

THE HETEROGENIC CHEMICAL SENSITIVITY OF THE CENTRAL NEURONES OF *LYMNAEA STAGNALIS* L.

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In the past years it has been demonstrated, that there are different chemical receptors on the membrane of the nerve cells. A particularly important role has been attributed to receptors playing part in the effect of the mediator substances. In general, the transmitters release from the presynaptic endings and act on the postsynaptic membrane, however, they can also directly influence the excitability of the soma and spontaneous firing of the neurone. A great part of the results related to this question has been obtained on CNS of Mollusca, where the readily accessible giant neurons make possible the intracellular recording and the direct application of drugs to the surface of the cell membrane.

The ACh is the most extensively studied active matter, the transmitter role of which has been demonstrated also with electrophysiological methods in the CNS of some Mollusca (KÉRKUT and THOMAS, 1963; CHIARANDINI et al. 1967; TAUC and GERSCHENFELD, 1960; ZEIMAL and VULFIUS, 1968). In recent years the possible transmitter role of 5-HT has been examined by a number of investigators and on the basis of their data in several molluscan species 5-HT can be regarded as a neurotransmitter substance (KÉRKUT and COTTRELL, 1963; GERSCHENFELD and STEFANI, 1966).

In addition to the above two matters a great number of chemicals has been tested on the neurones of invertebrates. Among these dopamine (GERSCHENFELD and TAUC, 1964) and several amino-acids (GERSCHENFELD and LASANSKY, 1964; SALÁNKI, 1968) are considered to be possible transmitter agents, but their mediator function has not yet been made certain.

It has been demonstrated, that the soma of a neurone can be sensitive to several kind of mediator substances. This fact has led a number of authors to classify the neurones in pharmacological categories on the basis of the effect of different drugs (TAUC and GERSCHENFELD, 1962; GERSCHENFELD and TAUC, 1964; TAUC, 1966). The typifying is based on the data obtained on *Aplysia* and *Helix* species. The chemical sensitivity of the giant neurones located in CNS of *Lymnaea stagnalis* was studied by a few investigators only. On this species the mediator function of ACh was demonstrated by ZEIMAL and VULFIUS (1968) and it was revealed that neurones can be classified into types D and H. The CNS of *Lymnaea stagnalis* has a significant activity of cholinesterase enzyme (VARANKA, 1968) supporting the mediator role of ACh.

In the cerebral ganglia biogenic monoamines were found and their localization histochemically was investigated (SAKHAROV and ZS.-NAGY, 1968).

The effect of L-glutamate was also tested on the neuronal activity and this amino-acid was effective on the D type cells only (SALÁNKI, 1968).

However, it was not yet investigated, how the drugs, others than ACh, being effective in other Mollusca, influence the activity of the giant neurones of *Lymnaea stagnalis*. Information is poor about the correlation between the chemical sensitivity and type of the neuronal activity, as well as about the problem whether or not the cells having identic localization and activity possess the same chemical sensitivity in different preparations.

Our aim was 1) to investigate the effect of ACh, 5-HT, dopamine and noradrenaline on the membrane potential and spontaneous activity of the central neurones of *Lymnaea stagnalis* and to classify the cells on the basis of these effects.

2) to clear up, whether there is any correlation between the chemical sensitivity and the type of the activity.

Material and method

Examinations were conducted on the abdominal and right parietal ganglia of CNS of *Lymnaea stagnalis*. The isolated ganglion ring was fixed in appropriate orientation by means of the surrounding connective tissue and nerves. The thick connective tissue was removed from the dorsal surface of the ganglion and so the cells became fairly visible through the thin tissue located under the thick one. The preparations were then placed in a chamber containing 3 ml saline (JULLIEN and RIPPLINGER (1948).

The experiments were conducted partly on the earlier identified neurones (SALÁNKI and KISS, 1969) partly on some recently identified ones (*Fig. 1*).

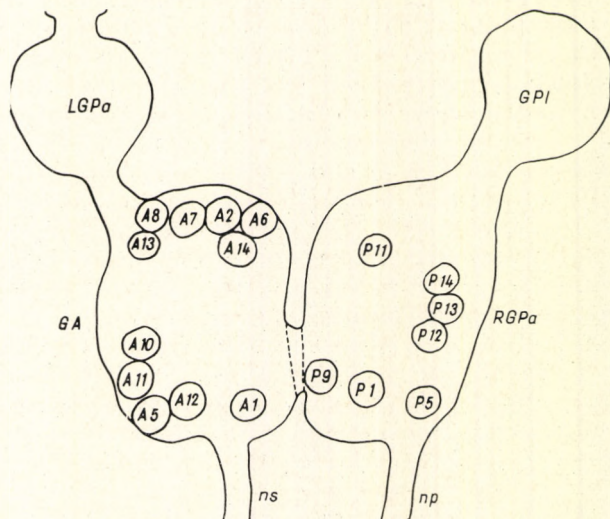


Fig. 1. Localization of the identified neurones

Membrane and action potentials were recorded by means of glass microelectrodes filled with 2.5 M KCl. Resistance of the electrodes ranged between 5 and 10 Mohm. The electrode was connected with a DISA negative capacitance high input impedance amplifier, or a FET negative capacitance high input impedance amplifier (VÉRÓ, 1971). During the experiments the signals were fixed on a magnetic tape and the desired portions were photographed later by means of a DISA Universal Indicator and photorecorder. In the case of the experiments, when the membrane potential was artificially shifted, the connection to the amplifier was made by inserting a bridge circuit.

The chemicals to be tested were added to the bath from a capillar of 0.7 mm diameter filled with 10^{-1} – 10^{-3} M solution of the drugs. After recording the control activity the substances were added instantaneously to the vicinity of the surface of the ganglion. Following this, the preparation was thoroughly washed as long as the control activity restored. On the same cell 2–4 drugs were tested depending on the condition of the cell. In the present experiments the following chemicals were used: Acetylcholine-chlorid (Sigma), Serotonin-creatininsulfat (Sandoz), 3-hydroxy-tyramine-HCl, dopamine (Sigma), L-Noradrenaline-bitartarat (Serva).

Results

1. Effect of ACh

All of the 18 examined neurones were sensitive to ACh. However, in a part of the experiments the ACh was ineffective on some of these cells. On the basis of the type of the ACh-effect the neurones can be classified into three groups:

a) The ACh-effect results in depolarization. This was connected in most of the cases with an increase of the firing rate (*Fig. 2a*). We could find 9 neurones of this type, 6 of these were located in the abdominal, 3 in the right parietal ganglion. A1, A2, A5, A10 and P1 cells have been described earlier, while the A12, A13, P12 and P14 were indentified recently. In addition to the identified neurones, a lot of others of small diameter can be classified into this category. Most of the cells belonging to this group are pacemakers having a regular spontaneous activity, however, there are in this group some cells with other type of activity, too. P14, and A2 as well as several non-identified neurones have synaptically driven activity with low frequency, moreover, the A2 cell in most of the cases was silent (*Fig. 2b*). The effect of ACh can be characterized by a short-time reaction and fast restoration. The latter occurs in most of the cases without any washing. In the case of some cells after the marked depolarization and increase of the firing rate a secondary inhibition can be observed following the restoration of the resting potential. The neurone A13 located in the abdominal ganglion has a special characteristic. This pacemaker neurone having no synaptic input responds to ACh with depolarization of several mV and at the same time the spontaneous activity disappears (*Fig. 2d*).

b) The ACh-effect results in hyperpolarization and inhibition of the activity (*Fig. 2c*). Three cells of this type are located in the parietal ganglion: the P5 cell and two other cells identified recently. On these cells the ACh-effect was prolonged and the control activity could restore only after long washing.

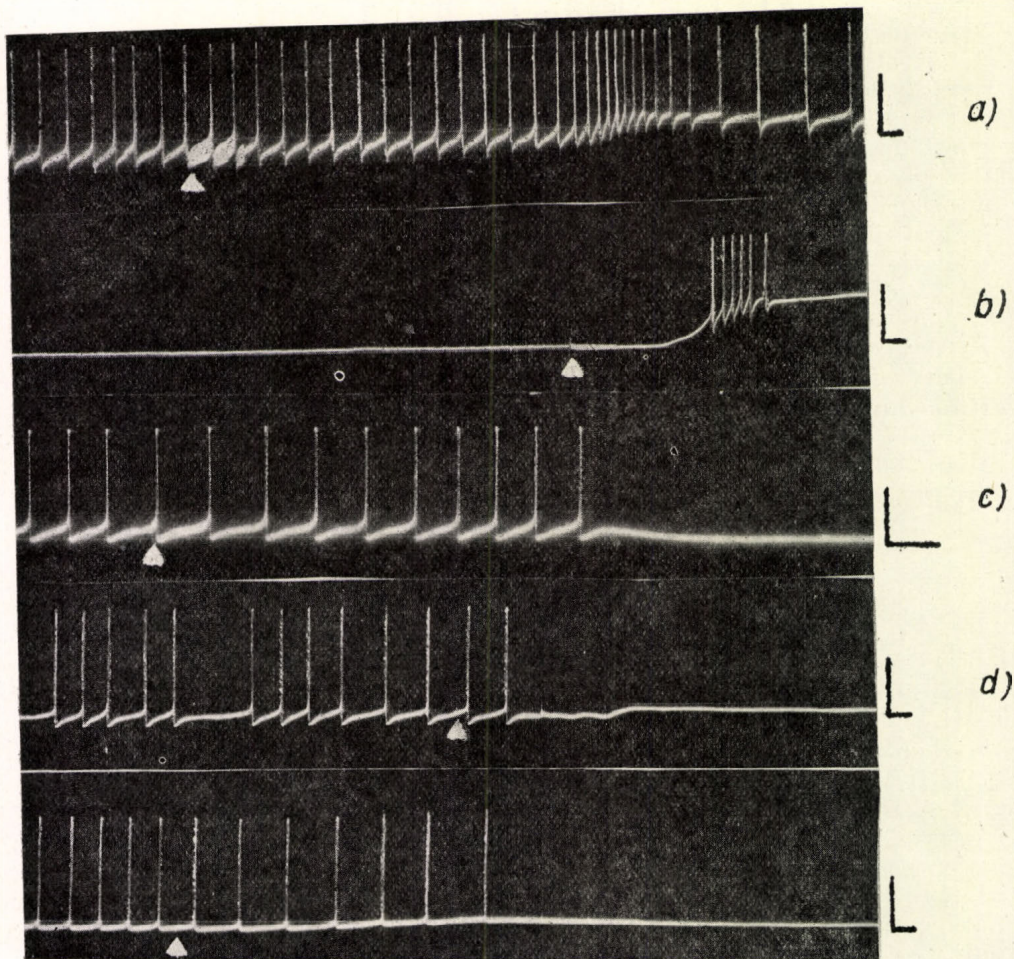


Fig. 2. Effect of ACh (Arrow marks the application of ACh)
 a) Effect depolarizing the membrane and facilitating the activity on neurone A5
 b) Activating effect on silent neurone A2
 c) Hyperpolarization and inhibition on neurone P5
 d) The special reaction of cell A13: depolarization and at the same time inhibition of spontaneous activity from two different preparations. Calibration 50 mV, 1sec.

c) Neurones belonging to this category cannot be classified either in D, or in H cells on the basis of their reaction given to ACh. Difficulty of the classification consists in the different effects of ACh caused on the identical cells of different preparations. The cells A6, A7 and A8 described in our earlier paper as well as the cells A11 and A14 identified recently belong to this category. In respect of their external appearance, these are neurones of most considerable size and they can be very clearly identified both visually and by their activity. All of them are located in the abdominal ganglion, four of them are in the vicinity of the connective between the left parietal and abdominal ganglion. The cells A6 and A14 were silent in most of the experiments. The

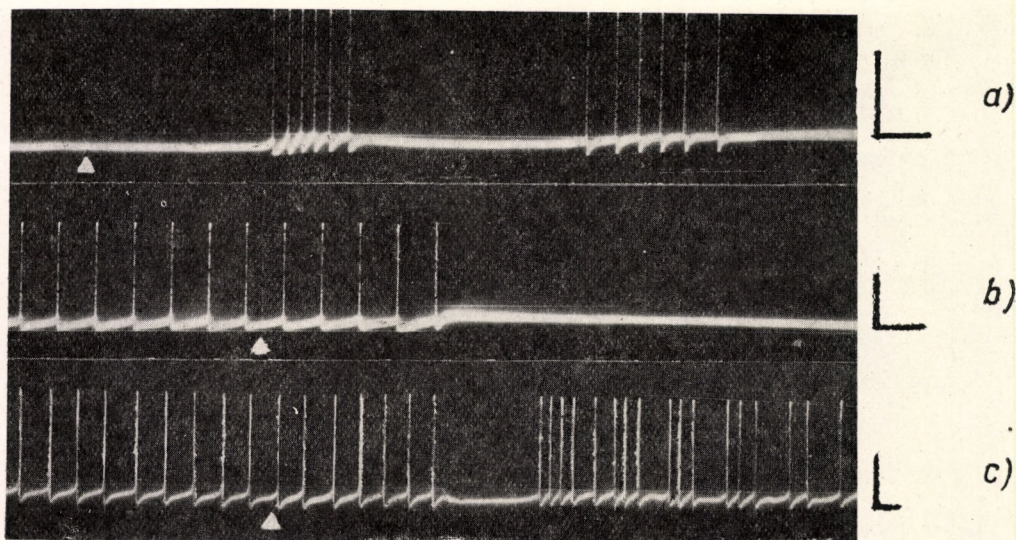


Fig. 3. Reactions to ACh of the neurones unclassifiable into typical D or H cells. (Arrow marks the application of ACh) Calibration: 50 mV, 1sec.

- a) ACh activates silent neurone A6
- b) ACh causes inhibition in the case of activity of high frequency
- c) Biphasic reaction given to ACh

A11 is a pacemaker with synaptic input being always active. The A7 and A8 look like oscillating neurones, however, as it was demonstrated earlier, they are in fact synaptically driven (SALÁNKI and KISS, 1969). About the reactions of these neurones one can tell at first approximation, that in general they respond to ACh with an excitatory effect when they are silent, or their firing rate is less than 1 cps and have a high membrane potential (Fig. 3a). However, if the frequency of their spontaneous firing is more than 1 cps, the ACh-effect results in inhibition (Fig. 3b). Further specific feature characterizing these neurones is that both the ACh and other investigated drugs cause frequently a biphasic reaction consisting of inhibition and excitation (Fig. 3c).

In one part of the cases the membrane potential of these neurones was higher, than the average value (40 mV), and the occasional high-frequency of their activity was connected with the depolarized condition of the membrane. Without any experimental intervention such a depolarization may be established by injury or by unusually strong synaptic bombardment. It was supposed that the variable effect of ACh is associated with the actual level of the membrane potential. To elucidate this problem the reactions caused by ACh were investigated at different levels of the membrane potential. It was found that at the artificially polarized levels the ACh-effect differed from that registered without polarization.

I. If the ACh causes an excitatory effect at the resting potential level, the direction of the reaction changes under the influence of a 30 mV depolarization, i.e. inhibition occurred (Fig. 4a).

II. If the ACh causes an inhibitory effect at the resting potential level, then under hyperpolarized conditions its effect results in 10–20 mV depolar-

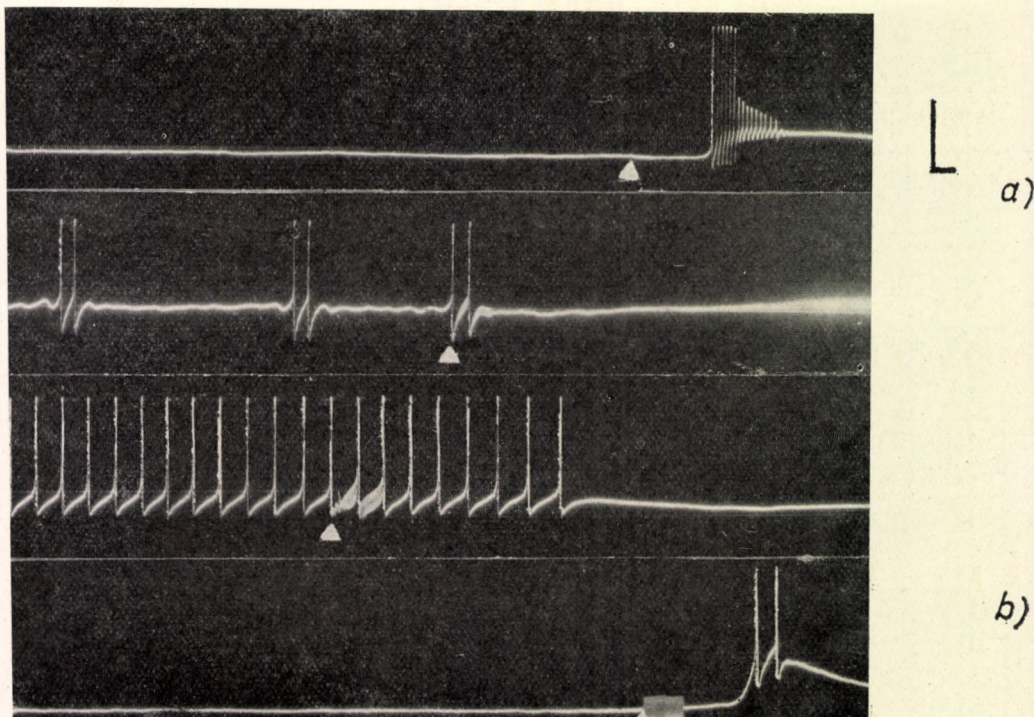


Fig. 4. Effect of ACh at different membrane potential levels on the same neurone. (Arrow marks the application of ACh) Calibration: 50 mV, 1sec

a) At the resting potential level ACh causes excitatory effect, the direction of the reaction changes under the influence of a 30 mV depolarization

b) At the resting potential level the effect of ACh results in inhibition, but it causes excitation under the influence of a 20 mV hyperpolarization

ization, leading in certain cases to the appearance of a series of spikes (*Fig. 4b*).

III. Alteration of the membrane potential influences also the biphasic reactions inasmuch as an appropriate level exists, at which only one of the phases remains.

2. Effect of 5-HT

5-HT causes a marked depolarization on the majority of the investigated cells, as well as increases the firing rate, or elicits a spike train if the cells performed no activity before (*Fig. 5a*). In single cases there was no reaction on the cell A1, while on the neurones reacted variably to ACh, in a number of the cases the 5-HT had a biphasic effect consisting of inhibition and excitation (*Fig. 5b*).

Only a single neurone was inhibited by 5-HT: it was the cell P11 located in the right parietal ganglion (*Fig. 5c*).

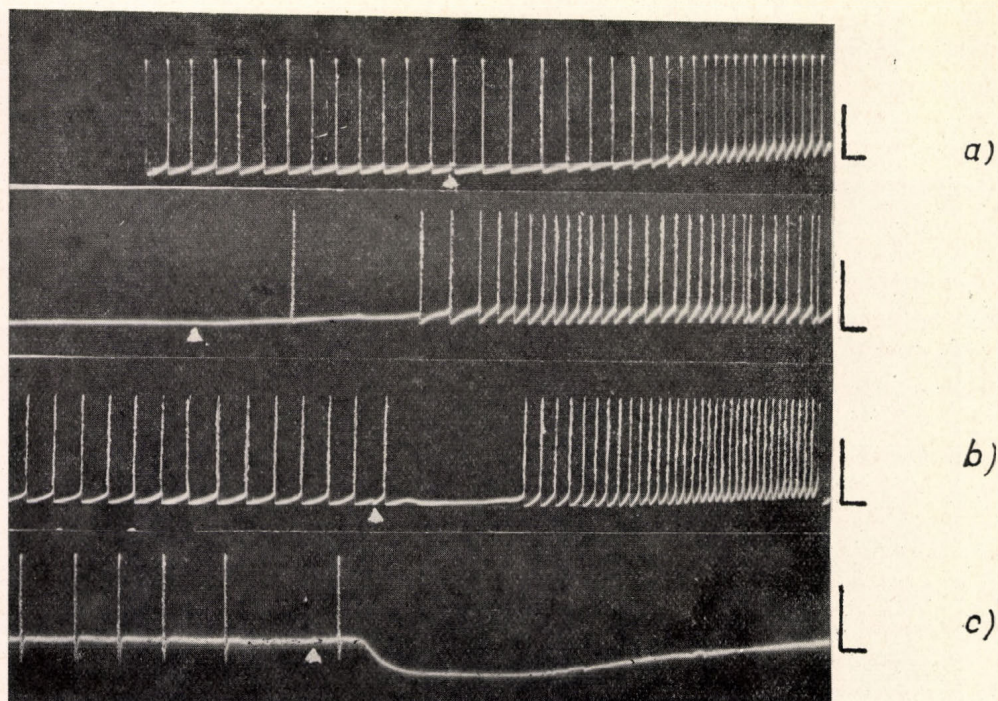


Fig. 5. Effect of 5-HT (Arrow marks the application of 5-HT) Calibration: 50 mV, 1sec
a) Increase in the frequency of spontaneous activity following the application of 5-HT and activation of a silent neurone
b) Biphasic reaction caused by 5-HT. There is a short inhibitory period followed by excitation
c) 5-HT causes hyperpolarization of the membrane potential and inhibition of the activity

3. Effect of catecholamines

Dopamine

There was only one neurone in all of the preparations the activity of which was stimulated by dopamine. It was the cell A11 located in the abdominal ganglion. On three other neurones marked as A2, A5 and A6 in single cases also excitatory effects were observed. (*Fig. 6b*). On cells A10, A1 and P11 hyperpolarization of the membrane potential accompanied by an inhibition of the activity takes place following the application of dopamine. In the case of neurone A10 this inhibition realizes as a long-lasting hyperpolarization (ILD) while on the latter two cells it is established by IPSP-s (*Fig. 6c*).

Noradrenaline

Excitatory effect produced by noradrenaline (*Fig. 6a*) could be observed on every neurone except cell A14, but there was no cell found whose activity would have been influenced by noradrenaline on every preparation.

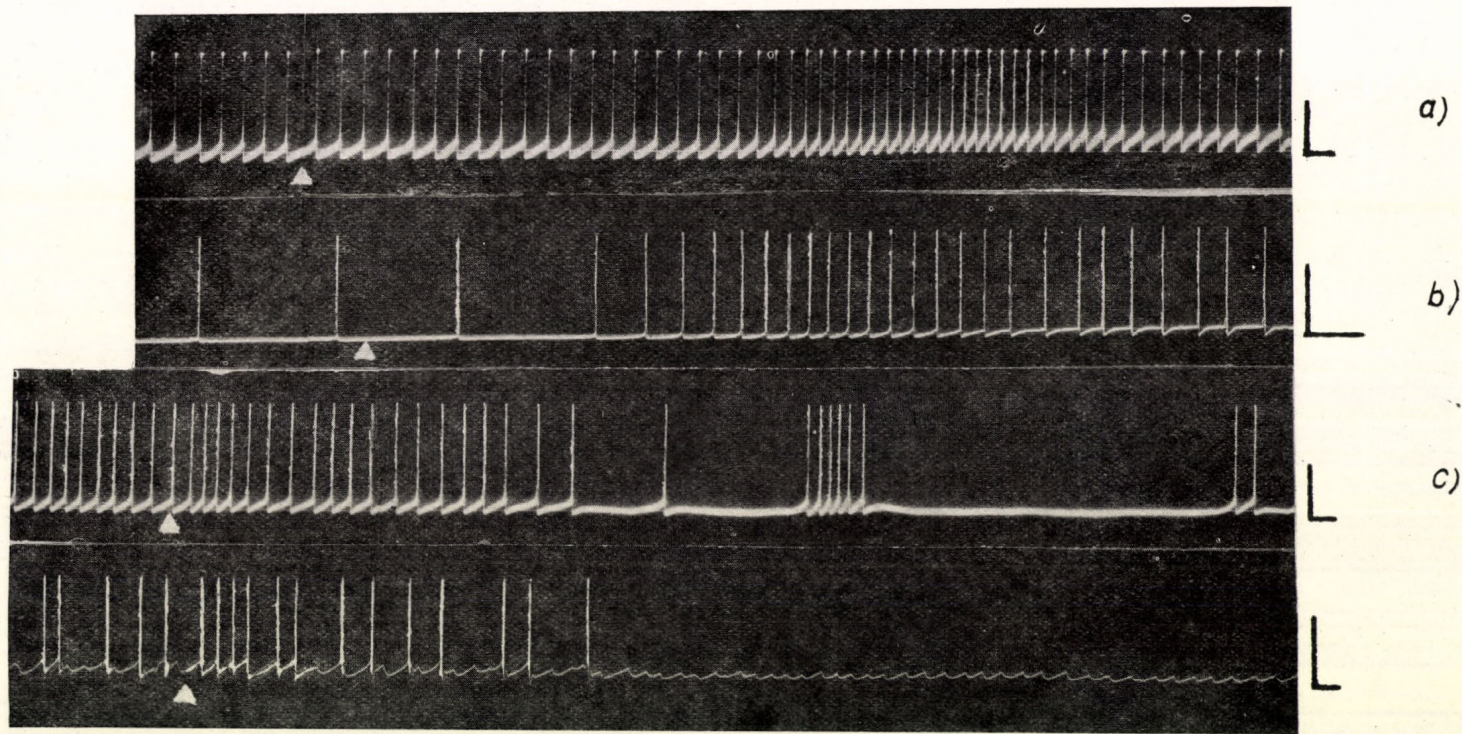


Fig. 6. Effect of catecholamines (Arrow marks the application of drugs)

a) Excitatory effect of noradrenaline

b) Excitation caused by dopamine

c) Inhibitory reactions given to dopamine

upper — ILD (CILDA cell) lower — IPSP-s (DInhi cell)

Calibration: 50 mV, 1sec.

Discussion

The establishment of the pharmacological categories described in the literature was made on the basis of the effect of ACh, 5-HT and dopamine. Beside these drugs noradrenaline was also tested by some authors (KERKUT and WALKER, 1961; GLAIZNER, 1968).

A considerable heterogeneity in the chemical sensitivity of different neurones and a great variety of the combination between the effects of different mediator substances were observed by GLAIZNER (1968) and WILGENBURG (1970).

The present results support the data of the latter authors, as we also have found a great variability in the sensitivity of the different identified neurones (*Table I*). Nevertheless, a variability can be found not only in this respect, but also the reaction of identical neurons located in different preparations were not always the same (*Table II*). In spite of these facts it is possible to

TABLE I

The more frequently occurring combinations of drug-effects in the different pharmacological categories.

	D				H			CILDA and DInhi		Other
Acetylcholine	+	+	+	+	-	-	-	+	+	0
5-hydroxytryptamine	+	+	0	+	0	+	0	+	+	-
Dopamine	0	0	+	+	0	0	+	-	-	-
Noradrenaline	0	+	0	+	+	0	0	+	0	0

TABLE II

The variability of the effect of the investigated chemicals on different preparations in the case of two identified neurones.

	A5						A6											
Acetylcholine	+	+	+	+	+	+	-	-	0	-	+	+	+	+	+	-	-	+
5-hydroxytryptamine	+	+	0	+	0	0	+	+	+	+	+	0	+	0	+	+	+	
Dopamine	0	+	0	0	+	+	0	+	0	+	0	+	0	+	0	+	0	
Noradrenaline	0	+	+	0	0	0	0	+	+	0	0	0	0	+	0	+	0	

+ = excitation

- = inhibition

0 = uneffectiveness

classify the neurones including also that of *Lymnaea stagnalis* in the known pharmacological types (*Fig. 7*). This is as follows:

1. D-cells (TAUC and GERSCHENFELD, 1962).

ACh causes depolarization of the membrane potential as well as increases their firing rate. D-cells have no inhibitory synaptic input. These criteria were found to be valid for cells A2, A5, A12, P1, P12 and P14. On the basis of the depolarization caused by ACh also cell A13 must be classified into this group in spite of the inhibition of its activity observed at the same time.

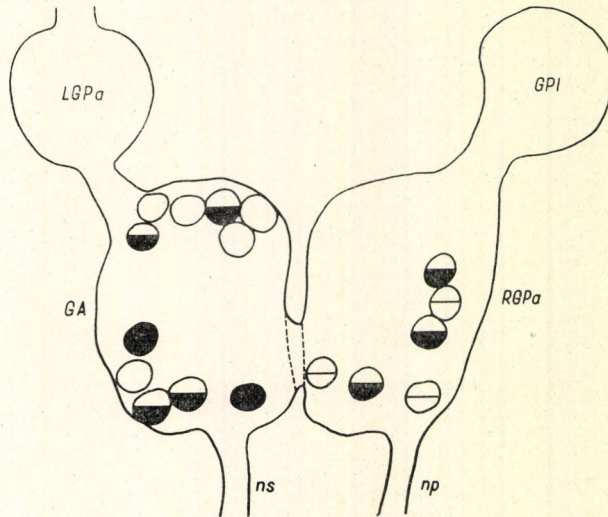


Fig. 7. The topography of the identified neurones distinguished on the basis of their chemical sensitivity full circles: CILDA and Dlnhi cell, half empty circles: D-cells, empty circles with line: H-cells, empty circles: cells with variable effect

2. *H-cells* (TAUC and GERSCHENFELD, 1962).

These cells can be characterized by hyperpolarization of the membrane potential as well as by an inhibition of their activity caused by ACh. It has been described that the membrane of the H-cells was particularly sensitive to dopamine considered as the excitatory, mediator substance of these neurones (GERSCHENFELD and TAUC, 1964). In the present investigations the inhibitory effect of ACh was not always connected with an excitatory effect caused by dopamine, but in a lot of the cases 5-HT or noradrenaline appeared to be excitatory substances. A similar result has been obtained on *Helix aspersa* by GLAIZNER (1968), and on *Helix pomatia* by WILGENBURG (1970).

3. *CILDA-cells* (GERSCHENFELD and TAUC, 1964).

Only one cell showed the properties characteristic for this group, it was cell A10. This is a pacemaker cell with synaptic input, which has from time to time long-lasting inhibition (ILD). The ILD can be elicited by the application of dopamine. At the same time the effect of ACh results in depolarization of the membrane potential and in the increase of firing rate, so this cell can be regarded as one of DILDA. Its activity can be stimulated also by 5-HT regarded by GERSCHENFELD and STEFANI as an excitatory mediator substance exclusively of the neurones belonging to this group (GERSCHENFELD and STEFANI, 1966). However, our results do not support the latter conclusion, because in the present investigations the 5-HT was effective on the majority of the neurones. A similar result was obtained on *Helix aspersa* by GLAIZNER (1968).

4. *Dlnhi-cells* (TAUC, 1966).

The cell A1 belonging to this group differs from the CILDA neurones only in one respect; the inhibition caused by dopamine is not realized as ILD, but as IPSP-s.

Six cells could not be classified into any of the above categories. In the case of cell A11 we could not find any excitatory mediator substance among the investigated drugs. The other five neurones could not be regarded as typical D or H cells because of their variable effect to ACh.

The chemical sensitivity of D and H cells has no relationship with their localization and type of activity, similarly, as it was found on *Helix pomatia* (SAKHAROV and SALÁNKI, 1969). Cells belonging to this two groups may be both pacemakers and synaptically driven neurones, and situate quite scatteredly. In the cases of CILDA type cells the correlation between the chemical sensitivity and the type of activity may be derived from the definition of this category. The neurones given variable reaction to ACh appeared to have the most constant localization and type of activity. These cells are gigantic, located close each to one another, and they belong to the driven neurones. Cell A11 is an exception, it is situated in the neighbourhood and having similar activity to the neurones A10 and A1.

According to the literature, the majority of the molluscan neurones are sensitive to ACh. However, there have been described on every investigated species cells, on the membrane of which this generally occurring mediator substance was ineffective. ZEIMAL and VULFIUS, (1968) examined the effect of ACh on *Lymnaea stagnalis* and they failed to obtain any reaction in 50 per cent of the neurones. In contrast with their findings we have found no cell insensitive to ACh. The reason for this fact presumably is that in the present experiments less neurones were investigated, but all they were well identified. The above mentioned authors worked on unidentified neurones, located partly in the deeper regions of the ganglia. In such conditions the ineffectiveness of the ACh in one experiment does not refer to a neurone being characteristically insensitive to ACh, as the ACh-sensitivity can be variable in the same cell. On the other hand, the above mentioned authors applied the ACh solution by perfusion, and according to our experience — presumably just because of the desensitization (ZEIMAL and VULFIUS, 1968) — using such a method much slighter effects can be obtained than using our method. Probably it is also connected with this problem, that while all the silent neurones have been regarded by ZEIMAL and VULFIUS insensitive to ACh in our experiments these cells often showed not only depolarization, but activation following the application of ACh.

On the basis of the results obtained by the examination of drug-effects at different membrane potential levels there is a reason to assume, that the responses given to ACh of those neurones, which cannot be classified as typical D or H cells, have a close relationship with the ACh equilibrium potential. It was demonstrated (CHIARANDINI and GERSCHENFELD, 1967; CHIARANDINI et al. 1967) that in the cases of both D and H cells a special value of the membrane potential could be estimated (E_{ACh}). If the membrane potential level is lower than this value, the direction of the reaction given to ACh changes from depolarization to hyperpolarization and conversely. Considering this fact the behaviour of these neurones can be explained as follows: either the membrane potential of the cells may alter in such an interval within which there is the E_{ACh} or the E_{ACh} itself may be variable. The first assumption is supported by the fact, that in our investigations the membrane potentials of the cells ranged between 30 and 60 mV, and most of the cells gave a response of D-type to ACh. On the D-cells of *Cryptomphallus aspersa* about 30 mV

E_{ACh} was measured (CHIARANDINI et al. 1967). On the other hand, it is an argument against this assumption, that on some other neurones also having a variable membrane potential the same reaction was obtained in each case. Also the role of the synaptic input cannot be negligible, as all the neurones being under discussion are synaptically driven cells. It may be supposed too, that in one case the synaptic input, another time directly the soma membrane is influenced by the applied drug. To confirm one of the above mentioned assumption further investigations are required.

Summarizing the effect of the examined drugs we are of the opinion that the ACh and 5-HT play the most important role in the CNS of *Lymnaea stagnalis*. The former matter seems to have a fundamental role in the functioning of the neurones exhibiting complex activity and connected with integrative functions, while the latter may be regarded, as the most important excitatory mediator in this species. It appears, that the 5-HT plays a more significant role in *Lymnaea stagnalis* than in the other investigated Gastropoda. In the two *Helix* species only 50 per cent of the neurones were found to be sensitive to 5-HT. The existence of 5-HT in *Lymnaea stagnalis* has been demonstrated histochemically (SAKHAROV and ZS.-NAGY, 1968) and its synthesis has been proved biochemically (HIRIPI, 1970). Nevertheless, the mediator function of 5-HT can be made only probable as long as the effects of its antagonists have not been examined. The dopamine and noradrenaline can be regarded, as less effective drugs. They cause reaction on less neurones than the ACh and 5-HT. According to our results the effect of the catecholamines has no close relationship with the reactions given to ACh and 5-HT, with the exception of the CILDA neurones. Dopamine plays a more important role defining a category in the case of two neurones, when it functions as an inhibitory mediator substance.

Comparing the number of the inhibitions and excitations caused by dopamine our results markedly differ from those obtained on *Helix aspersa* by GLAIZNER (1968). Following the application of dopamine as well as noradrenaline this author observed inhibitory reactions in most of the cases. We have found, that also in the case of dopamine the excitatory reactions are predominant and we have never obtained an inhibitory response given to noradrenaline.

Summary

The chemical sensitivity of some identified giant neurones located in the CNS of *Lymnaea stagnalis* was examined. Membrane and action potentials were recorded by means of intracellular microelectrodes. The ACh, 5-HT, dopamine and noradrenaline were added to the vicinity of the surface of ganglia from a capillar.

On the basis of the type of the effects of investigated drugs the neurones were classified into pharmacological categories. On the basis of the effect of ACh D and H cells were distinguished, however, there were unclassifiable neurones in these two groups. CILDA and DI_{inhi} cells were also found, which could be inhibited by dopamine.

It was demonstrated, that in the case of some neurones the effect of ACh had a relationship with the actual membrane potential level.

The cells showed a great heterogeneity with relation to their chemical sensitivity.

Furthermore, it was found that beside some analogy the effect of the investigated drugs markedly differs from that observed on other molluscs. It is suggested, that ACh and 5-HT have the most important function, as chemical mediator substances on *Lymnaea stagnalis*.

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LYMNAEA STAGNALIS L. KÖZPONTI NEURONJAINAK HETEROGÉN
KÉMIAI ÉRZÉKENYSÉGE

Kiss István és Salánki János

Összefoglalás

Lymnaea stagnalis központi idegrendszerében található identifikált óriás neuronok kémiai érzékenységét vizsgálták. A membrán és akciós potenciál elvezetése intracelluláris mikroelektrodával történt, az ACh-t, szerotonint, dopamint és noradrenalint kapillárisból applikálták a ganglion felszínére. A vizsgált anyagok hatáskombinációjának alapján a neuronokat farmakológiai kategóriákba sorolták. ACh hatása alapján D és H sejteket különböztettek meg, valamint olyan neuronokat, amelyek nem sorolhatók egyértelműen a két csoportba. CILDA és DINHI sejteket is találtak, amelyek dopaminnal gátolhatók.

Megállapítást nyert, hogy bizonyos sejteken az ACh hatása az aktuális membránpotenciál függvénye.

Az eredmények alapján a *Lymnaea* központi idegrendszerében található óriás sejtek nagyfokú heterogenitását állapították meg a kémiai érzékenység viszonylatában. Kimutatták továbbá azt, hogy bizonyos hasonlóságok mellett a vizsgált anyagok hatása erősen különbözik más puhatestű fajokon leírt irodalmi adatoktól. A szerzők szerint *Lymnaea*-n az ACh és a szerotonin játszhat legfontosabb szerepet a kémiai mediációban.