

CENTRAL REPRESENTATION OF INTERNAL
AND EXTERNAL SENSORY INFORMATION
IN THE CNS OF *HELIX POMATIA* L. AND
LYMNAEA STAGNALIS L.*

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The central representation of intero- and exteroceptors located in visceral organs and the osphradium were compared in the CNS of *Helix pomatia* L. (Gastropoda, Stylommatophora) and *Lymnaea stagnalis* L. (Gastropoda, Basommatophora), two pulmonate snail species inhabiting a terrestrial and anaquatic environment, respectively. Semi-intact preparations were used comprising the CNS connected by the corresponding nerves either to the cardio-renal, respiratory and genital systems or to the osphradium. Spike discharges of central neurons and the nerves were recorded simultaneously. The central representation of intero- and exteroceptors was found to be distributed throughout the CNS and involved about 300 neurons. The majority of the neurons received sensory information from all the studied visceral organs and the osphradium. Among the neurons responding to intero- and exteroceptors a multimodal reaction to tactile, chemical and osmotic stimuli prevailed while in the osphradium specific reactions also were demonstrated. Central neurons receiving sensory information from visceral organs and the osphradium form overlapping and reorganizing neural circuits using the same neurons in the regulation of heart activity, respiration or reproduction producing the appropriate behaviour. In the selection of sensory information the firing pattern appears to be the main determining factor as bursting neurons do not receive sensory information. The central representation of intero- and exteroceptors and its variability can be a model system for cellular studies of motivational state and self-perception.

Keywords: *Helix pomatia* L. – *Lymnaea stagnalis* L. – visceral organs – osphradium – intero- and exteroceptors – neural circuits – motivation

INTRODUCTION

The comparative approach in biology has been adopted for many generations of scientists resulting in great progress in understanding such fundamental problems of neurobiology as nerve excitability, identification of ion channels, receptors, single cell properties, network organizations, cellular memory events, etc. Simultaneously, the achievements in understanding the basic problems in one group of animals were extrapolated to others, leading to biological generalization and emphasizing that different kinds of organisms solve similar life or regulatory problems by using similar

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basic mechanisms, from sensory perception to cellular learning or memory consolidation.

However, comparative physiology paid less attention to modelling the cognitive physiology or the “sense of self”, although these events can also have their analogues between different species or even phyla. Among others, the regulation of homeostasis which is one of the best studied questions in the animal kingdom, can offer some models for cognitive neurobiology. In a broad sense, homeostasis assures the self-preservation under environmental alterations, while in a more specific sense, it reflects the internal conform state of the individuals. In this respect, all the systems connected with the control or protection of homeostasis in invertebrates can be used for modelling various questions of cognitive physiology.

Due to limited number of the neurons in the CNS of gastropod molluscs both internal and external information can be traced in a cell to cell manner from sensory to central computational units and the corresponding information can be decoded.

In our laboratory several types of semi-intact preparations of *Helix pomatia* and *Lymnaea stagnalis* were developed contributing to the identification of the central representation of sensory information originating from intero- or exteroceptors as well as to an understanding of the regulation of visceral organs [10, 11, 14]. In these studies the cardio-renal, respiratory and genital systems were used for the analysis of interoceptive information, while the exteroceptive information that was studied originated from the osphradium [6, 7, 14].

The aim of our present study was to compare the intero- and exterosensory perceptions and their central representation in two molluscan species (one of them being terrestrial and the other aquatic). Further on, according to the central representation of various intero- and exteroceptive sensory information the overlapping or independent character of neural networks regulating different sensory modalities or functions are discussed.

MATERIALS AND METHODS

The experiments were performed on adult specimens of the pond snail, *Lymnaea stagnalis* L. (Pulmonata, Basommatophora) and the edible snail, *Helix pomatia* L. (Pulmonata, Stylommatophora) collected from their natural habitat during the months May–April. The animals were fed with fresh lettuce.

In the course of the experiments the following types of semi-intact preparations were used:

1. CNS and the cardio-renal system including heart, pericardium, liver and kidney connected by the intestinal nerve
2. CNS and the cardio-renal and genital systems including additionally to the above organs the female duct, hermaphroditic gland, hermaphroditic duct, spermatheca, accessory genital mass and prostate gland connected by the intestinal nerve
3. CNS and cardio-renal system as well as the pneumostome (the respiratory opening) connected by the intestinal and the right parietal nerves

4. CNS and the osphradium linked by the osphradial nerve, which is the ramification of the inner right parietal nerve

The preparations and experimental protocols have been described in detail [5, 6, 11, 12, 13]. During experiments the intracellular activity of central neurons and the extracellular discharges on the corresponding nerves were registered simultaneously. The heart contractions and the opening or closing of the pneumostome were also recorded synchronously with nerve activity (see: Figures). For the stimulation of intero- or exteroceptors tactile, chemical or osmotic stimuli were used, respectively [5, 13]. The compositions of the physiological salines used can also be found in earlier papers [5, 13, 14].

RESULTS

Representation of sensory inputs originating from the cardio-renal, respiratory and genital systems in CNS of Helix pomatia L.

In this series of experiments the visceral organs were stimulated either by tactile or chemical stimuli applied to their surface and the corresponding responses were recorded on nerves and in central neurons [11, 12]. According to the findings a large number of central neurons received sensory information from each of the visceral

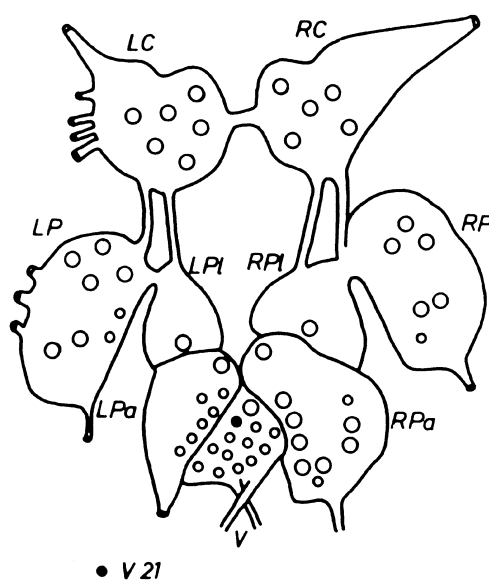


Fig. 1. Distribution of neurons involved into the regulation of cardio-renal system in CNS of *Helix pomatia* L. The symbols are as follow: LC, RC – left and right cerebral ganglia, LP, RP – left and right pedal ganglia, LPL, RPL – left and right pleural ganglia, V – visceral ganglion, LPa, RPa – left and right parietal ganglia [11]

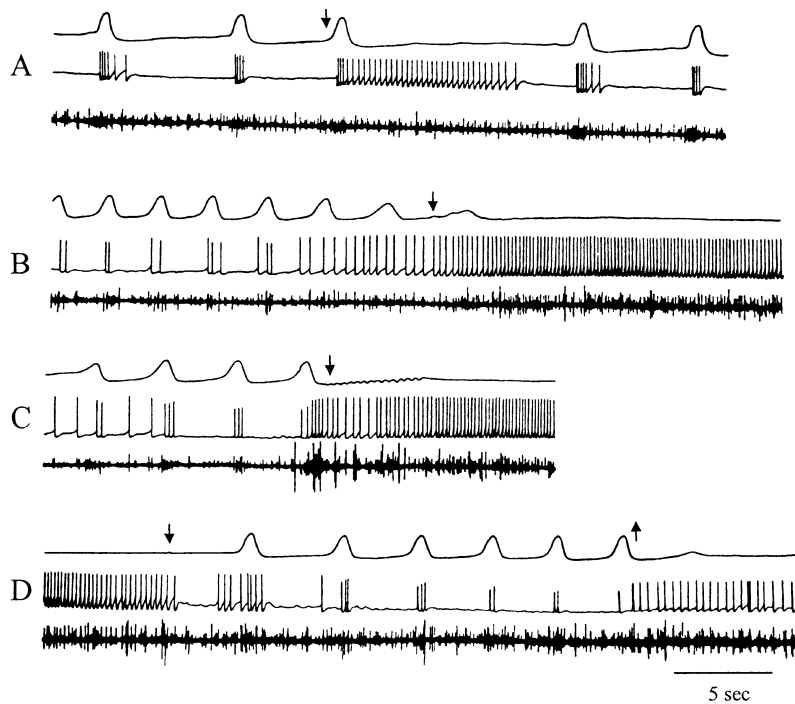


Fig. 2. Changing in firing pattern of the multifunctional interneuron V21 in *Helix* CNS. A – phasic pattern of the neuron V21 shifted to tonic one following tactile stimulation of the heart. The heart contractions were inhibited during tonic firing of the neuron V21. B- and C – the same as A following stimulation of the pericardium and kidney, respectively. D – recovery of phasic pattern of the neuron V21 restored the heart contractions. In each record, heart beats are seen above, the discharges of the neuron are shown in middle, while the nerve activity is seen below [11]

organs studied. The target neurons were distributed throughout the central nervous system. The overwhelming majority of the neurons received information from the cardio-renal, respiratory and genital systems alike [11, 13, 14].

The results obtained in the semi-intact preparation including only the cardio-renal system connected to the CNS showed that the neurons receiving sensory inputs from the cardio-renal system or regulating heart activity can be identified in the left and right parietal (LPa, RPa), left and right pleural (LPL, RPL) visceral (V) and left and right pedal (LP, RP) ganglia (Fig. 1). In *Helix pomatia* among the identified central neurons involved in the regulation of the cardio-renal system two heart inhibitory, two heart excitatory, one heart relaxing and two multifunctional interneurons were identified [11, 13]. In addition to the identified central neurons about 300 small unidentified neurons reacted to input activation originating from cardio-renal system [11, 13].

Using the semi-intact preparation with two peripheries (e.g. cardio-renal and respiratory systems) it was found that nearly all the neurons identified as a member of

the cardio-regulatory circuit also are involved in the regulation of the pneumostome and receive permanent sensory information from respiratory organs, too [11, 13].

The same set of neurons regulating the cardio-renal and respiratory systems was found to participate in the regulation of the genital system, too (Fig. 1), receiving sensory information from each of its units [10, 11, 13].

In the *Helix* CNS, among the identified neurons a multifunctional interneuron, V21, was found to be involved in the regulation of all the studied visceral organs. The neuron V21 is characterized by a firing discharge being a phasic or a tonic one (Fig. 2). The phasic firing pattern of the neuron V21 showed a close correlation with single heart contractions and these phasic discharges turned to tonic ones in response to sensory activation from any of the cardio-renal organs leading to heart inhibition (Fig. 2).

The multifunctional neuron V21 also receives interoceptive information from respiratory and genital organs, turning its phasic firing pattern into a tonic one. However, the shape and time course of this alteration in firing pattern can vary considerably depending on the origin of sensory information. The responses of interneuron V21 to the activation of sensory inputs originating from the prostate gland,

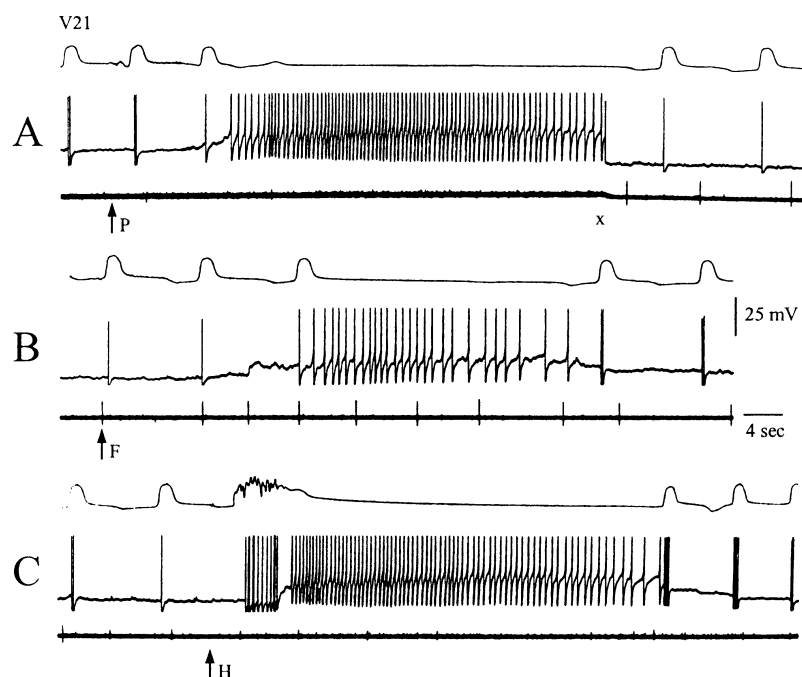


Fig. 3. Response of the interneuron V21 to the stimulation of genital organs. Turning of phasic pattern to tonic one is seen on the interneuron V21 to the stimulation of the prostate gland (P, A), female gland (F, B) and the heart (H, C). Although the intensity of tonic firing appearing in answer to the stimulation the above organs is different it led uniformly to the inhibition of heart contractions. Heart activity recovered simultaneously with phasic firing of the neuron V21

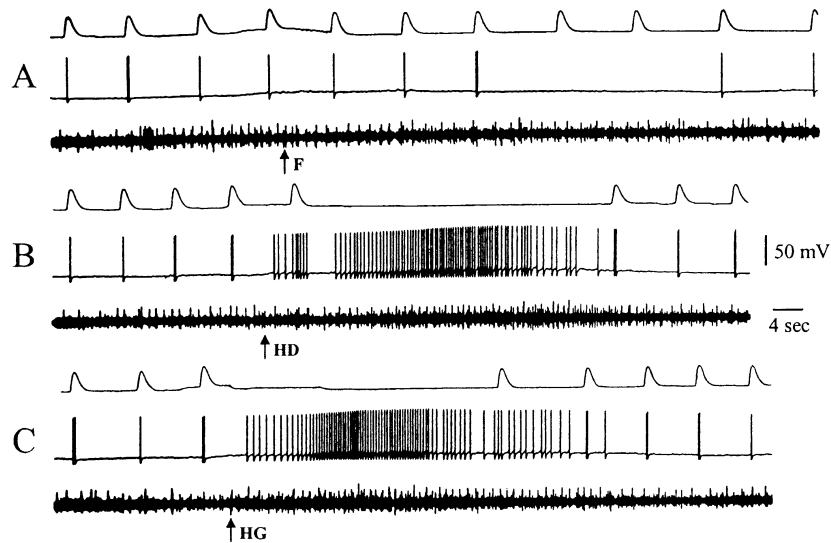


Fig. 4. Modulated input sensitivity of interneuron V21 to the stimulation of the genital organs. Tactile stimuli were applied to the female duct (A), hermaphroditic duct (B) or gland (C). The insensitivity to the stimulation of female duct can be seen, while the inputs from hermaphroditic duct and gland remained intact on the neuron V21

female duct, hermaphroditic gland and duct were found to be very similar to that of heart stimulation (Figs 3 and 4). The tonic firing of neuron V21 in response to sensory activation of the genital organs led uniformly to heart inhibition, too (Figs 3 and 4). However, the duration and intensity of the response of interneuron V21 to the stimulation of genital organs were variable or the response could even be totally absent, as it is demonstrated for the female duct (Figs 3B and 4A).

The results showed that stimulation of genital organs either caused uniformly a change in firing pattern of the interneuron V21 or failed to influence the neuron during a certain type of pattern. This means that central neurons can select between the sensory information coming from genital organs depending on their motivational state.

The central neurons reacted both to tactile and chemical stimuli applied to the visceral organs [11, 13]. It has been shown that acetylcholin, 5-hydroxytryptamine, dopamine and octopamine introduced to the heart also activated sensory inputs to the same central neurons which were related to tactile stimulus activated inputs, too [11, 13].

Summarising the results it can be stated that the central neurons regulating visceral functions respond to several sensory modalities and regulate more than one visceral functions. The distribution of interoceptive sensory information to central neurons indicate that the number of the cells permanently informed on the state of the visceral organs is much higher than that of the neurons taking part in the regulation of the given visceral organ. It became evident too, that the same neuron can be shared

alternatively by dynamically organized and reorganized neural networks, depending on the momentary need of the organism for adequate adaptation to environmental alterations. It was found that in the molluscan CNS a number of moto- and interneurons are multifunctional and react to visceral sensory informations [11].

*Representation of exteroceptive information in the CNS of *Lymnaea stagnalis* L. originating from the osphradium*

The osphradium is a peripheral multisensory organ developed only in molluscs inhabiting aquatic environments. In *Lymnaea*, the osphradium is located at the entry of the mantle cavity along the path of the respiratory currents and adapted to analyse the physico-chemical properties of the environment [6, 7, 18]. The osphradium is known to respond to hypoxia, hypercapnia, mixtures of amino acids, different classes of odorants and osmotic pressure [5, 18, 20]. The chemo- and osmosensitivity of single osphradial neurons have been described earlier [5, 7, 20]. However, the demonstration of the central representation of this multisensory organ in CNS of *Lymnaea* is still insufficient and the transferring of the environmental information has not been compared to that of visceral organs.

In these experiments the transfer of exteroceptive sensory information from the osphradium to central neurons was studied and their target central neurons were compared to those of the neurons receiving sensory information from cardio-renal and respiratory organs. Here, the semi-intact preparation including the CNS and osphradium with the osphradial nerve connecting them was used.

In the CNS of *Lymnaea stagnalis* central neurons regulating visceral functions have been identified [1, 8, 19, 21] and compared to those of *Helix pomatia* [13, 14]. However, central representation of the osphradium has not been related to the regulation of visceral functions. In *Lymnaea* the best-studied units of the cardio-respiratory regulatory neural network were shown to comprise neurons forming a respiratory central pattern generator (RPeD1, VD4 and IP3) connecting to their followers from the A-, J-, K-, I-clusters and the neuron RPaD1 [1, 19, 21]. In the *Lymnaea* CNS more than 500 central neurons were found to receive inputs from the heart or pneumostome [21]. The distribution of the inputs from the osphradium presumably transferring information from the environment to the CNS was shown to overlap with the main elements of the cardio-respiratory network, with the result that the environmental signals can modify directly adaptive forms of behaviour or functions such as heart rate, respiration, locomotion, mating behaviour, escape from predators, etc. [6, 7, 9, 15, 18].

Although in semi-intact preparation of *Lymnaea* the firing pattern of the neurons varied considerably, responses to osphradial stimulation were recorded consistently. The results showed that the main units of central pattern generator receive inputs both from the visceral organs and the osphradium (Fig. 5). The central neurons RPaD1, RPeD1, VD1-4, IP3 and the members of the A-, I-, J-, K-clusters reacted with characteristic alterations in their firing pattern to chemical stimulation of the

osphradium being identifiable on the osphradial nerve, too. Both specific and variable responses were revealed on central neurons to the stimulation of the osphradium (Fig. 5).

The neurons VD1-3 receive sensory inputs from the osphradium and send efferent signals to the same organ (Fig. 6) behaving similarly to the multifunctional interneu-

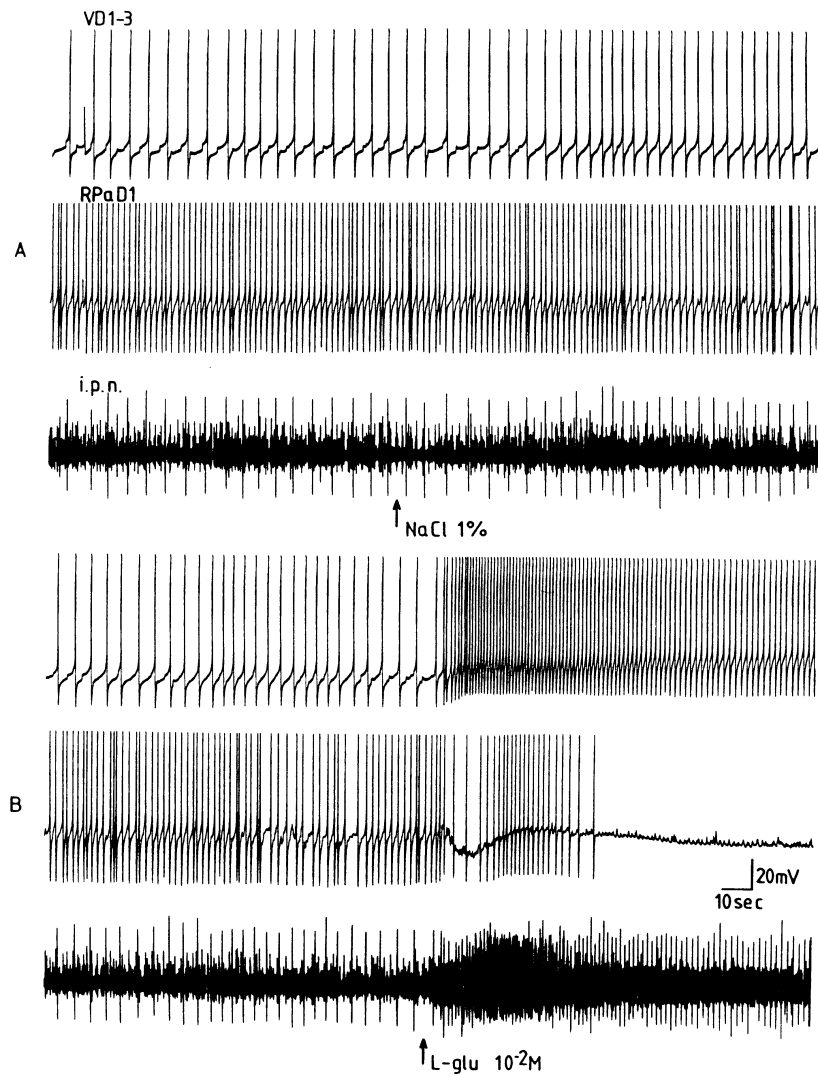


Fig. 5. Central representation of sensory information running to the neurons VD1-3 and RPaD1 from osphradium during application of NaCl (A) and L-glutamate (B) to its surface. The afferent impulsion running from the osphradium to the central neurons can be seen on the osphradial nerve (i.p.n.). The firing pattern of these neurons underwent more dramatic changes using L-glutamate as peripheral stimuli than that of the NaCl [14]

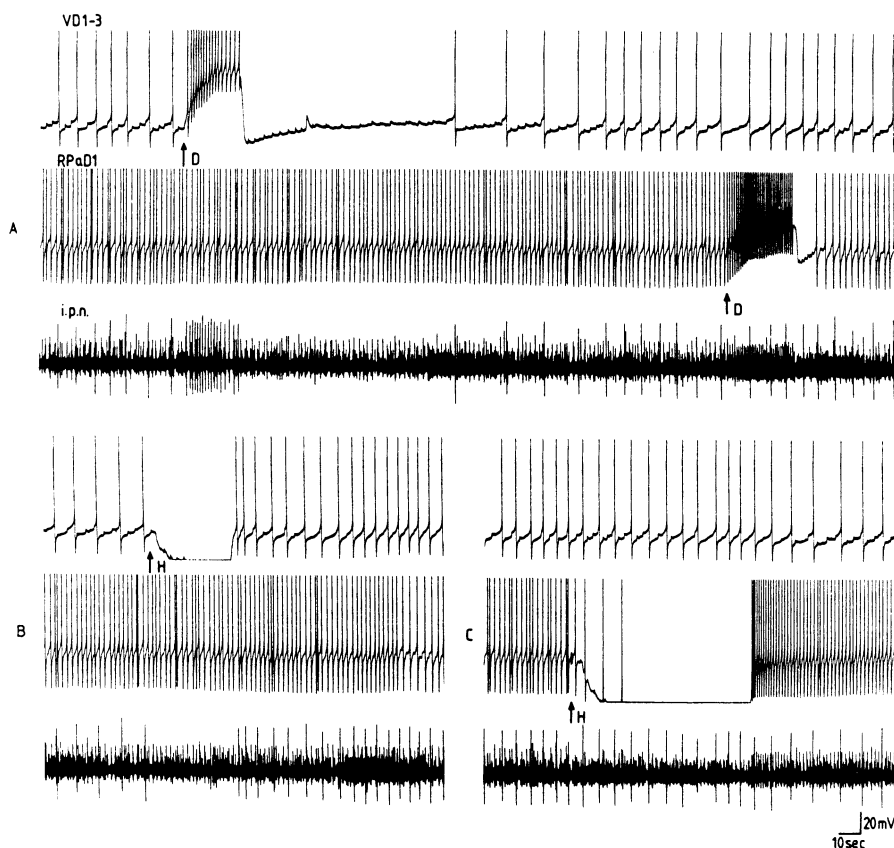


Fig. 6. Efferent signalisation running to the osphradium from central neurons VD1, and RPaD1 was revealed by de- or hyperpolarization of the soma membrane of the neurons. In firing pattern of the osphradial nerve the largest amplitude component was shown to originate from the neuron VD1 (A, B), while the middle amplitude signals originated from the neuron RaD1 [14]

ron V21 in *Helix* [10, 11]. The overlapping character of the neural networks regulating intero- and exteroception was found in both molluscan species used in these experiments.

The responses of the neurons were found to be different depending on the chemical stimuli applied to the osphradium. The responses of the neurons VD1-3 and RPaD1 were rather weak following application of NaCl to the osphradium (Fig. 5), while L-glutamate elicited a robust increase in the firing frequency of the neurons VD1-3, with simultaneous hyperpolarization leading to the blockade in the discharge of the neuron RPaD1 (Fig. 5). In the activity of the osphradial nerve, the afferent and efferent signals were clearly separated and related to the central neurons in question (Figs 5 and 6). Both de- or hyperpolarization of the soma membrane of the neurons VD1-3 altered the largest of the amplitude components of the nerve activity (Fig. 6).

Depolarization of the neurones VD1-3 led to an increase in the firing frequency of the largest component of the nerve activity (Fig. 6). At the same time, de- or hyperpolarization of the neuron RPeD1 left the largest component of nerve activity unchanged altering another, lower-amplitude component of nerve activity (Fig. 6).

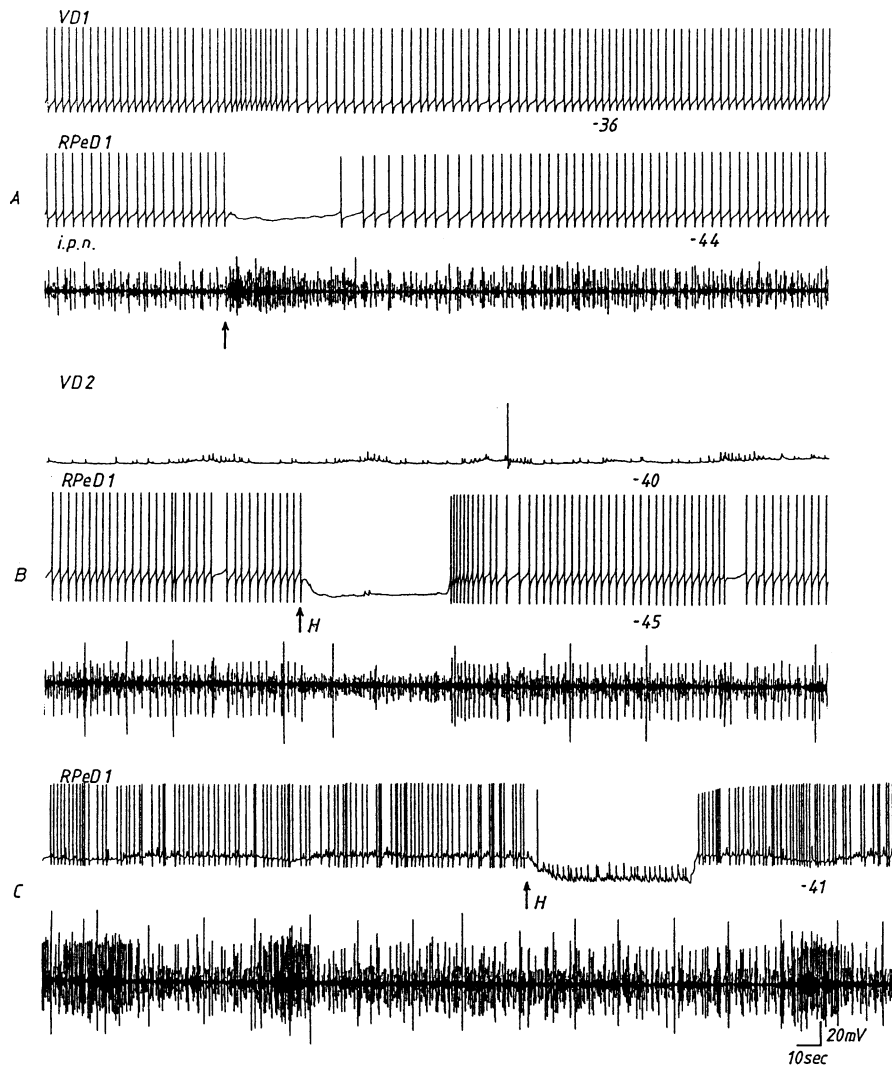


Fig. 7. Spontaneous variations in firing pattern and osphradial inputs on the neurons VD1 and RPeD1. A – osphradial inputs (arrow) to the neurons firing in tonic mode. B – activation of the interneuron IP3 traced on the neurons VD2 and RPeD1 modifying their firing pattern when their efferent pathways remained intact tested by hyperpolarization (arrow H). C – during phasic discharges of the neuron RPeD1 the efferent pathway was not identifiable in nerve activity but the activation of respiratory rhythm generator was seen

However, some of the central neurons proved to be multifunctional, involved both in afferent and efferent signalization. One such cell was the well-known neuron RPeD1.

Studying central representation of the osphradium it became evident that responses of the same neurons to the same stimulation of osphradium can highly vary or can even be absent depending on the simultaneous activation of a variety of inputs.

The relationship between the firing pattern of central neurons and input activation of intero- and exteroceptors

The variations in central representation of the osphradium in the *Lymnaea* CNS were reflected by the different responses of the same neurons to the same stimulation of the osphradium, which was either due to spontaneous changes in their firing pattern in response to the activation of some unknown inputs or to the effect of neurotransmitters applied to the CNS.

It can be seen on the activity patterns of the neurons VD1-RPeD1 that osphradial stimulation can activate the interneuron IP3 leading to the activation of the conjoint units of the central pattern generator appearing both in the activity of the neuron RPeD1 and osphradial nerve (Fig. 7). However, burst-type firing of central neurons

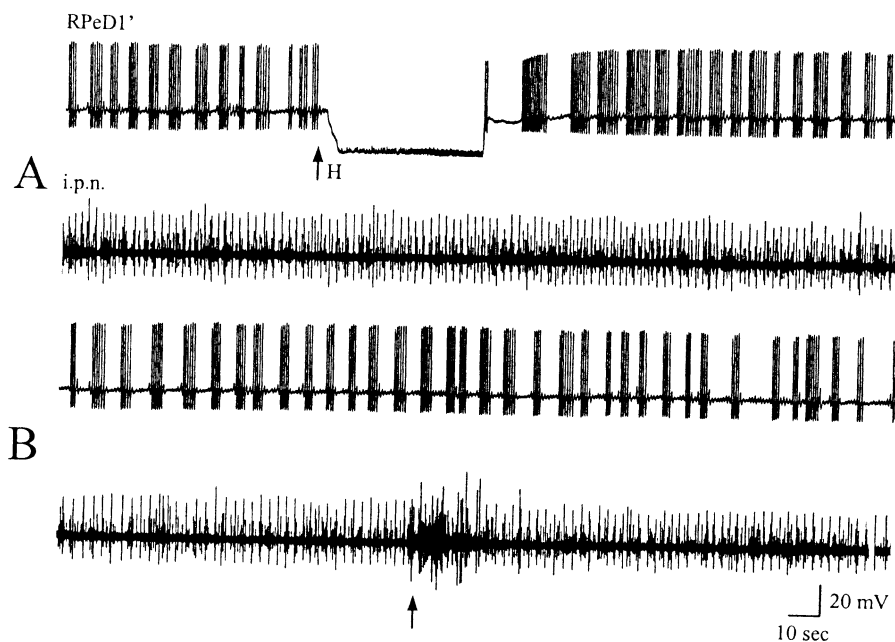


Fig. 8. Variability in the central representation of osphradium and the efferent signalization of its target neuron. During ongoing bursting discharges the neuron RPeD1 was separated from the neural network and both its efferent (A) and afferent (B) pathways were inactivated

can prevent the receiving of sensory information from the osphradium with simultaneous generation of some irregular oscillation in response to osphradial stimulation. The application of neurotransmitters (GABA, 5HT, etc.) to the CNS elicited a long-lasting activation of respiratory pumping (Fig. 8) accompanied by a bursting pattern of the neuron RPeD1 resulting in insensitivity to the osphradial inputs. The sensory information from the osphradium can be interrupted also on the other target neurons if they generated long-lasting respiratory central pattern activity (Fig. 9).

This variability in responses to sensory information can be a consequence of the permanently altering environment, e.g. the presence of combination of signal molecules in the synaptic area or in the vicinity of the neuron modulating their sensitivi-

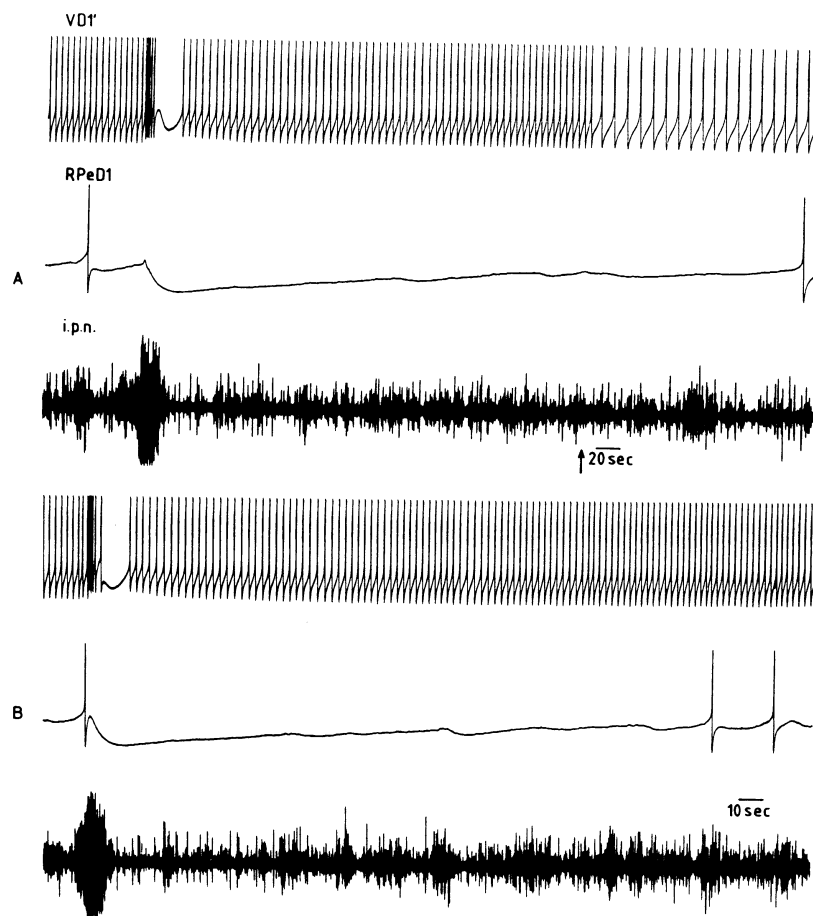


Fig. 9. Insensitivity of the neurons VD1 and RPeD1 to sensory inputs of osphradium (A, arrow) during activation of respiratory central pattern generator. The central pattern generator was activated by GABA application to the CNS

ty [12]. The oscillation and pattern alterations proved to be the main indicators and factors in sensory perception and neural circuit reconstruction in the molluscan CNS [13, 14].

DISCUSSION

According to prevailing theory, in the process of perception different sensory modalities are considered to be located to different brain areas and operating independently from each other. However, the studies on invertebrates challenged this view suggesting that cross-modal interactions are rather the rule and not the exception in perception [17]. Recently, the latter theory has been questioned also on the vertebrates, since it was shown that in mammals the cortical pathways previously thought to be sensory-specific are modulated by signals from other modalities [17].

Semi-intact preparations, developed from gastropod molluscs, contributed considerably to an understanding of multisensory interactions at the cellular, neural network and behavioural levels [4, 5, 7, 9, 11, 15, 21]. Furthermore, the results obtained on molluscs can serve as models of perception at cellular and circuit levels, being mainly the subject of mammalian physiology.

The results demonstrated that central representation of intero- and exteroceptors of visceral organs and osphradium is distributed throughout the CNS of the two molluscan species studied. Further on, a large number of central neurons receive information from different receptors and visceral organs and respond with varying responses to sensory signals. As the sensory information is transmitted to a large number of central neurons [11, 21] it can modify the reaction of the whole nervous system and contribute to the selection of information of vital importance according to the homeostatic need of the organisms.

For selection of sensory information an alteration in firing pattern can be a candidate (Figs 7 and 8). Studying either the visceral organ or osphradium it became evident that the sensory information is eliminated when the central neurons display bursting pattern (Fig. 8). However, the patterns of central neurons are modified permanently due to activation of various synapses resulting in a mosaic-like representation of the sensory information at the circuit level [12–14] leading to reorganization of the network corresponding to the need of the given behaviour. In functioning of the network it is important that adaptation of neurons to a changing environment and homeostasis could assure their ability to discriminate between incoming stimuli and to form relevant messages to elicit a corresponding function or behaviour.

In *Lymnaea*, oxygen sensitive receptors were demonstrated in the lung cavity [3, 4, 18] and since the interneuron RPeD1 was found to ramify to blood vessels supplying the lung area, it was suggested that this neuron can be activated by a decrease in oxygen content in the blood switching the respiratory cycle [19, 21]. Our results indicate that the neurons including RPeD1 can directly react to the alterations of the environment with the aid of osphradial receptors sensing the changes in water contamination and oxygen tension, adapting in this way the regulation of the cardio-respiratory and genital system to the momentary need of the organism. This means that

the respiratory cycle of *Lymnaea* can be inhibited by RPeD1 as an answer to environmental changes transferred from osphradium to CNS and, likewise, one behaviour can dominate over others depending on the neural circuits activated [9, 15, 21, 22] and reflecting the sensory information.

The variability in central representation of intero- and exteroceptors found in our studies can be regarded as a model of motivation at cellular level (Figs 5 and 6). Recently, in the crayfish rapid alteration in heart and ventilatory activities evoked by environmental disturbances were demonstrated [16] reflecting the internal status of the animal. Schapker et al. [16] use the above reactions as a sensitive indicator of an animal's perception of the changes in its immediate surroundings providing information on the duration of an altered internal state of animals. Although they failed to determine the transfer and central target of these changes they suggest an analogy with the regulatory role of the vertebrate autonomous nervous system.

In *Lymnaea*, the hypoxia-induced activity was recently explained also by peripheral perception, differing considerably from the previous explanations [2, 8]. Our results proved that in *Helix* and *Lymnaea* the multifunctional interneurons which are involved in the regulation of a wide variety of physiological functions and behaviour receive constant sensory information from their external and internal surroundings [6, 7]. This sensory information can lead to the "perception of self" and motivated state in every moment of information processing which will determine the involvement of the given neuron in particular regulatory circuits [14]. In both of the studied species the information conveyed from visceral organs to the CNS has a decisive role in the normal regulation of vital functions. In *Lymnaea*, the peripheral stimuli originating both from the osphradium and visceral organs were shown to be sources for driving the respiration by the neuron RPeD1, while in *Helix* sensory inputs from visceral organs modulated and regulated the firing pattern of central neurons [14]. The osphradium is a multisensory peripheral organ perceiving all the chemical and osmotic changes in its surroundings and transferring sensory information to a number of central neurons, including RPeD1. Our results proved that environmental changes directly affect heart activity, respiration, etc. as this information is transferred by sensory stimuli to the central neurons regulating various forms of behaviour [8, 9, 15, 21, 22]. However, as it was demonstrated, sensory information originating either from visceral organs or the osphradium is distributed to a large number of central neurons and the population of the neurons can store this information until the regulatory neuron (e.g. RPeD1) is prevented from receiving sensory information due to its ongoing bursting pattern (Fig. 8). This analogy to motivational state could be analyzed at cellular level in this simple system. This system is a useful model also for studying reorganizing neural circuits [12, 13].

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