharynx. This suggests that outward movement of the prey may also be a trigger for contraction.

Individual motor acts combine with one another to make up a feeding sequence. As few as 2, or as many as 7 different motor acts combine to make up a sequence. Two of the acts, retraction and contraction, may abort a sequence. Retraction can abort a sequence if it occurs after protraction (Fig. 3), or after protraction with flaring, making a sequence composed of 2 or 3 motor acts. If feeding is not aborted following protraction and flaring, prey seizure composed of strike and snap occurs. If a small prey is eaten, prey seizure may be sufficient to bring prey entirely into the pharynx (Fig. 4). The pharynx is then retracted, making a sequence of 5 acts. If a large prey is eaten, prey seizure may be followed by expansion and retraction, making a sequence of 6 acts (Fig. 7). If food is too large to enter the pharynx in one expansion, a number of expansion movements can occur. The large piece of food can also induce contraction leading to expulsion instead of expansion (Fig. 8), which also makes a sequence of 6 acts. Finally, contraction and concomitent expulsion can occur after expansion, making a sequence of 7 acts.

Failure to ingest a piece of food in one sequence does not necessarily mean that prey will be rejected: a second attempt at prey seizure can occur. The second attempt need not begin with protraction and lip flaring, but rather may commence directly with strike and snap, or with expansion. A flow diagram summarizing the sequence of events that occur in prey ingestion is shown in Fig. 10.

Studies on *Aplysia* (Rose 1972; Kupfermann 1974; Weiss et al. 1977), *Archidoris* (Rose 1971), *Helisoma* (Kater and Rowell 1973; Kater 1974; Kaneko et al. 1978), *Pleurobranchaea* (Davis et al. 1973; Siegler et al. 1974; Siegler 1977), *Limax* (Gelperin et al. 1978; Reingold and Gelperin 1980), *Lymnaea* (Benjamin and Rose 1979; Rose and Benjamin 1979) and *Tritonia* (Willows 1978; Bulloch and Dorsett 1979a, b; Willows 1980) have emphasized that the pattern of feeding movements is stereotyped and repetitive, due to the activation of various types of central pattern generators. Sensory input serves to initiate and modulate the pattern generator. A similar view of feeding in *Navanax* was proposed by Woollacott (1974) based upon studies of movements elicited by stimulation of the cerebro-buccal connectives in a number of reduced preparations. By contrast, the present study suggests that natural feeding movements seem to be a chain of a number of acts, which combine to form feeding sequences appropriate to a specific prey stimulus. The difference between our data and that on other gastropods in part may reflect ecological differences. Other gastropods studied to date graze upon plants, or sessile animals. By contrast, *Navanax* consumes prey about as active and sometimes almost as large as itself. Greater flexibility may therefore be needed to produce a feeding response appropriate to this type of food. Also, the repetitive phase of feeding studied in other gastropods is the protraction-retraction swallow that draws food into the mouth and gut; this follows the initial bite that leads to entry of food into the mouth. The present study addresses itself only to movements leading to prey capture, which may be less stereotyped than are subsequent movements in other gastropods as well.

Radial musculature producing expansion is prominently active during 2 feeding acts: lip flaring and expansion. Lip flaring involves expansion of the anterior pharynx, while expansion involves activity of the radial muscles in the whole pharynx. Expansion movements observed in the present study are poor monitors of the activity of motoneurons and muscles producing these movements. Radial musculature may also be more prominently active during prey seizure than we have observed (Fig. 5), but mechanical factors prevent forces due to muscle contraction from being translated into movements. Small, localized expansions may also be easily missed. Expansion movements which were not monitored may be at least partially responsible for the strike movement. In the strike, the pharynx lunges forward toward the prey; movement of the pharynx occurs with respect to the rest of the animal. Also, the animal sometimes appears to move forward with respect to its surroundings. The forward translocation of the pharynx and the whole *Navanax* may be due to expansion producing negative jet propulsion.

Circumferential musculature is prominently active during 2 phases of feeding: lip closure and contraction. Circumferential musculature may also be active during flaring, causing the posterior pharynx to be constricted behind the anterior pharyngeal expansion. The role of circumferential musculature during flaring and constriction are more readily observed in partially dissected preparations than in intact animals. The entire behavior of peristalsis is also best observed after animals are partially dissected. Discussion of circumferential involvement in these movements will be deferred to a future paper.

A specialized subpopulation of circumferential muscles forming an anterior sphincter has been described (Cappell et al. 1979; Zimering et al. 1981). It is possible that some or all of these muscles are responsible for the snap, the fastest and most stereotyped movement observed.

Protraction and retraction are produced in part by the activity of muscles extrinsic to the pharynx. Protraction and retraction muscles have been described by Murray (1971), and Spray et al. (1977) have identified motoneurons for some of these muscles. The extrinsic muscles described to date cannot be the exclusive source of these movements, since animals in which either all protractor or all retractor muscles are chronically cut are still able to ingest prey (unpublished observation).

In the present paper we have demonstrated that externally observable feeding can be divided into a number of acts which can be combined with one another to provide considerable flexibility in producing feeding sequences appropriate to a particular prey stimulus. The behavioral studies on intact animals also shed light upon the function of particular groups of muscles, and upon particular aspects of neural circuitry which have been previously studied. However, studies upon intact animals are limited, in that the pharynx is not directly visualized. The data presented above can be extended by observations of feeding behavior in partially dissected preparations, where the pharyngeal movements can be directly seen (Susswein et al. 1979).

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