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THE ROLE OF THE *MELIBE* BUCCAL GANGLIA IN FEEDING BEHAVIOR

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A series of anatomical, physiological and behavioral experiments were conducted to determine the role of the *Melibe* buccal ganglia in feeding. The small, paired buccal ganglia are located on the surface of the esophagus, communicate with each other via a long buccal-buccal connective, and with the brain via bilaterally symmetrical cerebral-buccal connectives. They also innervate the anterior and posterior regions of the esophagus, and the paired salivary glands. Stimulation of the cerebral-buccal connectives causes slow rhythmic contractions of the esophagus, and stimulation of either the anterior or posterior buccal nerves results in single contractions of the esophagus. Removal of both buccal ganglia does not impair the ability of animals to capture food, but it has a significant impact on the transfer of captured prey through the esophagus. These data, taken together, indicate that the *Melibe* buccal ganglia do not influence the capture of food, but rather control movements of the esophagus which are necessary to transport food from the mouth to the stomach.

KEY WORDS: *Melibe leonina*, buccal ganglia, feeding behavior, swallowing, lesions, gastropod feeding.

INTRODUCTION

Gastropod buccal ganglia innervate extensive areas of the buccal mass, pharynx, salivary glands, esophagus, and stomach and serve important functional roles in the control and modulation of feeding behavior. Due to their suitability for investigations of the neural basis of behavior buccal ganglia have been studied extensively in a number of different species (*Aplysia*, Kupfermann, 1974; Cohen *et al.*, 1978; Lloyd *et al.*, 1988; *Helisoma*, Kater, 1974; *Limax*, Gelperin *et al.*, 1978; *Lymnaea*, Benjamin and Rose, 1979; Elliot and Benjamin, 1985a, b; *Pleurobranchaea*, Gillette and Gillette, 1983; *Tritonia*, Willows, 1980; Lloyd and Willows, 1988; Willows *et al.*, 1988; *Planorbis*, Arshavsky *et al.*, 1988). Although the feeding behaviors, and the types of prey consumed, differ widely between gastropods, certain organizational and functional characteristics of buccal ganglia appear to have been conserved during the course of evolution (Benjamin, 1983). In general,

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buccal ganglia contain sensory neurons, motor neurons that innervate the feeding organs, a network of interneurons which generate the biting, chewing and swallowing rhythms, and regulatory neurons that modulate the output of the network.

Recordings from buccal nerves in semi-intact preparations of several species indicate that the buccal ganglia play a major role in the acquisition and processing of food. They generate the various rhythmic feeding patterns and control the intrinsic muscles of the radula and buccal mass, as well as the salivary glands, pharynx, and esophagus (Benjamin, 1983). Additional evidence indicating that buccal ganglia play a critical role in the consummatory aspects of feeding behavior comes from studies in *Aplysia*. When Kupfermann (1974), cut both the cerebral-buccal connectives between the brain and the buccal ganglia, thereby preventing activation of the buccal motor programs by descending interneurons and sensory neurons, he observed that food would still elicit appetitive aspects of feeding, such as head waving, but animals were unable to eat the food.

Swallowing and movements of the buccal mass that transport food through the esophagus to the stomach, also appear to be under the control of neurons in the buccal ganglia. Willows (1980) has identified buccal ganglion neurons which are involved in swallowing behavior in *Tritonia diomedea* and characterized their rhythmic activity. Both ingestion and egestion motor programs have been recorded from isolated and semi-isolated *Pleurobranchaea* buccal ganglia (Croll and Davis, 1981). Finally, Lloyd *et al.* (1988) have demonstrated that identified peptidergic neurons in the buccal ganglia of *Aplysia* control gut motility. Thus, it appears as if gastropod buccal ganglia contain neural circuits which control chewing, swallowing, egestion, and the transport of food through the esophagus to the stomach, as well as aspects of food acquisition.

The nudibranch *Melibe leonina* has a unique feeding behavior for a gastropod, which is related to the fact that it lacks both a radula and buccal mass (Agersborg, 1921; Gosliner, 1987). It uses movements of its large oral veil to capture food and bring it in contact with the mouth (Agersborg, 1921; Hurst, 1968; Ajeska and Nybakken, 1976; Watson and Trimarchi, this issue). In addition, *M. leonina* lacks structures for chewing food and therefore prey are engulfed whole and transported, without chewing, to the stomach. While the process of capturing food is rather complex, the gut movements controlled by the buccal ganglia are relatively simple.

Despite the fact that *Melibe* lack a buccal mass, they have retained a pair of small buccal ganglia. Their general anatomy and pattern of innervation suggest that they are involved in the control of gut motility. In the present study we tested this hypothesis by examining how removal of the buccal ganglia affected feeding and the movement of food through the alimentary canal. In addition, we mapped the buccal ganglia and demonstrated that stimulation of the buccal nerves cause contractions of the esophagus. These data suggest that the *Melibe* buccal ganglia are not necessary for the capture of prey, but rather are responsible for controlling the transfer of food from the mouth to the stomach.

METHODS

Animals

All animals were collected, using SCUBA, from eel grass beds located around the San Juan Archipelago (Washington), and shipped to the University of New Hampshire Coastal Marine Laboratory. Animals were maintained in seawater tables which were continuously perfused with filtered seawater from Portsmouth Harbor (6–12°C). Every 3–4 days the *Melibe* were fed a small amount of the material which was filtered from the flow-through seawater system. During the time of our feeding experiments this filtrate consisted primarily of barnacle nauplii.

Anatomy of the Buccal Ganglia

The nervous system of freshly dissected animals was observed with a dissecting scope, drawn and photographed.

Stimulation of the Buccal Ganglia Nerves

To determine the potential motor function of particular buccal nerves we stimulated them in partially dissected animals. *Melibe* were pinned in a perfusion chamber and an incision was made in the skin, extending from over the mouth to just above the junction of the esophagus and the stomach. The incision was held open with pins, so that suction electrodes could be placed on different nerves, and a thread connected to a Grass FT.03 force transducer could be attached to various locations along the musculature of the alimentary canal. A Grass S88 stimulator and isolation unit was used to supply pulses of various strengths, durations and frequencies to the suction electrode. The output of the force transducer was recorded on a Grass Model 79 polygraph.

Lesioning the Buccal Ganglia

Animals to be lesioned were placed on their side in a Sylgard-lined dish, and held in place with pins that secured the animals but did not penetrate their integument. A 0.5 cm incision was made in the integument of the neck region (Figure 1), and the exposed buccal ganglia were removed with a fine forceps. Care was taken to cause as little damage as possible to the surrounding musculature, connective tissue and non-buccal nerves. Once both buccal ganglia were removed the incision was sutured closed using fine silk thread glued to a minuten pin. The entire surgical procedure lasted approximately 15 minutes. Sham-operated animals were treated identically except the buccal ganglia were not removed. Control animals did not undergo surgey ($n=9$).

All animals were then placed in aquaria, where they fed on *Artemia* (concentration of 1500/L) for five days. *Artemia* are not a natural food source for *Melibe* in the Puget Sound, and they are digested very slowly; thus the quantity of *Artemia* present in the

digestive tracts of experimental animals can be used as an indicator of post-surgery feeding efficacy.

After feeding for 5 days the animals were weighed, and dissected for analysis of gut contents. The number of *Artemia* in each of the four gut regions (esophagus, stomach, gastric sac, intestine) were counted. Other observations recorded were the color of the stomach diverticuli, the size, color and viability of the salivary glands, locomotor activity, and posture of each animal. After the 5 day recovery and feeding period 11 of the lesioned animals and 9 of the sham-operated animals were either dead, or dying; leaving 10 healthy lesioned and 14 healthy sham-operated animals for data analysis. Data were tabulated and non-parametric statistical analysis, Mann-Whitney U, was conducted on the resulting data.

RESULTS

Anatomy of the Buccal Ganglia

Melibe buccal ganglia are located lateral to the esophagus, just posterior to the mouth (Figure 1, Figure 2). In comparison to the buccal ganglia of most gastropods they are quite small (200 μm in diameter), with fewer neurons (approximately 30–40/ganglion, Falk *et al.*, 1990). They are separated by an unusually long buccal-buccal connective, which positions them on opposite sides of the esophagus. There are 2 major nerves projecting from each buccal ganglion, in addition to the buccal-buccal connective. The posterior root runs along the surface of the esophagus, branching extensively and apparently innervating this tissue at various points along its length (Figure 1). At the base of the stomach diverticuli the posterior root connects to the gastric ganglion (Hurst, 1968).

The buccal anterior root bifurcates close to the ganglion (Figure 2). One branch becomes the cerebral-buccal connective and the other projects anteriorly. This anterior root innervates the salivary gland, anterior esophagus and the most posterior region of the mouth (Figure 1). Another very small root exists the buccal-buccal connective near its midpoint and innervates the esophagus immediately under the buccal ganglia.

Removal of Buccal Ganglia

Both lesioned and sham-operated animals followed a similar time course of recovery from surgery. Approximately twelve hours post-surgery the animals were behaving normally; carrying out activities such as swimming, mating and laying eggs. Of more interest, all animals appeared to feed normally (Figure 3), extending and contracting their oral veil in the stereotypical manner described in the the previous paper (Watson and Trimarchi, this issue).

After three to four days the surgical wounds were fully healed and the sutures had been sloughed off (Figure 4). Approximately 50% of the lesioned and sham-operated animals began to die at this time, and most of these subjects were dead after 5 days. The cause of death in these surgically treated animals was not clear, but

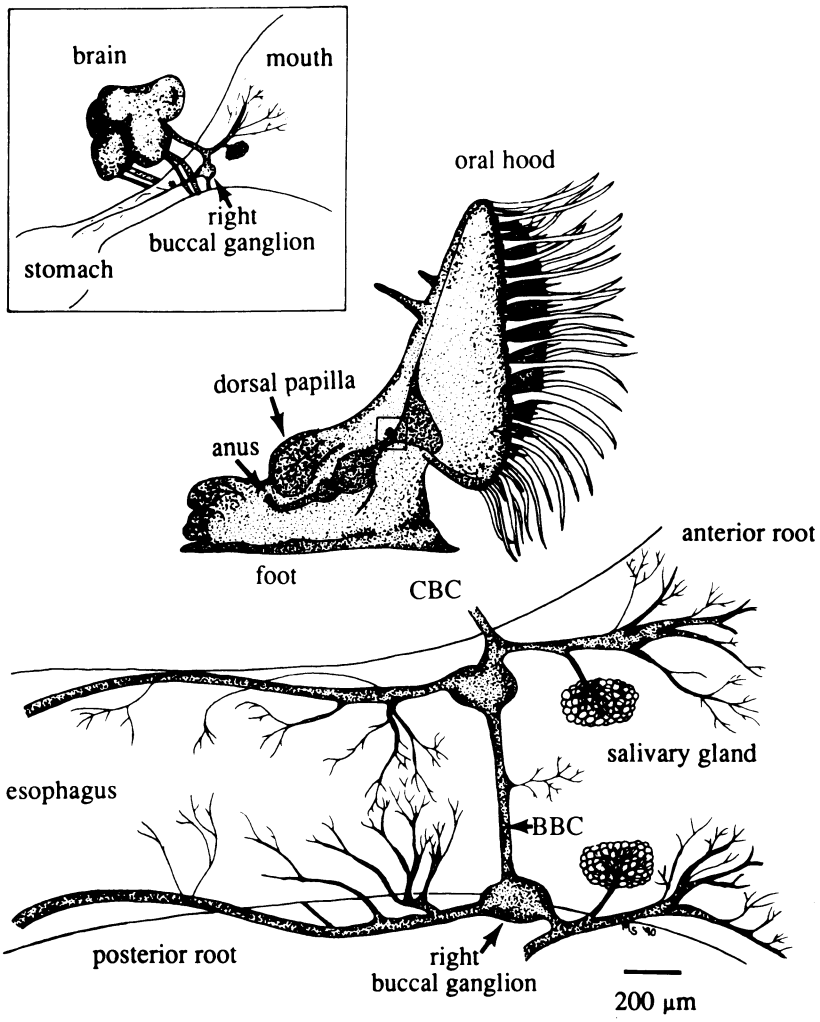

Figure 1 The anatomy of the *Melibe* buccal ganglion. An overview of the location of the internal digestive organs is illustrated in the center drawing. The boxed area is shown magnified in the upper left of the figure, to demonstrate the orientation of the brain, one buccal ganglion and one salivary gland. A magnified ventral view of the paired buccal ganglia is presented at the bottom of the figure. Note the extensive branching of the anterior and posterior buccal nerves, as well as the innervation of the salivary glands. Calibration bars are not presented for the top two figures because of the variability between animals of different sizes. The calibration bar in the bottom figure is typical for a large (5 inch long) *Melibe*.

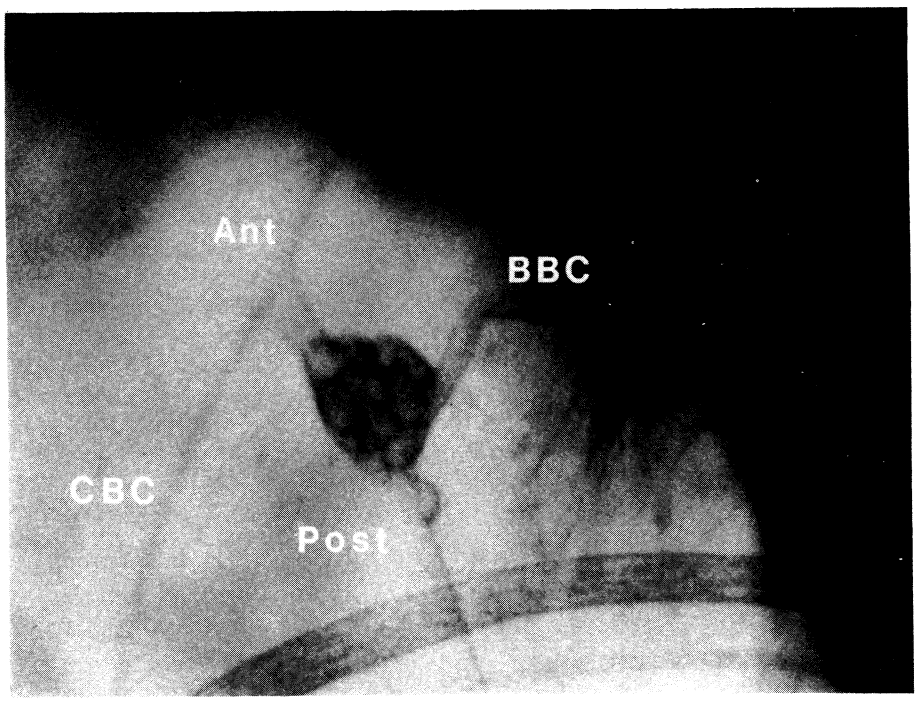

Figure 2 Photomicrograph of one buccal ganglion in a partially dissected *Melibe*. The ganglion is small compared to most gastropods, containing few cells (30–50). Most of the cell bodies are fairly large (>40 μm dia.) and readily penetrated with microelectrodes. There are three nerves emanating from this buccal ganglion. The buccal nerve extending to the upper left is the anterior root (Ant), which bifurcates, with one root innervating the anterior esophagus (which appears dark in this micrograph), and the other becoming the cerebral-buccal connective (CBC). Although the brain is out of the field of view, note the large commissure extending from the lower left to the lower right of the photomicrograph. The bent nerve which leaves the right side of the buccal ganglion is the buccal-buccal connective (BBC). The other buccal ganglia is out of the field of view, because the buccal-buccal connective is so long. The buccal nerve running toward the bottom of the photograph is the posterior root (Post), which innervates the esophagus.

because approximately equal numbers of sham-operated and lesioned animals died, removal of the buccal ganglia was probably not the immediate cause. Healthy, post-surgical animals displayed a normal behavioral repertoire.

After 5 days all animals were dissected and the number of *Artemia* in the entire digestive tract, from mouth to anus, were counted. Control animals captured slightly more total prey than sham-operated or lesioned animals (Table 1, Figure 5), suggesting that the efficacy of food capture was slightly altered by the surgical procedure. However, the difference was small, and statistically insignificant ($p=0.470$). More importantly, sham-operated and lesioned animals captured comparable numbers of prey (Table 1, Figure 5), demonstrating that both

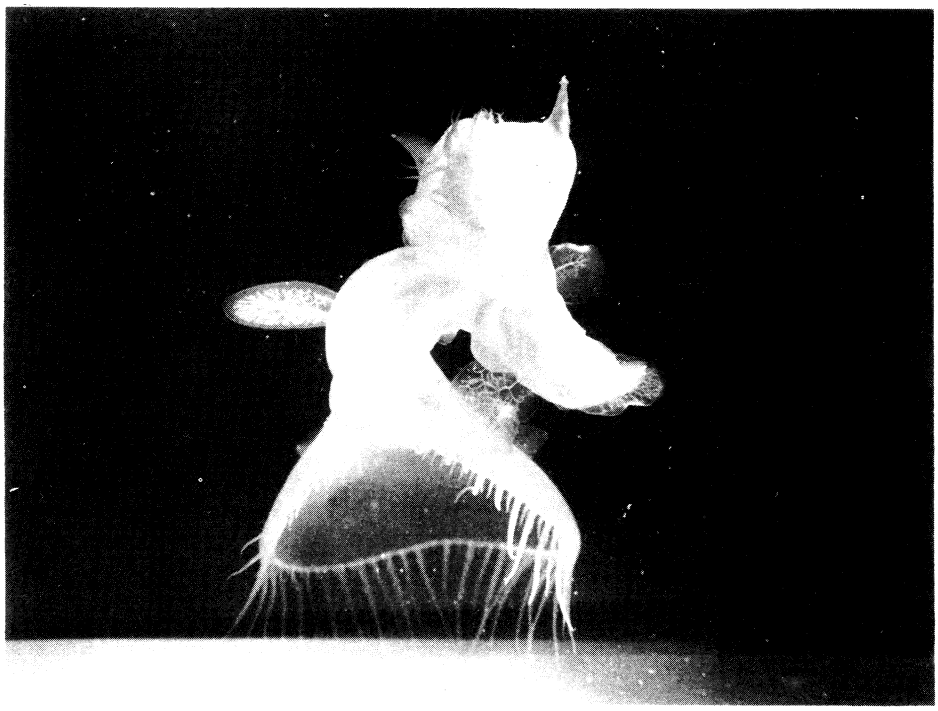

Figure 3 A lesioned and a normal *Melibe* feeding. Both animals, as well as those that were subjected to sham operations, exhibited normal, stereotyped food capture behaviors, indicating that removal of the buccal ganglia did not affect this aspect of feeding behavior. The animal on the bottom is a normal animal in the opened phase of a feeding cycle and the animal on the top is a lesioned animal in the closing phase of a feeding cycle.

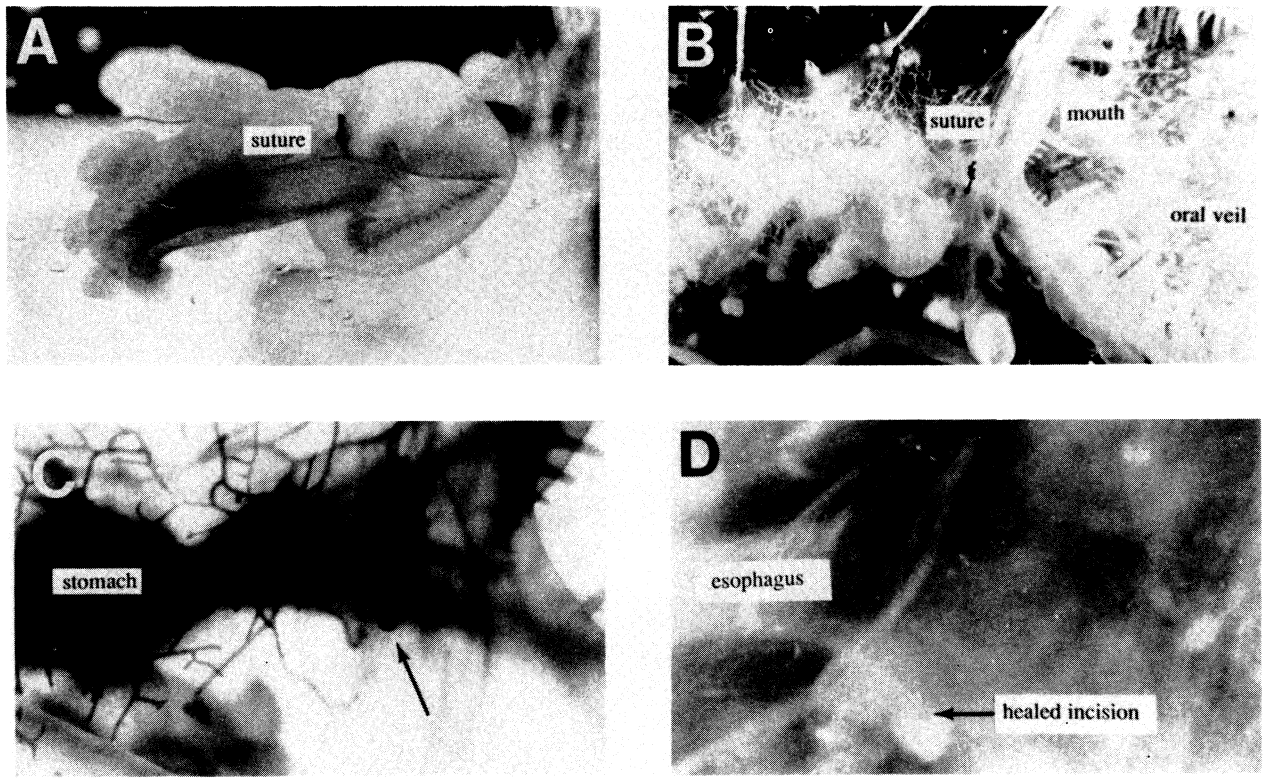

Figure 4 The progress of recovery from surgery. A. A lesioned *Melibe* swimming in an aquarium 5 minutes after surgery. B. A lesioned animal pinned in a dish to illustrate the location of the incision and the suture. The animal shown here was pinned through the integument to limit movement for photography, but during surgery animals were restrained without pinning them in this manner. C. A higher magnification view of a 1 day old suture, showing its location (arrow), just above the buccal ganglion. D. A fully healed incision, after the suture has been sloughed off, four days post-surgery.

Table 1 Quantity of *Artemia* present in different gut regions after a 5 day post-treatment feeding regime. Mean values ± S.E.M., with the percent of total food consumed in parenthesis. All the different gut regions are illustrated, and labeled in Figures 1 and 6, except for the gastric sac, which is a small area between the stomach and the beginning of the intestines. The esophagus column includes animals that were in either the esophagus or mouth.

Treatment	*Esophagus*	*Stomach*	*Gastric Sac*	*Intestine*	*Total*
Control	12.2± 12.2 (1.2)	807.9 ± 407.7 (82.6)	31.1 ± 11.8 (3.2)	126.3 ± 43.8 (12.9)	977.6 ± 404.4
Sham-Operated	56.7± 42.2 (8.1)	488.4 ± 183.7 (69.9)	60.9 ± 38.7 (8.7)	95.7 ± 69.3 (13.6)	701.6 ± 285.8
Lesioned	361.5 ± 175.8 (50.9)	282.2 ± 111.3 (39.7)	28.3 ± 11.4(4)	38.4 ± 11.5 (5.4)	710.4 ± 263.5

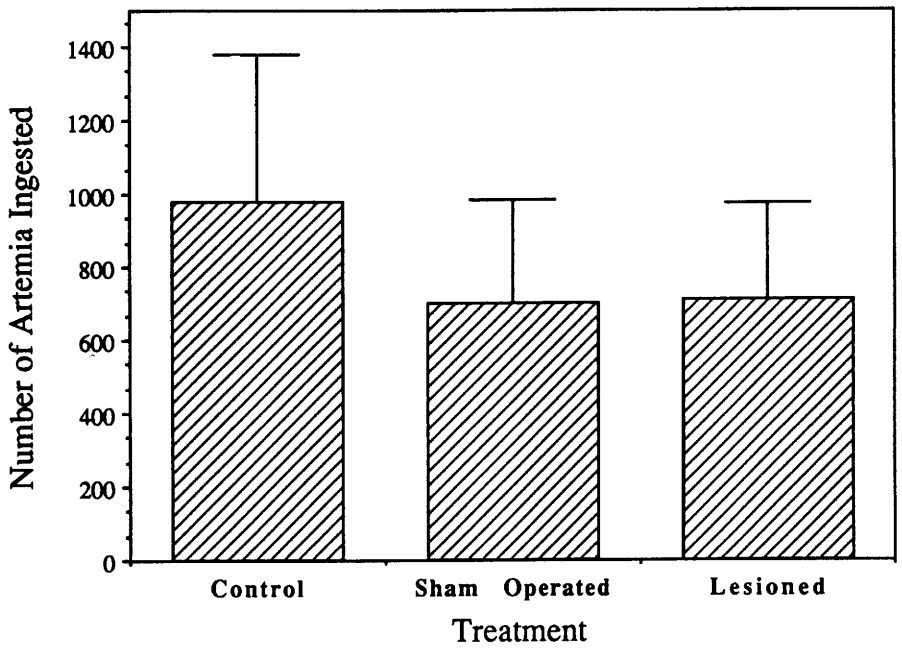

Figure 5 Effect of surgery on prey capture. Although the surgery itself had a slight effect on the ability to capture prey, there was no statistically significant difference in the amount of food captured by the three groups of animals during the 5 day post-operative period ($p=0.475$). Error bars indicate standard error of the mean (control, $n=9$; sham-operated, $n=14$; lesioned, $n=10$).

qualitatively and quantitatively the removal of the buccal ganglia had no effect on the capture of food ($p=0.475$).

Despite similarities between sham-operated and lesioned animals in the total amount of food captured there were major differences in the way food was distributed in their digestive tracts (Table 1, Figure 6). In sham-operated invididuals, as with control animals, most of the prey captured were in the stomach (69.6% and 82.6% respectively). In contrast, only 39.7% of the prey captured by lesioned animals were in the stomach, because a large percentage of the captured *Artemia* (50.9%) were still in the mouth and esophagus (Figure 6). These data indicate that removal of the buccal ganglia had a significant effect on the transfer of food from the mouth to the stomach.

Stimulation of Buccal Ganglion Roots

Stimulation of inputs to the buccal ganglion (CBC, cerebral-buccal-connective) in semi-intact preparations typically produced a series of 3–6 slow (1 every 10–20 sec),

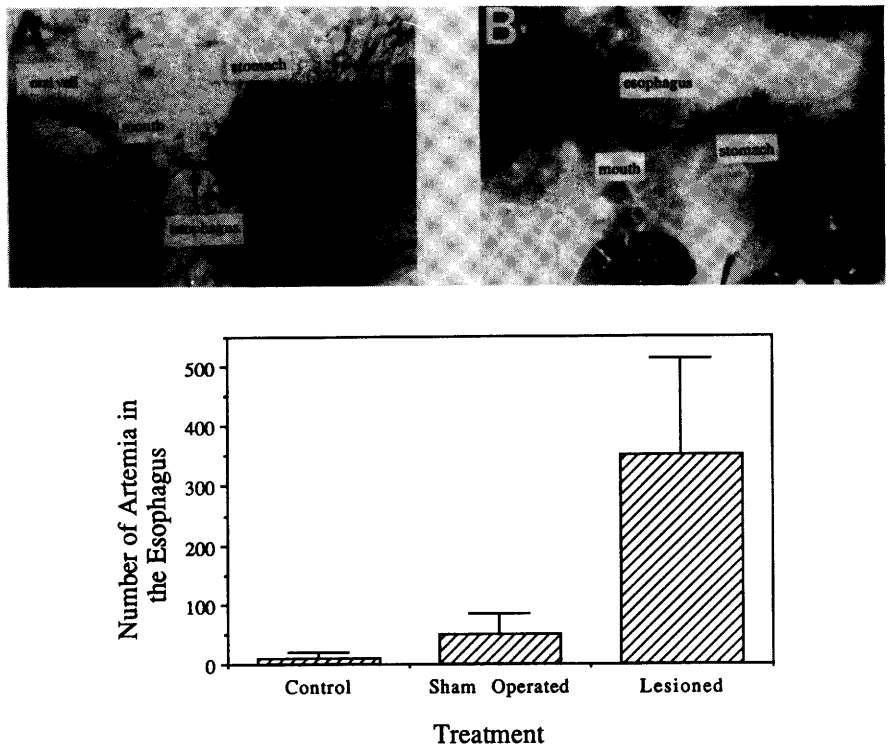

Figure 6 Influence of buccal ganglia removal on the transfer of food from the mouth to the stomach. Top: Normal animals dissected after 5 days of feeding had enlarged stomachs which were full of *Artemia* (A), while in lesioned animals most of the food was stuck in the anterior esophagus (B). Bottom: The mean number of *Artemia* observed in the esophagus of animals from each experimental group after a five day post-treatment feeding regime. While the quantity of prey in the anterior guts of control and sham-operated animals were similar ($p=0.479$), there were significantly more prey in the same regions of the alimentary tract in lesioned animals ($p=0.017$); up to 80% of the total food ingested. The error bars are standard error of the mean (control, $n=9$; sham-operated, $n=14$; lesioned, $n=10$).

rhythmic contractions of the esophagus (Figure 7A). Stimulation of the anterior nerve produced lateral contractions of the anterior esophagus and posterior mouth, while stimulation of the posterior nerve caused dilation and longitudinal contractions of the posterior esophagus (Figure 7B, C). These data suggest that there is a pattern generating network in the buccal ganglia which is activated by input from the brain, and motorneuron axons emanating from the buccal ganglia capable of producing peristaltic-like movements of the esophagus.

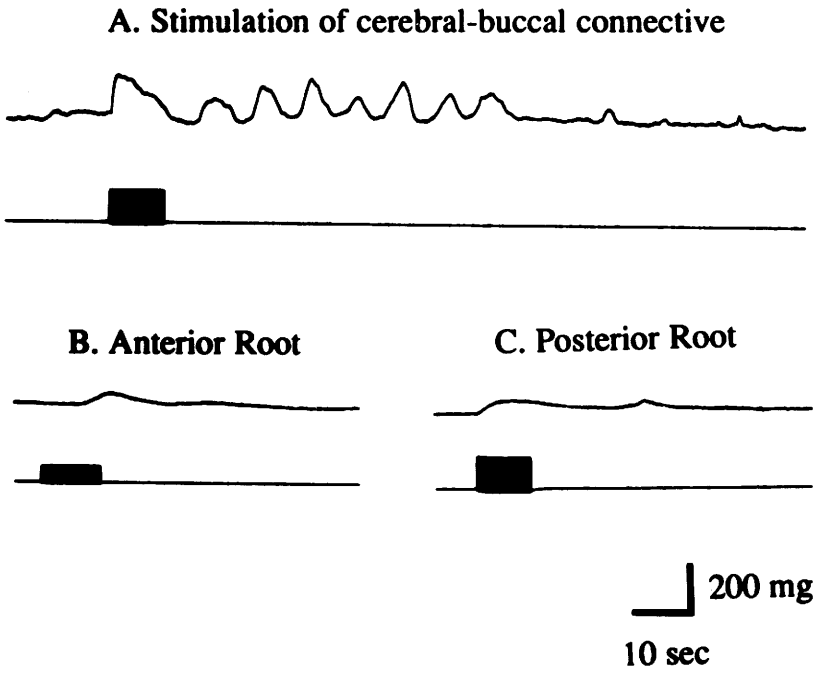

Figure 7 Stimulation of buccal roots. Top trace = tension, bottom trace = stimulation monitor. A Stimulation of the cerebral-buccal-connective (CBC, 5 volts, 10/sec, 5msec/pulse, 10 sec train) caused a series of rhythmic contractions of the gut, as recorded with a force transducer attached to the posterior region of the esophagus. Stimulation of the anterior root (B) or the posterior root (C) using similar stimulation parameters as in A (except anterior root stimulation was at 2 volts), resulted in individual, long-duration contractions of the anterior and posterior regions of the esophagus, respectively. Observations of the guts during stimulation indicated that the anterior esophagus contracted primarily in the lateral direction, while the posterior gut shortened longitudinally, leading to some dilation. The delay between stimulation and response illustrated in B. does not occur consistently with stimulation of the anterior root.

DISCUSSION

The innervation pattern of the *Melibe* buccal ganglia, the deficits in feeding behavior resulting from their removal, and the response of the esophagus to stimulation of the nerves emanating from the ganglia, suggest that they play a major role in transporting food from the mouth to the stomach. If this is true, then the *Melibe* buccal ganglia only serve a subset of the roles buccal ganglia in other gastopods perform. Results obtained from examination of feeding in other gastropods indicate that buccal ganglia typically innervate and control the organs whose movements are responsible for both the acquisition of food (i.e. buccal mass, pharynx, and radula) and the subsequent transfer of that food to the stomach, such as the esophagus (Benjamin, 1983; Audesirk and Audesirk, 1985). In contrast this study on *Melibe* illustrates that individuals from which the buccal ganglia were removed, maintained the ability to capture prey effectively, even though they had difficulty swallowing the prey they captured. Thus, we conclude that, unlike most gastropod buccal ganglia, the buccal ganglia of *Melibe* are not involved in the control of food aquisition organs (i.e. oral veil), but instead perform the more restricted role of food transfer.

One must be conservative when interpreting lesion experiments because removal of one tissue, a pair of ganglia in this case, may damage adjacent cells or neural pathways. For example, in our experiments removal of the buccal ganglia may have damaged axons from the brain which pass through, or by, the buccal ganglia on their way to the esophagus, and the behavioral deficits we observed may be due to damaging these axons, not removal of the buccal ganglia. While this remains a possibility that must be examined more rigorously there are several additional lines of evidence which also support our conclusions. First, we have performed cobalt chloride backfills of the anterior and posterior roots of the buccal ganglia and in neither case do we see stained cell bodies in the brain. This suggests that most, if not all, of the axons in these roots emanate from somata in the buccal ganglia. Second, recordings obtained from the CBC in semi-intact and isolated preparations have never revealed any rhythmic activity that would be capable of driving gut peristalsis. Third, application of the peptide SCP_B to a preparation consisting of only the buccal ganglia connected to the esophagus, results in rhythmic contractions of the esophagus, and if the SCP_B application is repeated after the removal of the buccal ganglia, esophageal peristalsis does not occur (Nina Kaplan, personal communication). Finally, recordings from isolated buccal ganglia reveal that they are capable of generating rhythmic activity and that stimulation of the CBC leads to a series of bursts which have a time course comparable to the rhythmic esophageal contractions we recorded in semi-intact animals following stimulation of the CBC (Watson, in preparation). Therefore, we conclude that esophageal contractions are primarily, if not exclusively, controlled by the buccal ganglia, and other modulatory influences from sources such as the brain, act indirectly by influencing the buccal ganglia.

The aforementioned results also suggest that the buccal ganglia of *Melibe* contain a central pattern generating network which drives peristalsis of the esophagus upon receiving input from the brain. In fact, because *Melibe* lacks both a buccal mass and a radula, control fo the esophagus appears to be the primary function of this small

network of neurons. This same function may be incorporated into a subset of neurons in the larger ganglia of other gastropods. For example, Lloyd *et al.* (1988) and Lloyd and Willows (1988) have demonstrated that SCP_B-containing neurons in the buccal ganglia of the gastropods *Aplysia* and *Tritonia* control rhythmic peristalsis of the esophagus during feeding. The buccal ganglia of *Melibe* also contain a pair of SCP_B-immunoreactive neurons which innervate the esophagus, are active during feeding and may be homologous to the cells in *Aplysia* and *Tritonia* (Watson and Willows, 1986; Willows and Watson; 1986). Thus, during the course of evolution *Melibe* may have lost many of the neurons responsible for controlling the buccal mass, radula and lips but retained a group of neurons to regulate gut motility.

While it appears as if the slow rhythmic movements of the oral veil responsible for the capture of food are controlled by a central pattern generator in the brain, and swallowing movements are generated and regulated by the buccal ganglia, the precise temporal relationship between these two activities has yet to be determined. Thus far, we have been unable to visualize esophageal movements during feeding. Our stimulation experiments, both with semi-intact animals, and isolated buccal ganglia suggest that input from the brain is capable of triggering a series of rhythmic esophageal contractions and so we hypothesize that during normal feeding every contraction of the oral veil is accompanied by several contractions of the esophagus. This idea is consistent with the data obtained by Lloyd *et al.* (1988) with chronic electrodes implanted on the esophageal nerve of *Aplysia*. They found that each swallowing movement is accompanied by a series of bursts in the esophageal nerve. Further studies involving more sophisticated methods for both visualizing gut movements and recording from buccal ganglia roots during feeding are necessary to reveal how the two rhythmic components of feeding in *Melibe* are coordinated.

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