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ORIGIN OF AUTOMATICITY AND NEURAL REGULATION OF PERISTALSIS IN THE GASTROINTESTINAL TRACT OF *APLYSIA* AND *LYMNAEA**

SHORT COMMUNICATION

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We examined whether the enteric nervous system (ENS) is capable of controlling autonomous peristalsis, which occurs in the crop of *Aplysia* as well as in the esophagus of *Lymnaea.* Interestingly, "pacemaker neurons", which lead peristaltic rhythm, were found in the gizzard in *Aplysia* and in the crop in *Lymnaea*; both of these structures are located distal to the regions exhibiting peristalsis. Thus, the bursting activity of the ENS first occurred in lower regions and then progressed in an ascending direction (i.e. in the opposite direction of peristalsis). The two species are thought to differ in terms of the mechanisms involved in producing peristalsis.

Keywords: Enteric nervous system – gastrointestinal tract – peristalsis – *Aplysia* – *Lymnaea*

The enteric nervous system (ENS) consists of a network of neurons that are intrinsic to the gastrointestinal tract in a wide variety of animals. We have shown that both neurogenic and myogenic automaticity are involved in the gastrointestinal motility of *Aplysia kurodai* and *A. juliana* [4, 5] and also *Lymnaea stagunalis* [5, 6]. In these studies, the peripheral neurons in the posterior gizzard in *Aplysia* and in the crop in *Lymnaea* demonstrated autonomous rhythmic bursting activity that was followed by excitatory junction potentials and subsequent contractions of the GI tract. In *Lymnaea*, peristaltic movements are observed in the esophagus. Downward peristalsis is driven by the rhythmic bursting activity of peripheral neurons; this activity propagates in an upward direction from the crop toward the esophagus [6]. We examined whether ENS neurons are capable of controlling the ordered autonomous peristalsis observed in the crop of *Aplysia*, and then compared the mechanisms of peristalsis generation between *Aplysia* and *Lymnaea*.

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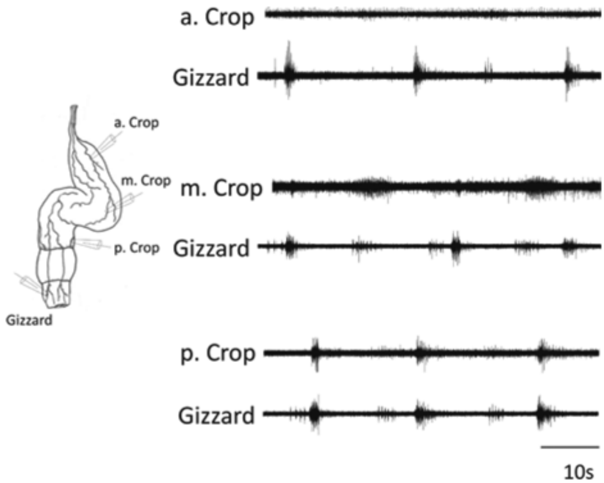

Fig. 1. Simultaneous extracellular recordings using suction electrodes from the plexus on the anterior (a. Crop), median (m. Crop), or posterior (p. Crop) portions of the crop (upper traces) and the posterior gizzard (lower traces). Synchronous rhythmic bursting activity of the peripheral neurons was observed between the posterior gizzard and the crop, with the exception of the a. Crop. To the left is a schematic drawing of the upper part of the gastrointestinal tract demonstrating the recording sites on the esophagus, crop, and anterior and posterior gizzard

The GI tract, containing the esophagus, crop, and gizzard, was isolated from the central nervous system and the rest of the animal in *Aplysia* (Fig. 1, insert). Synchronous bursting activities were obtained in simultaneous recordings from the neurons in the median or posterior crop and the posterior gizzard (Fig. 1). A previous experiment indicated that the pacemaker area that drives the rhythmic activities is located in the gizzard [4]. The bursting activity propagates upward to the median portion of crop with a short (<10 ms) latency as observed in *Lymnaea* from the crop to the esophagus. The bursting activity in the posterior gizzard is known to evoke rhythmic contraction for triturating foods with teeth lining the inner surface of the gizzard [4]. It has been demonstrated that digestive fluid containing small pieces of food regurgitates from the gizzard to the crop during contractions. Ingested foods transported through the buccal mass and esophagus by the centrally generated rhythmic movements [2] meet with digestive juices inside the crop. The crop functions as a reservoir in which food is mixed with digestive juices; the liquefied products of digestion are then propelled into the gizzard. Howells [3] reported that the posterior portion of the crop underwent peristaltic contractions timed apparently independently of those of the anterior region, which are thought to be controlled by the central neuronal networks. We found that the contractions of the gizzard were followed by peristalsis from the median to the posterior crop (Fig. 2). The peristalsis started at the median crop just after the start of contraction of the anterior gizzard, suggesting that the neuronal bursting activity in the median crop, in synchrony with that in the posterior gizzard, may be responsible for initiation of peristalsis.

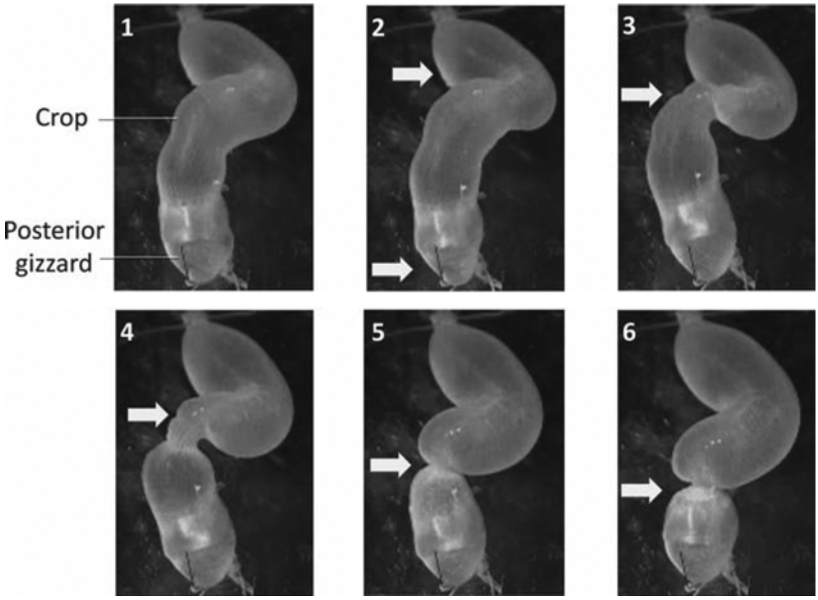

Fig. 2. Contractions of the posterior gizzard followed by descending peristalsis in the crop. Just after the contraction of the anterior gizzard was evoked (lower arrow in 2), peristaltic movement started at the median crop (upper arrow in 2) and descended slowly along the posterior crop toward the gizzard over a course of several seconds (arrows in 3–6). Consecutive photographs were taken with one second intervals

The "pacemaker region", where the rhythm of peristaltic movement originates, was found in the gizzard in *Aplysia* and in the crop in *Lymnaea*, both of which are located distal to regions that undergo peristalsis. Thus, the bursting activity of the ENS first occurred in the gizzard of *Aplysia* or in the crop of *Lymnaea* and then propagated in an ascending direction along the crop or esophagus, respectively. This fact gives rise to the following question: How dose constriction travel in a descending direction, i.e. in the opposite direction of peristalsis? In *Lymnaea*, observations of the relationship between neuronal activity and esophageal motility have suggested that proximally decreasing time lag between the neuronal burst and the peak contraction (Time to peak: T-p) is crucial in producing peristalsis [6]. In the esophagus of *Lymnaea,* numerous motor neurons are scattered throughout the ENS. While neuronal activity propagates up the esophagus, activated neurons exert their motor effects on the esophagus one by one in an ascending direction. However, the resultant peristalsis moves in a descending direction according to regional differences in T-p (Fig. 3, right). In the crop of *Aplysia*, however, peripheral neurons are sparsely located and no peripheral motor neurons have been identified. As shown in Figure 2, it took more than several seconds for the peristaltic wave to travel downward along the crop toward the gizzard. The conduction velocity of this wave was much slower in the crop of *Aplysia* than in the esophagus of *Lymnaea* [6]. Therefore, constriction at the lower crop was observed several seconds after the bursting activity was evoked. Based on

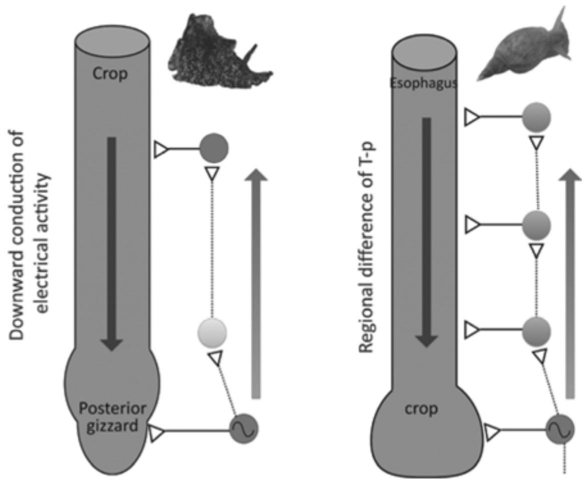

Fig. 3. Summary diagrams. Different mechanisms underlying peristalsis of the gastrointestinal tract are proposed to occur in *Aplysia* (left) and *Lymnaea* (right). In both cases, rhythmic neuronal activity originates in the lower portion (the so-called pacemaker region) and propagates in an ascending direction, the opposite of the peristaltic wave. See text for details

these facts, it cannot be assumed that the mechanism underlying the generation of peristalsis in *Lymnaea* is the same as that found in the crop of *Aplysia*. Another possible mechanism is proposed here, as illustrated on the left in Figure 3. Neural activity may only function to initiate peristalsis at the median crop and may not be necessary for peristaltic conduction. Some types of electrical activity, such as slow waves, which are generally recorded in correspondence with peristalsis in the gastrointestinal tracts of mammals [1], might propagate along the crop, although we have not succeeded in recording these yet.

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