Review Article

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Feeding Behaviours in Gastropod Molluscs

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Abstract

Molluscs are second largest phylum of the animal kingdom which transmits disease directly or they may serve as intermediate host/ vectors for parasites of human and animals. Gastropods have evolved specialized behavioral patterns to detect, acquire and ingest food. The most striking feature of gastropod feeding is its flexibility. In most gastropods, feeding consists of a variable sequence of food-finding movements, followed by a series of rhythmic movements in which food is consumed. Most snail species are herbivores, feeding plant material whereas other species are scavengers, feeding on dead plant or decomposing animals, while others are predators. Food-finding movements are often effected by muscles of the head and foot that also produce movements unrelated to feeding. A well-developed olfactory system plays an important role in snails for locating food, homing or pheromone communication and in predator risk assessment.

Keywords: Chemo-receptors; Feeding; Gastropods; MAPK; Octopamine

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Introduction

Molluscs contribute the second largest invertebrate groups on earth next only to insects and they have adapted to terrestrial, marine and freshwater habitats all over the globe, although most molluscs are marine [1]. Snails may directly transmit disease, or they may serve as intermediate host/ vectors for parasites of human and animals [2]. Layton et al. [3] described in his review that few species of gastropods are external or internal parasites of other invertebrates including mites and a wide variety of nematodes. The slug mite, *Riccardoella limacum*, is known to parasitize several dozen species of mollusks, including slugs, such as *Agriolimax agrestis, Arianta arbustrum, Arion ater, Arion hortensis, Limax maximus, Milaxbudapestensis, Milax gagates* and *Milax sowerbyi* [4]. Gastropods have evolved specialized behavioral patterns to detect, acquire and ingest food [2]. Bouchard [5] reported that food-related behavior includes all actions exhibited by an animal in response to hunger or to searching and perception of food and an interesting observation is that most of the snail species tend to keep company when feeding, as they do in other situations. Murphy [6] reported that feeding behaviours in a number of gastropod mollusks are the most striking feature of gastropod feeding is its flexibility. Wentzell et al. [7] reported that in most gastropods, feeding consists of a variable sequence of food-finding movements, followed by a series of rhythmic movements in which food is consumed. Thus, examining gastropod feeding addresses a problem of general interest to all neurobiologists, understanding how the nervous system generates a flexible series of movements. However, the neurones and the neural circuitry that organize and modulate gastropod feeding are amenable to the detailed cellular analysis that has provided seminal insights into the modulation of withdrawal reflexes in gastropods by serotonin and small peptides [8]. Ju and Bassett [9] reported in his article neural systems generating feeding have begun to provide rich insights into how complex regulatory phenomena arise from the properties of individual neurones and their interconnections. Investigations in some genera, notably *Aplysia*, have taken a top-down approach, beginning by characterizing behavior and then proceeding to the nervous system. Feeding has been studied in both carnivorous and herbivorous gastropods [8]. Olivera et al. [10] reported that many carnivorous gastropods are limited to whatever prey can be chased down at a snail's surroundings, but the Conidae have developed a series of venomous needles, and after injecting the prey with toxins it becomes immobilized and can easily be consumed. Valarmathi [11] reported a number of investigations and observations that snail species have an ability to choose and to recognize their preferred food stuffs subsequently. The objective of this study was to clarify the roles of the various structures involved in food- feeding behavior of the Gastropod mollusk.

Food of the Snails

The diet of gastropods differs according to the group considered [12]. Kiss [13] reported that most snail species are herbivores, feeding plant material and terrestrial species consume leaves, bark, seedlings and fruit, while marine species can scrape algae off the rocks on the sea floor. Other species are scavengers, feeding on dead plant or decomposing animals, while others are predators [13].

Feeding Habits

In gastropods the feeding habits are as varied as their shapes and habitats, but all include the use of some adaptation of the radula [14]. Steneck and Watling [15] reported that many gastropods are herbivorous, rasping off particles of algae from a substrate. They also reported that some herbivores are grazers, some are browsers, and some are planktonic feeders. Some snails are scavengers, living on dead and decayed flesh and some others are carnivorous, tearing prey apart with their radular teeth [16]. It is also reported that most pulmonates (air breathing snails) are herbivorous, but some live on earthworms and other snails. Some sessile gastropods, such as slipper shells, are ciliary feeders that use the gill cilia to draw in particulate matter, which they roll into a mucous ball and carry to their mouth and in ciliary feeders the stomachs are sorting regions and most digestion is intracellular in the digestive gland [17]. Beninger [18] reported that most bivalves are suspension feeders. They have Gland cells on the gills and labial palps secrete copious amounts of mucus, which entangles particles suspended in the water going through gill pores [18]. Ciliary tracts move the particle-laden mucus to the mouth. In the stomach the mucus and food particles are kept whirling by a rotating gelatinous rod, called a crystalline style. Solution of layers of the rotating style frees digestive enzymes for extracellular digestion. Ciliated ridges of the stomach sort food particles and direct suitable particles to the digestive gland for intracellular digestion. Mooi et al. [19] reported that some, such as oyster borers and moon snails, have an extensible proboscis for drilling holes in the shells of bivalves whose soft parts they find delectable and some even have a spine for opening shells. Shipworms feed on the particles they excavate as they burrow in wood [20]. They also reported that the symbiotic bacteria live in a special organ in these bivalves and produce cellulase to digest wood. Jantzen et al. [21] reported that other bivalves such as giant clams gain much of their nutrition from the photosynthetic products of symbiotic algae living in their mantle tissue. Villanueva et al. [22] reported that cephalopods are predaceous, feeding chiefly on small fishes, molluscs, crustaceans, and worms. Their arms, which are used in food capture and handling, have a complex musculature and are capable of delicately controlled movements and they are highly mobile and swiftly seize prey and bring it to the mouth. Strong, beaklike jaws grasp prey, and the radula tears off pieces of flesh [22]. Ponte and Modica [23] reported that octopods and cuttlefishes have salivary glands that secrete a poison for immobilizing prey. Digestion is extracellular and occurs in the stomach and cecum. In addition to internal factors, such as hunger, internal clock and stage of maturity, external ones may contribute to the feeding behavior, as well [23]. External factors that influence foraging behavior include abundance and distribution of food material, presence of competitors, risk of predators, season and time of day. Food preference determines the food ingested by an animal which in turn improves its physiological condition and fitness [24]. Tobie et al. [25] reported in his review that the concept of food preference comprises two features of the food, attractiveness and palatability. Therefore, the diet choice of an animal may be constrained by nutrient requirements or digestive limitations. Mand et al. [26] reported that snails need to consume a considerable amount of calcium to develop and preserve their shells as hard as possible. Lah et al. [27] reported that the low acceptability of natural food could possibly relate to volatile and nonvolatile chemical compounds present indifferent plant species or to a low nutritional contents. They also noted that food preference of gastropods does not correlate linearly with energy content of the available food, but instead it correlates with the efficiency of digestion. Hagele and Rahier [28] reported that many terrestrial gastropods have narrow and distinct dietary preferences and regularly occur in close association with their food species, while others tend to feed on a variety of items found in their natural habitat and it is also observed that herbivorous gastropods may also consume decomposing materials including those of animal origin. Tiwari and Singh [29,30] reported the behavioural responses of snail *L. acuminata* against different amino acids and carbohydrates and found that the greater attraction of the snail *L. acuminata* to starch and maltose in the bait is possibly due to fact that in nature starch is the major carbohydrate stored in aquatic plants and maltose is released by some epiphytic algae which form a part of the snail modular system where snail are found. Kumar et al. [31] studied that the behavioral responses of snails to binary combinations of carbohydrate and amino acid in bait formulation. Among all the binary combination of carbohydrate+amino acid+molluscicide after 2h of experiment, highest attraction of snail (54.71%) was observed towards the Snail Attractant Pellets (SAP) containing starch+histidine+limolene. Srivastava et al. [32] reported that feeding of baits containing sub-lethal concentration of (80% of 24h LC_{50}) eugenol caused a significant reduction in fecundity, hatchability and survival of young snails. Srivastava et al. [33] reported that feeding of bait containing 40% of 24hLC_{50} of piperine with attractant starch caused maximum (1124 eggs/20 snails) and minimum (327 eggs/20 snails) fecundity in the month of June and November, respectively. Whereas feeding of bait containing 40% of 24hLC_{50} of piperine with attractant serine caused maximum (1028 eggs/20 snails) and minimum (352 eggs/20 snails) fecundity in the month of June and November, respectively. Srivastava and Singh [34] reported that the effect of sub-lethal feeding of bait formulations containing molluscicidal component of *Syzygium aromaticum* (eugenol) with attractant (starch/serine) on biochemical changes in the ovotestis/nervous tissue of snail *Lymnaea acuminata* in each month of the year Nov-2011-Oct-2012. Bait containing eugenol caused significant reduction in the level of free amino acid, protein, DNA, RNA and AChE activity in the snail *Lymnaea acuminata*. Srivastava and Singh [35] reported that feeding of SAP containing papain on certain biochemical parameters in the gonadal/ nervous tissue of the vector snail *Lymnaea acuminata* and noted that feeding of snail attractant pellets containing papain (40% of 24hLC_{50}) caused significant reduction in the level of protein, amino acids, DNA, RNA and AChE activity in the *Lymnaea acuminata*.. Tripathi et al. [36] noted trapping of snails with the help of light stimulant of different wavelengths acts as an attractant. Presence of different types of photoreceptors in the eyes of *Lymnaea acuminata* plays the vital role in attraction. Under natural condition, the spectral composition of light in the water is different because sunlight is compressed in the long wavelength part of the spectrum due to water's high absorption of red light.

Structure of the Feeding System

Elliott and Susswein [8] reported in his review that the food-finding movements are often effected by muscles of the head and foot that also produce movements unrelated to feeding and after food has been localised, in herbivorous gastropods it is ingested by repeated movements of the radula, a sheet of semi-hardened tissue covered with rows of chitinous teeth. They also reported that many carnivorous molluscs capture prey *via* specialised organs that may be adaptations of structures present in herbivores e.g. the pharynx in *Pleurobranchaea* or that may be unrelated to such structures (e.g. buccal cones in *Clione*). Gill [37] reported in his dissertation that in most gastropods, food is eventually engaged by the radula, which is controlled by the buccal muscles and these muscles cause the radula to protract out of the mouth towards the food and then to pull the food into the buccal cavity, or to rasp the food, with a retraction movement. Wentzell et al. [38] reported that in some gastropods like *Aplysia* and *Pleurobranchaea*, a fold in the centre of the radula acts as a hinge that allows the two radula halves to open and close and their buccal mass is innervated by the paired buccal ganglia, which connect to the cerebral ganglia by the paired cerebrobuccal connectives. They also reported that the cerebral ganglia innervate the anterior portion of the animal, including many structures related to feeding, such as the rostral foot, the head, the sensory anterior and posterior tentacles (rhinophores), the lips and the mouth. Hartenstein [39] reported that the cerebral ganglia also innervate extrinsic buccal muscles, which cause forward and backward movements of the whole buccal mass. These ganglia also communicate with the rest of the central nervous system.

Role of Octopamine in Feeding

Vehovszky et al. [40] reported that the distribution of octopamine immuno reactive neurons was described in the central nervous system of *Lymnaea* spp. where they occurred in the buccal, cerebral and pedal ganglia. Brown et al. [41] reported that the highest concentration of Octopamine (OA) was measured in the paired buccal ganglia in *Aplysia, Helix* and *Lymnaea* and these ganglia contain the main elements of the feeding network: one of the most studied neuronal systems in gastropods. Benjamin [42] reported that in *Lymnaea stagnalis* the feeding network in the buccal ganglia is composed of motoneurons (B1, B2, B3, . . . B10 cells) central pattern generator inter neurons (N1, N2, N3 interneurons) and higher order inter neurons (SO, N1L). They reported that these nerve cells act together with the cerebral interneurons to produce a rhythmic pattern (active feeding) which corresponds to the alternating cycles of the radula movements and the motoneurons play no part in the production of the rhythm, which is generated by the central pattern generator interneurons [42]. Crabe et al. [43] described in his review that the protractor premotor cells (N1) are cholinergic, whereas the retractor N2 inter- neurons probably use glutamate and these cells are activated during feeding by the modulatory interneurons SO, N1L and CGC, of which the first two are cholinergic and the latter serotonergic. They also reported that these modulatory cells are stimulated by inputs from chemo-and mechano sensory cells, which probably use Nitric Oxide (NO) as a transmitter. Straub and Benjamin [44] reported that in feeding, serotonin (5HT) is thought to be the predominant modulator substance, released mainly by the giant neurons (CGCs) located in the paired cerebral ganglia. Dopamine (DA) is considered to be another possible feeding modulator in gastropods as it initiates the feeding pattern in isolated CNS [44]. Miller et al. [45] reported that in *Aplysia*, a DA-containing buccal neuron is identified, which is capable of initiating the feeding activity of the buccal network. In addition, the role of modulatory peptides cannot be ruled out in feeding. Santama et al. [46] reported that In the buccal ganglia of *Lymnaea stagnalis* myomodulin, buccalin, Small Cardioactive Peptide (SCP), and FMR Famide-related peptides were shown to co-localize with`classical' transmitters in the cell body of both feeding motoneurons (B2, B3, B7 cells) and inter neurons (N1, N2, SO, CGC). Although OA-immunoreactive neurons have been visualized and the existence of OA receptors has also been proved both in *Lymnaea* and Helix CNS [46].

Role of Chemo Receptors in Locating Food

The major chemosensory organs of gastropods include the anterior and posterior tentacles and lips of terrestrial pulmonates [47]. Batts [48] reported that terrestrial pulmonates are characterized by two pairs of tentacles on the head region. Pola et al. [49] reported that the anterior tentacles are small and situated near the lateral margins of the mouth and the posterior (optic) tentacles are much larger and are situated more dorsally and posteriorly on the head. Srivastava et al. [50] updated in his chapter that snails of the Basommatophora have one pair of tentacles and a single osphradium and the osphradium, consisting of only a ciliated channel or pit located near the mantle collar, is not as well developed as in prosobranchs. They also described that at the blind end of the channel is a specialized sensory epithelium receiving innervation from a small associated peripheral ganglion. Lindberg and Ponder [51] reported that a number of different organs have been implicated as chemoreceptors in the prosobranchs. They showed that applications of food extracts to the cephalic and metapodial tentacles, the anterior margin of the foot and the siphon tip all elicited behavioural responses and the mantle tentacles have received special attention as chemoreceptors since they appear to be the primary sensory organs mediating avoidance behaviour of the limpet *Acmaea (Notoacmea)* to sea stars. The tips of the mantle tentacles bear densely packed ciliated sensory cells [52]. Srivastava et al. [50] also described in his chapter that another organ in *Tegulu* for sensing sea star odours. The osphradia in prosobranchs appear to be involved in chemoreception. While Archaeogastropoda generally have paired osphradia the Mesogastropoda and the Neogastropoda generally only have a single osphradium. These structures are often more developed in prosobranchs than in the pulmonates. The well developed osphradia in *Buccinum* or *Busycon* look superficially like miniature ctenidia with their bipectinate structures and all osphradia receive intensive innervation, thus suggesting a sensory role [53]. Croll [53] also reported that chemosensory organs of the opisthobranchs are the rhinophores. Gobbeler and Kolb [54] reported that like the posterior tentacles of the pulmonates, the rhinophores are situated dorsally on the head region and contain an extensively innervated specialized epithelium. Kiss [13] reported that a well-developed olfactory system plays an important role in snails for locating food, homing or pheromone communication and in predator risk assessment. For example, it is observed that odor strongly influences locomotor behavior of *Helix pomatia* because the snail steadily crawls toward attractive odorants. Terrestrial gastropods use their olfactory organ in searching for food and selecting a place to live [1]. Some terrestrial gastropods can track the odor of food persistently comparing stimulus intensity by paired sensory receptors on both sides of the body using their tentacles (tropotaxis) or track airborne chemical plumes (anemo-taxis) delivered by wind [13]. Nikitin et al. [55] reported in his research article that in terrestrial snails the concentration of odor reaching the olfactory organs is important for displaying adequate experience-dependent feeding behavior. Although chemoreception is the most important sensory modality informing gastropods to the presence of food in the environment [56]. Groendahl et al. [57] reported that gastropod feeding responses are subjected to modification by experience, including hunger, habituation, sensitization, satiation, quality of food, intensity of the feeding chemostimulus, and associative learning. It has been investigated that the snails use chemical senses as the principle modality for locating food sources as like other gastropods mollusks [57]. Ribeiro et al. [58] shows that the Mitogen-Activated Protein Kinase (MAPK) can be detected in the *Lymnaea* Central Nervous System (CNS), and that MAPK activation by phosphorylation is necessary for food-reward classical conditioning. They also reported that Phosphorylated MAPK was detected in the nuclei of neurons in the feeding circuitry located in the buccal ganglia and in neurons and neuropile located in other parts of the CNS, including the lip nerves. These lip nerves contain the axons of primary chemosensory [58].

Conclusion

Gastropods especially terrestrial snails and slugs, aquatic snails are major pests of agricultural/horticultural plants and carrier of most devastating diseases in cattle/human population. Control of these pestiferous gastropods is one of most neglected field in pest control measures. Initial control of these snails was performed by biological/mechanical methods. Simultaneously, chemical control was also very effective in control of pestiferous gastropods because gastropods use chemoreception for feeding and locate distant food sources, and to discriminate between potential foods. Amino acids appear as likely candidates for attractants and phagostimulants for gastropod feeding. Gastropod feeding responses are subjected to modification by experience, including hunger, habituation, sensitization, satiation, quality of food, intensity of the feeding chemostimulus, and associative learning. It has been investigated that the snails use chemical senses as the principle modality for locating food sources as like other gastropods mollusks.

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