Neuroscience and Behavioral Physiology, Vol. 24, No. 1, January-February, 1994

1. NERVOUS SYSTEMS OF THE SNAIL

Nervous System and Neural Maps in Gastropod *Helix lucorum* L.[1]

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UDC 612.822

Translated from Zhurnal Vysshei Nervnoi Deyatel'nosti imeni I. P. Pavlova, Vol. 42, No. 6, pp. 1075-1089, November-December, 1992.

Received March 30, 1992; revision submitted May 20, 1992.

The present review summarizes the literature and provides new data concerning nervous system structure and the identification of individual neurons in the snail Helix lucorum. Information about especially well-known neurons is provided in a table, and maps of the identifiable neuron's location in ganglia are correlated with the results of retrograde staining via various cerebral and subesophageal nerves. References concerning the morphology of snail central nervous system and identifiable neurons are given.

INTRODUCTION

The structure of the nervous system of snails was described in several classic articles at the beginning of this century [19, 38, 39, 49]. These papers describe the structure of the ganglia, give the nerves names, and show their targets. Snails have been intensively used in neurophysiological studies aimed at describing principles of the functioning of neural networks, determining the involvement of identified neurons, providing a detailed description of nervous system structure, and mapping identifiable neurons. The goal of the present paper is to provide a concise, comprehensive review which can be understood by a newcomer to the field.

The various species of *Helicoidea* used in experimental investigations are all similar in many respects. Given the similarities in behavior and organization of locomotion, the utilization of a particular snail depends mostly on its availability. *Helix pomatia* is most commonly used, a common edible garden snail found throughout central Europe and in the East up to the Moscow region. *H. lucorum taurica* is found in the Crimea, whereas another subspecies, *H. lucorum martensia,* is found in the Caucasus. In southern and western Europe, *Helix aspersa* (synonym *Cryptomphallus aspersa)* is typical. Although these snails are smaller in size, they are fully developed within 6 months and are easier for laboratory rearing. Recently, a new species of large snails was introduced into experimental practice from Northern Africa: *H. aspersa maximus,* which is also more suitable for maintaining in the laboratory. In the physiological (but not zoological) literature, all these snails are referred to as "terrestrial" snails (in Russian, grape snails). Cell maps in these species are very similar, and it seems useful to describe all of them in a similar manner. However, the neural maps reported in the literature have not used uniform numbering schemes (i.e., a given neuron may be numbered differently from map to map). This suggests another goal of our work: not only to describe homological cells in different species, but also to compare different descriptions within one species.

Structure of the Nervous System

Systematically, the snails in question are described as follows: Phylum *Mollusca,* Class *Gastropoda,* Subclass *Pulmonata,* Superfamily *Stylommatophora,* Family *Helicidae.* As in other molluscs, numerous neurons are located in the periphery: in the skin, foot, and other organs [49]. These peripheral parts of the nervous system are almost unexplored; most

[1]Translated by P. M. Balaban.

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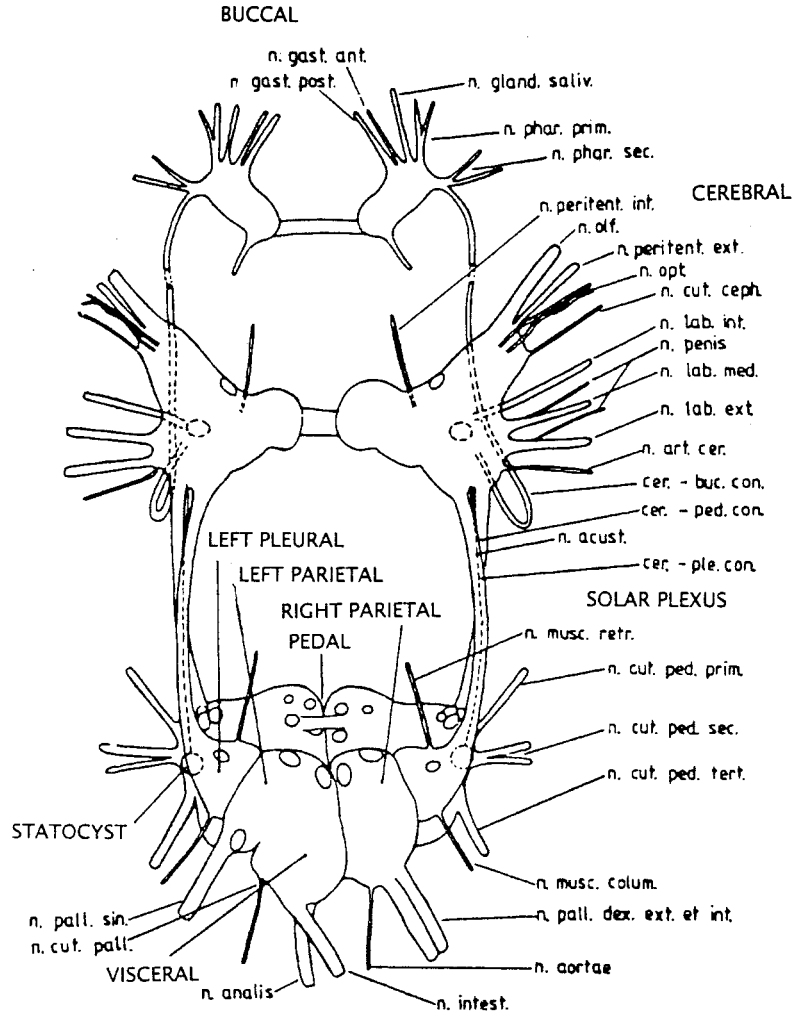

Fig. 1. Schematic representation of the central nervous system of the snail (*Helix*) with major nerves and ganglia labelled. Dorsal surface. Modified from [49]. Nerve of buccal ganglia: n. gast. post.) *nervus gastricus posterior*; n. gast. ant.) *nervus gastricus anterior*; n. gland. saliv.) *nervus glandulae salivalis*; n. phar. prim.) *nervus pharyngealis primus*; n. phar. sec.) *nervus pharyngealis secundus*. Nerves and connectives of cerebral ganglia: n. peritent. int.) *nervus peritentacularis internus*; n. peritent. ext.) *nervus peritentacularis externis*; n. olf.) *nervus olfactorius*; n. opt.) *nervus opticus*; n. cut. ceph.) *nervus cutaneus cephalicus*; n. lab. int.) *nervus labialis internus*; n. lab. med.) *nervus labialis medianus*; n. lab. ext.) *nervus labialis externus;* n. penis*) nervus penis;* n. art. cer.*) nervus arteriae cerebralis*; n. acust.) *nervus acusticus*; cer.-buc. con) cerebro-buccal connective; cer.-ped. con) cerebro-pedal connective; cer.-ple. con.) cerebropleural connective. Nerves of parietal, pleural pedal and visceral ganglia: n. musc. retr.) *nervus musculi retractoris pharyngealis*; n. cut. ped. prim.) *nervus cutaneus pedalis primus*; n. cut. ped. sec.) *nervus cutaneous pedalis secundus*; n. cut. ped. tert.) *nervus cutaneous pedalis tertius*; n. musc. colum.) *nervus musculi columellaris*; n. pall. dex. ext. et int.) *nervus pallialis dexter externus et internus*; n. aortae) *nervus aortae*; n. intest.) *nervus intestinalis*; n. analis) *nervus analis*; n. pall. sin.) *nervus pallialis sinister*; n. cut. pall.) *nervus cutaneous pallialis.*

work has been focused on the central ganglia which are fused in a circumesophageal ring. The ring contains 5 pairs of ganglia and a visceral ganglion. A view of these ganglia is presented in Fig. 1. A short description of the nerves described in this figure follows.

Buccal Ganglia. *Nervus glandulae salivaris* has salivary glands as its target, whereas anterior and posterior parts of the buccal mass are innervated by *nn. pharyngealis primus, secundus.* The pharynx and stomach are innervated by *nn. gastricus anterior, posterior.*

Cerebral Ganglia. *N. olfactorius* innervates olfactory ganglia in ommatophores (tentacles with eyes on their ends). *N. opticus* contains two branches, and innervates the eye and ommatophore retractor muscle. The skin and muscles (except retractor) of the commatophore are innervated by two nerves: *nn peritentacularis internus, externus.* The gravitational organ (statocyst) located in pedal ganglia is innervated by *n. acusticus.* The skin of the head is innervated by *n. cutaneus cephalicus,* the penis by *n. penis,* and the cerebral arteria by *n. arteriae cerebralis.* The lips, oral cavity, and

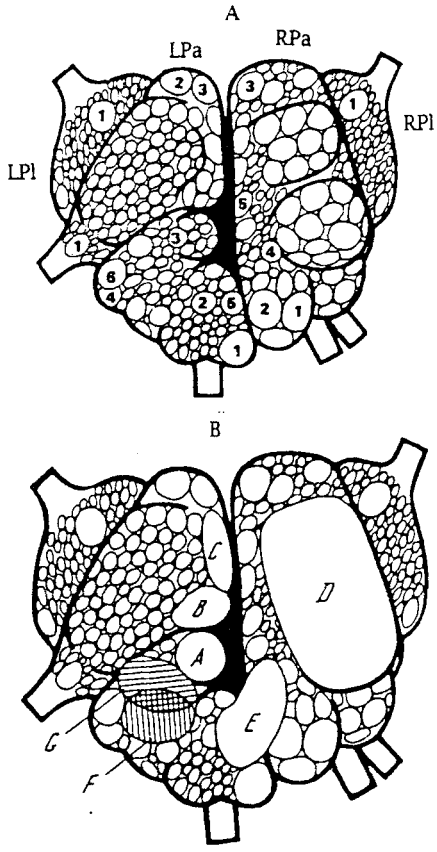

Fig. 2. Maps of the dorsal surface of parietal, pleural, visceral ganglia. Modified from [18]. With numbers on this and subsequent figures identified neurons are labelled (A); neural groups are labelled with letters (B). LPl, RPl) Left and right pleural ganglia. LPa, RPa) Left and right parietal ganglia. For nerve abbreviations see legend of Fig. 1.

rhinophores (small tentacles) are innervated by three nerves: *nn. labialis externus, medianus, internus.* Connectives connect cerebral ganglia to the pleural, pedal, and buccal ganglia.

Subesophageal Ganglia Complex. Ten pairs of nerves *(nn. musculi pedalis,* not shown on Fig. 1) originate from the ventral surface of pedal ganglion. These nerves innervate muscle and skin of the ventral part of the foot. The three pairs of *nn. cutaneus primus, secundus, tertius* innervate the skin on the dorsal surface of the foot. *N. musculi columellaris,* which innervates the columellar muscle (a major retractor of the body into the shell) and *n. musculi* retractor *pharyngealis,* which innervates a part of columellar muscle capable of contracting independently (pharynx retractor) take off from the pleural ganglia. The parietal ganglia nerves *nn. pallialis sinister, dexter* innervate the mantle, mantle bolster, and pneumostome. The central artery is innervated by *n. aortae,* and part of the skin surface is innervated by *n. cutaneous pallialis. N. analis* (which innervates the mantle bolster, and diaphragm) and *n. intestinalis,* the nerve innervating all internal organs (heart, liver, kidney, intestines and esophagus) take off from the visceral ganglion.

Identifiable Cells in the Snail

It was established long ago that many neurons in the invertebrate nervous system have constant location, shape, pigmentation, etc. Maps of neuronal location were published with a description of neurons identifiable from preparation to preparation [18, 20, 37, 480]. Figures 2-4 illustrate the neural maps which are used in several laboratories.

Identification Problem. Certain neurons are recognizable in every species. Usually, these are giant and large neurons. For identifying those neurons which exhibit individual variability, the following parameters are considered [18]: a) visual (size, location, pigmentation); b) electrophysiological (type of spontaneous activity, membrane potential, shape of action potential, characteristic synaptic input, pharmacological characteristics, response to polarization); c) morphological (shape of branches, nerve targets); and d) functional (interrelations with other neurons in the network, roles in eliciting behaviors, responses to external stimuli). Currently fewer than 100 of the 18000 neurons (besides the procerebrum) neurons have been individually identified. Table 1 presents data concerning most of the identified cells in *Helix.* Neurons are numbered according to [16].

Investigation of small network functioning normally involves nonstandard identification of small neurons and neuronal groups and, hence, can not be included in any kind of table. In order to consistently identify such neurons, one must obtain experimental data and refer to literature devoted to the cells in question.

Methods of Mapping. The shape and location of neurons normally should be described not only on the basis of visual experience and view of the cell on the ganglion surface, but also on morphological reconstructions from serial slices [16]. Recent monographs [43, 44] provide methods for describing neural branches, synaptic contacts, and specific transmitters within the cell. We will mention here only two major methods for revealing neuronal structure. First is the anterograde transport of an injected dye (or any other substance which may be colored later) from soma to branches in order to reveal the cell processes. By this method one can reveal the processes of a single cell in all nerve targets and ganglia. The second approach is the retrograde transport of a dye via the cut end of a nerve, which reveals the community of cells sending processes to the given nerve. Usually only one process of a neuron may be stained by the retrograde method. Both fluorescent dyes (DiI, DiO, Lucifer Yellow, Carbofluorescein) and dyes visible in white light may be used. As an example of the latter type of staining, heavy metal ions may be precipitated by S2- ions or by rubeanic acid (the resulting precipitate stays inside the cell). Another example is the reaction of intracellularly injected horseradish peroxidase and diaminobenzidine which stains the cell black. Staining may be intensified by silver or colloidal gold. By using two different methods or two different colors, one may double-label two cells or two clusters which send processes to different nerves in a given preparation. Detailed description of these methods can be found in cited monographs.

Such mapping techniques have been extensively used in studies of snails. Some results are shown in Figs. 5-7. Other reviews of this issue focus on buccal ganglion (U. Altrupp), sensory systems (O. Zaytzeva), cardio-respiratory systems (Bychkov et al.,), and cerebral ganglia (G. Kemenes).

Data Concerning Branches of Neurons. Summary view of neurons which can be labelled by retrograde staining via some nerves (Figs. 5-7) have been compiled from works of different authors and our experiments (see references in the legends). Occasionally, data from *H. lucorum* and *H. Pomatia* are combined, which is possible due to similar neuronal locations in these species. In some instances only nerves from one side were stained, which presents a unilateral view. Hence, the level of symmetry of neural branches is not known in these cases. It should be noted that no cellular somata were stained via the optical branch of the optical nerve (Fig. 5). Neural elements stained via *nn. opticus, columellaris, penis* are traced up to the somata (Fig. 5). Sometimes some neurons are located at different depths within a ganglion; this is not shown in the figures. It should be also noted that many neurons send branches to different nerves, and staining via these different nerves may show more neurons on the map than there are in the ganglion.

Functional Identification of Neurons

Intracellular recording of activity of one or more cells in a preparation with preserved receptors and effectors allows one to assign a certain function to a cell on the basis of: a) latency and type of response to adequate external stimuli; b) appearance of effector reactions to intracellularly-induced firing of the cell; c) dynamics of synaptic and spike reactions under repeated stimulations; d) correlation between firing of neuron and spontaneous movements of effectors; e) neuronal morphology. The morphological criterion for evaluating a given neuron as a primary sensory or a motoneuron is prevalent. The former has a morphologically traceable connection with receptors, whereas the latter can be traced to muscle. Morphological identification of interneurons (i.e., cells having inputs from neurons and making contact with the neurons) is impossible.

To identify the functional role of a given interneuron, a complex set of criteria should be used. Unfortunately, there is no set procedure for this important stage of identification. The complexity arises from the need to establish the role of a neuron in behavior, when the behavior itself is poorly formalized.

As an example let us take the problem of functional identification of giant parietal neurons which have been described as command for avoidance (withdrawal) behavior [16] by some authors and as a polyfunctional neuron by others [2].

More than 40 years ago, a very important idea was introduced concerning the existence of individual neurons responsible for a complex behavioral act [56, 60]. This idea was first introduced during the course of analyzing the escape behavior of invertebrates. The main implication is that there are individual cells which "make the decision" in the given network to initiate a very definite type of behavior, or can gate the behavioral start on the basis of sensory information. These cells were presumed to be the final stage of integration of sensory information. Interneurons with this function were called "command neurons" [58].

A debate concerning the concept of command neurons still persists in the literature. This is not really surprising since the problem under discussion is actually the classic

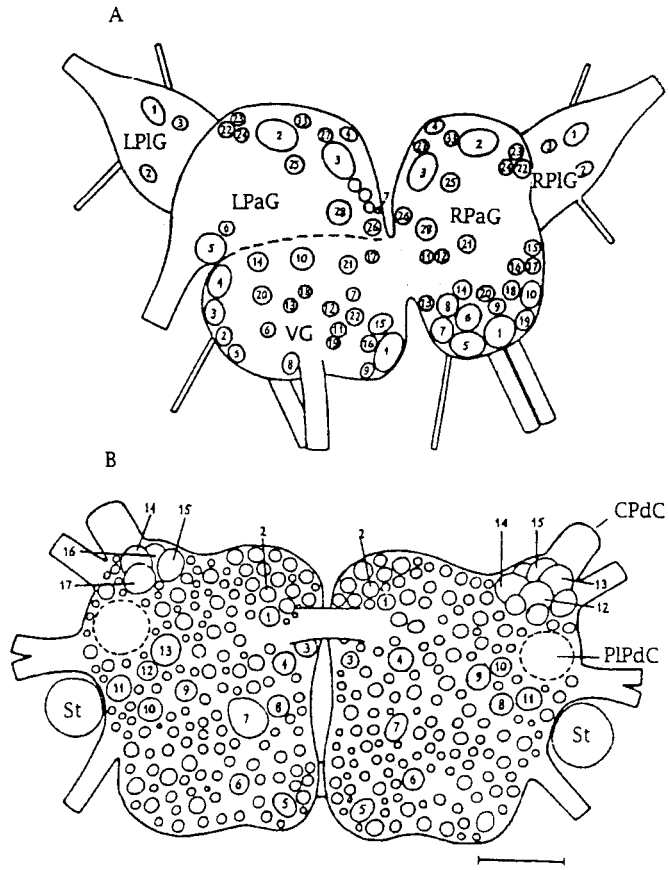

Fig. 3. Maps of dorsal surface of parietal, pleural, abdominal (A), and pedal (B) ganglia. Modified from [16] — A; [5] — B. LPlG, RPlG) Left, right pleural ganglia. LPaG, RPaG) Left, right parietal ganglia. VG) Visceral ganglion; St) statocyst; CPdC, PlPdC) cerebro-pedal, pleuro-pedal connectives. Calibration 500 microns.

neurobiological problem of localization of functions. What is the mechanism which dictates that a given behavior is initiated rather than some alternative one? Are there localized centers, or individual neurons (in invertebrates, for instance) which initiate a predefined behavior upon being activated? The command neuron concept gives a clear answer, i.e., that sets of "neural buttons" whose activation initiates certain behaviors may exist in the nervous system. According to this concept, the decision to start the variety of behavioral acts is statistically localized in certain specialized neurons. In other words, certain neurons should have an invariant behavioral function. An alternative hypothesis states that behavior is the net outcome of the network as whole, and behavior can be controlled only by the whole network [50, 59].

Experimentally, the command neurons have been described in crustaceans, molluscans, insects, and fishes (for review, see [16, 26, 42]. Two types of command neurons are described: one type only elicits the behavior, while another gates it, i.e., the initiated behavior may occur only during their activity. In any event, the command neurons may be distinguished from the pattern-generating neurons which control the duration and phase relationship. The role of command neurons consists of activating the pattern-generating neurons. Despite the popularity of this concept, it has

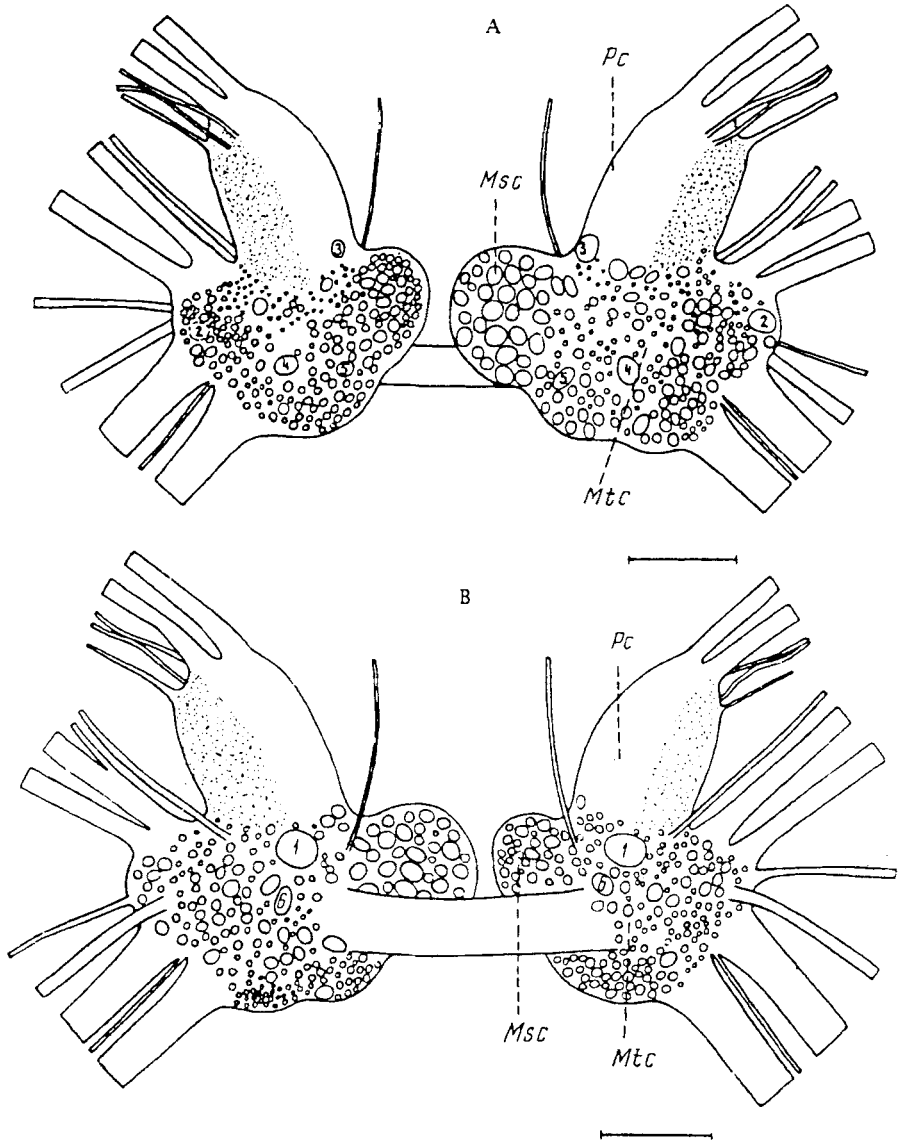

Fig. 4. Maps of dorsal (A) and ventral (B) surfaces of cerebral ganglia. Modified from [5]. Pc) Procerebrum; Msc) mesocerebrum; Mtc) metacerebrum. Calibration 500 microns.

some implicit contradictions. I. Kupfermann and K. Weiss [40] made progress toward clarifying the concept when they formulated criteria for defining command neurons on the basis of a causal analysis. A putative command neuron should not only participate in the given behavior, but also should be necessary and sufficient for the initiation of that behavior. This definition implies that reversible exclusion of the putative command neuron from the network reversibly eliminates the controlled behavior.

Often command neurons are related to motorneurons [34], but this generalization does not apply to all available experimental data. Command neuron function is not restricted to muscle activation, but rather seems to consist of activation of a set of motorneurons. Moreover, command neurons obtain convergent sensory information [20, 36] and can integrate sensory information. All known data conform to the definition of the command neuron, which has fixed connections with a certain set of motor elements in the nervous system, as the final stage of sensory information integration [22].

It is noteworthy that each neural system has its phylogeny, and the participation of interneurons in direct motor control may reflect their primary role in the early stages of ontogeny. Another trend is obvious in the description of the functional roles of neurons: with increased information about the participation of a given neuron in network functioning, uncertainty about its function increases, due to the regular appearance of data concerning new connections [54]. Besides, during an analysis of the separate behavioral acts (each of which may have its own command neuron) constituting a behavior, one inevitably observes doubling of the same functions by command neurons as predicted by T. Bul-

TABLE 1. Identified Neurons In the Snail

Name	Spontaneous Activity	Transmitter	Function	Nerves Containing Branches Of Neuron	Reference
RPa2	silent	FMRFa	command neuron, triggers ipsi-lateral contractions of the skin, mantle bolster, and pneumostome	Nn. pall. dex., sin.; n. analis; ipsilateral nn. musculi ped. III-VII, IX, X; nn. cut. ped. primus, sec.	[14, 16, 29]
LPa2	silent	FMRFa	as above	same + ipsilateral n. cut. ped. tert.	[4, 14, 16, 18, 29, 32]
RPa3	silent	FMRFa	command neuron, contraction of mantle bolster	Nn. pall. dex., sin.; n. analis; ipsilateral nn. musculi ped. III-VII, IX, X; nn. cut. ped. primus, sec.; contralateral nn. cut. ped. prim., tert.; n. cut. pall.	[1, 4, 14, 15, 16, 18, 29, 32]
LPa3	silent	FMRFa	as above	Nn. pall. dex., sin.; n. analis; ipsilateral nn. musculi ped. III-VII, IX, X; nn. cut. ped. primus, sec.	[1-4, 14-16, 18, 29]
LPa5	silent	FMRFa	as above	Nn. pall. dex., sin; n. analis; n. cut. pall.	[14, 16, 18, 29]
RPa1	bursting	peptide (?); FMRFa	regulates heart beating	N. intestinalis	[12, 13, 16, 18, 29, 45, 47, 53]
RPl1	irregular	FMRFa	command neuron: contraction of ipsilateral rostral part of the body	Cer.-Pl. conn.; ipsilateral nn. cut. ped. prim., sec.; n. musculi pedalis I-IV	[16, 18, 29, 32]
LPl1	as above	as above	as above	same + n. cut. ped. tert. sin.	[16, 18, 29, 32]
RPa2	silent	FMRFa	command neuron, triggers ipsilateral contractions of the skin, mantle bolster, and pneumostome	Nn. pall. dex., sin.; n. analis; ipsilateral nn. musculi ped. III-VII, IX, X; nn. cut. ped. primus, sec.	[14, 16, 29]
RPl2, LPl2	silent, occasional AP	FMRFa	contraction of ipsilateral eye retractor	Ipsilateral pedal ganglion, n. pall.	[16, 29, 32]
LPd7	regular AP	?	integrative neuron triggering pneumostome movements	N. pall. sin.; n. analis	[5, 32, 35, 55]
LGC1 RGC1	silent, occasional AP	5-HT	modulatory neuron for feeding behavior	Cer.-bucc. conn., n. lab.ext.	[5, 9, 10, 16, 18, 24, 30, 33, 46]
LC3, RC3	irregular bursts	FMRFa	motoneuron of eye retractor	contralateral n. opt.	[5, 11, 16, 29]
RPd*	irregular AP	5-HT	modulators of avoidance behavior	Left nn. cut. ped. primus, sec., tert.	[6, 28, 61]

RPd* — rostrally located group of neurons in pedal ganglia.

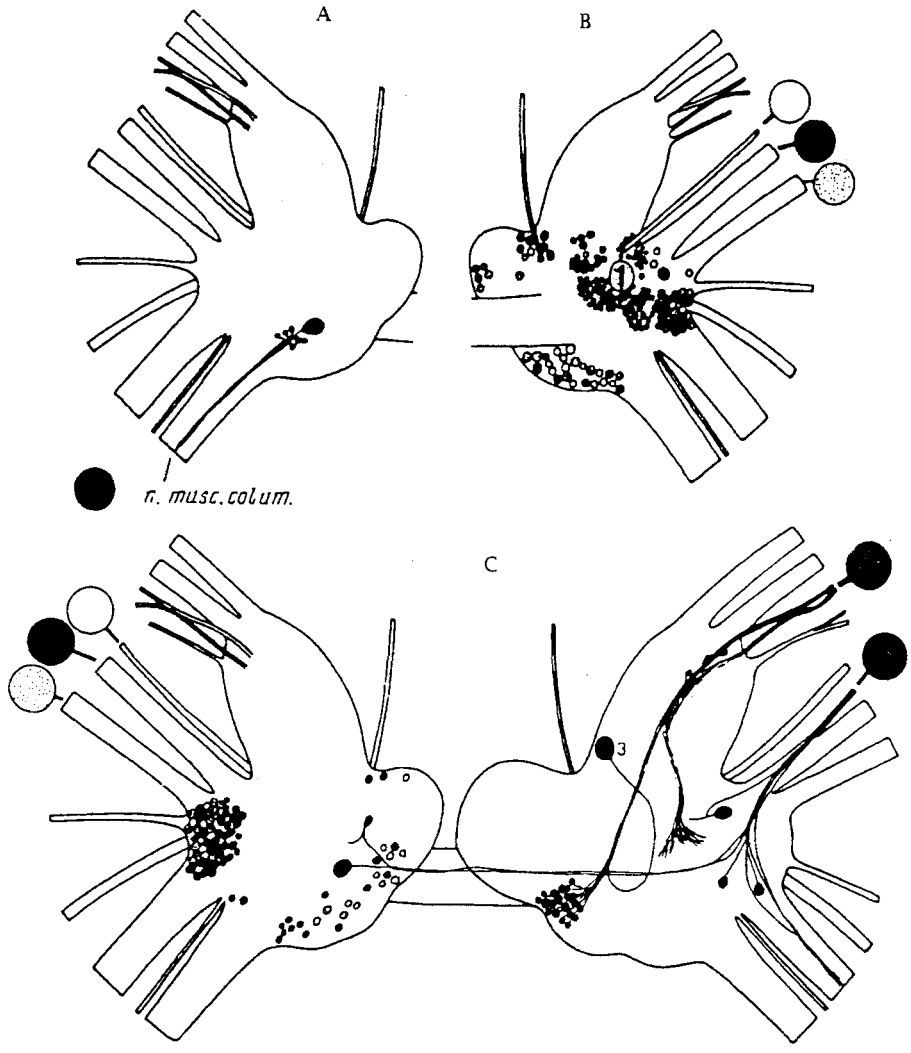

Fig. 5. Maps of location on dorsal (A, C); and ventral (B) surfaces of cerebral ganglia of the snail of the family Helicidae. Data concerning cells sending branches to nerves are taken: *nervus columellaris*) *Helix lucorum* [17]; *nerve labialis internus, medianus, externus*) *Helix pomatia* [30] and *Helix lucorum* (our unpublished data), *nervus opticus*) *Helix lucorum* [11]; *nervus penis* (branch innervating *musculus retractor penis*) - *Helix pomatia* [27]. Neurons sending processes to corresponding nerves are labelled by the symbols by which the nerve is labelled.

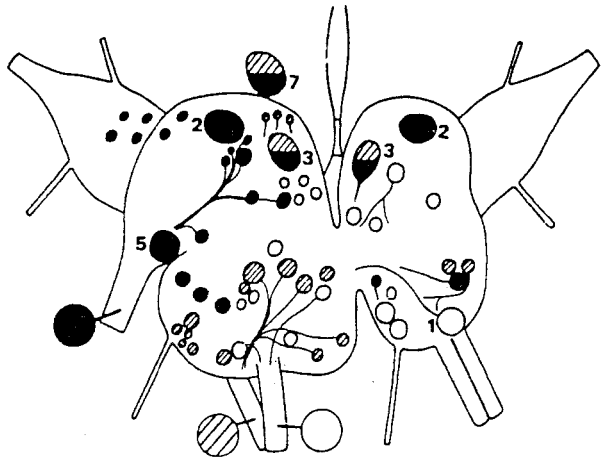

Fig. 6. Scheme of location of cell somata (dorsal surface), giving branches to the left pallial, anal, and intestinal nerves. Data from *Helix pomatia* [47, 51, 52, 53] and *Helix lucorum* (our unpublished data) are summarized. Neurons sending processes to corresponding nerves are labelled by the symbols by which the nerve is labelled.

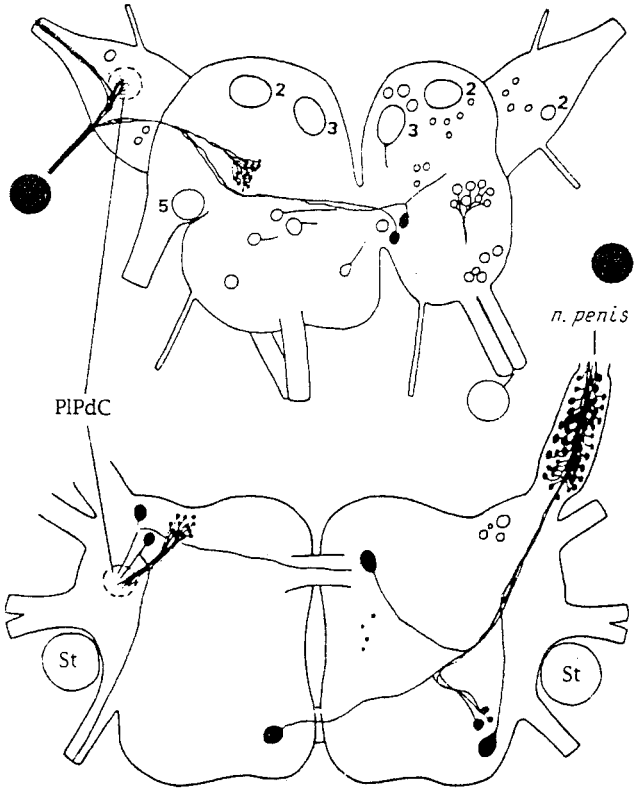

Fig. 7. Scheme of location of cellular somata and nerve fibers sending processes to *nervus columellaris*, *nervus penis* (branch innervating *musculus retractor penis*), and *nervus pallialis dexter*. Dorsal surface of subesophageal ganglia. Data are taken from: *nervus penis*) *Helix pomatia* [27]; *nervus columellaris*) *Helix lucorum* [17]; *nervus pallialis dexter*) *Helix pomatia* [47] and *Helix lucorum* (our unpublished observations).

lock [22]. In such cases it is only possible to estimate the role of a class of cells in behavior and, on the basis of knowledge of hierarchical structure of behavior and separate behavioral acts, suggest the role of an individual neuron.

Recently, giant parietal neurons of the snail were found to produce negative feedback in the simple reflex pathway [8]. Rather than contradicting their trigger function in withdrawal behavior, this observation illustrates the complexity of neural systems which underlie behavior. One could simply label all neurons with nontrivial properties as "polyfunctional" [2] without considering the functional identification of the cell, but this approach would be problematic in that an unlimited number of neurons fall into such a class. Polyfunctionality of neurons occurs early in phylogeny, whereas specialized functions correspond to increased complexity of behavior and body structure in phylogeny. Apparent accuracy in usage of the term "polyfunctional" becomes a refusal to view the organization of behavior as a reflection of the hierarchical structure of nervous system. The notion of "function" is of a higher order than "sensory," "motor," or "command."

Analysis concerning the principle of the distribution of function in the system also may be productive. For instance, the "orchestration" hypothesis [31] included all available data in a description of the interaction of neurons during a grasshopper jump and provided a direction for future research. In such a system, there is no place for command neurons, but there are some other functional classes of interneurons. Given the present level of knowledge of details of behavioral organization in the snail, one should not limit oneself to a single paradigm. Consequently, functional classification of individual neurons is rather loose and reflects the level of our knowledge.

Functional Identification of a Neural System

In quite a few cases one can not specify the function of an individual cell in an analysis of behavior. In such instances the primary analysis is performed at the level of the relationships among distinct neuronal groups. As an example, we will consider the description of neurons related to sexual behavior.

Sexual organs in the snail are innervated by a nerve originating from the cerebral ganglion *(n. penis)* and the pedal ganglion nerve *(n. cutaneus pedalis primus dexter)*. The cerebral ganglia of *Stylommatophora* consists of the procerebrum, mesocerebrum, and post (meta) cerebrum. Mesocerebral neurons are involved in the control of sexual behavior. Neurons in the right mesocerebrum are larger and more numerous than in the left [23]. The cellular processes of mesocerebral cells innervate the symmetrical ganglion and the right pedal ganglion. Because mesocerebral cells are uniformly sized and colored, no individual cells can be identified. Extracellular stimulation of the mesocerebrum, as well as intracellular stimulation of individual cells, leads to a high-latency movement of the sexual organs [23]. On the basis of available data, it has been assumed that the motoneurons responsible for the movements of sexual organs are located in the pedal ganglia.

It has been shown immunochemically that some neurons of the mesocerebrum contain the neuropeptide FMRFamide

[29] which is known to inhibit neurons involved in withdrawal behavior [21]. Also, data describing enkephalin-containing cells have been recently published [41], which are extremely interesting in terms of the participation of mesocerebral cells in reinforcement.

Extracellular stimulation of mesocerebral cells with pulsed current elicited a significant decrease in the responses to tactile stimulation of the command neurons for withdrawal behavior, as well as inhibition of spontaneous activity in pedal serotoninergic cells. It was also found that mesocerebral stimulation decreased both the number of spikes in command neurons and the amplitude of the behavioral response [7].

The available data make possible the following generalizations concerning the mesocerebral cells. 1) There exists one-way inhibition between mesocerebral and giant parietal (command for withdrawal) cells. Mesocerebral cells inhibit the response of these neurons to noxious stimuli. This effect corresponds to behavioral changes during activation of sexual behavior; the threshold to noxious stimuli increases. 2) Activation of the mesocerebrum simultaneously inhibits serotoninergic neurons participating in sensitization of withdrawal reactions. More effective inhibition of withdrawal is achieved by this additional influence.

Such analysis is a necessary preliminary step before neural relations may be investigated at the level of individual cells.

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