

**ON THE ROLE OF CHOLINERGIC, ADRENERGIC AND  
TRYPTAMINERGIC MECHANISMS IN THE REGULATION OF A  
“CATCH” MUSCLE (*ANODONTA CYGNEA* L.)**

JÁNOS SALÁNKI and ELEMÉR LÁBOS

*Biological Research Institute of the Hungarian Academy of Sciences, Tihany, Hungary*

Received: 21st February, 1969

The regulation of tonic and phasic activity in the “catch” muscles of Molluscs differs significantly from that found in smooth and skeletal muscles (HOYLE, 1964). Investigations on the chemical basis of regulation existing in this type of muscles being rather specific also in their structure (HANSON and LOWY, 1960; ZS.-NAGY and SALÁNKI, 1965; MILLMANN, 1967) were carried out mainly on the anterior byssus retractor muscle (ABRM) of *Mytilus* (see TWAROG, 1967) and on different Gastropoda preparations (KOSHTOYANTS, 1936; FÄNGE and MATTISSON, 1958; MINKER and KOLTAI, 1961; GREENBERG and JEGLA, 1963; JAEGER, 1964). There are data referring to the role of cholinergic, adrenergic and tryptaminergic mechanisms. In general acetylcholine (ACh) is considered as tonus-increasing, while serotonin (5HT) as tonus-inhibiting agent (FLOREY, 1967). At the same time usually no importance is attributed to the role of adrenergic mechanisms. In cases adrenergic substances were effective, their action was similar mostly to 5HT, in less of the cases to ACh (JAEGER, 1963; HOYLE, 1964; HILL, 1958; GREENBERG and JEGLA, 1963).

In contrary to the fact, that the adductor muscles of *Anodonta cygnea* are characteristic “catch” muscles, up to now direct pharmacological investigations were not carried out on them. The effects of sympathetic and parasympathetic drugs were tested on the whole animal by GEIGER (1929), while the response of the adductor after applying serotonin, adrenaline and ACh to the ganglia were investigated by SALÁNKI (1963) and PUPPI (1963a, b). The pharmacology of the non-definitive adductor of the larvae of *Anodonta* (glochidia) is known better (LÁBOS et al. 1964; LÁBOS, 1966).

The aim of our investigations was to answer the question, which of the main possible chemical mechanisms (cholinergic, adrenergic, tryptaminergic) may exist in the regulation of tonic and/or phasic activity of the adductors at the level of the muscle fibres, or in the neuromuscular transmission.

**Material and methods**

Investigations were carried out on the posterior adductor muscle of *Anodonta cygnea* L. The adductor was not isolated from the whole of the animal, but we made it mechanically independent of the anterior adductor. The



functioning of the muscle was registered on a kymograph; the upward movement of the lever indicated contraction (closing of the shells).

To render the muscle within reach, above the heart a part of the shell was abolished, and using subcutan needle drugs were injected directly into the middle of the posterior adductor. The volume of the solution varied between 0.2—0.5 ml. The substances were dissolved in physiological saline (MARCZYNSKI, 1959). In each animal also a control was made when only the physiological solution was injected.

In a number of the experiments the spontaneous activity of the adductor was registered and influenced. In other cases the answer of the adductor was evoked by an indirect way: either the cerebro-visceral connectives (CVC) were stimulated by square wave impulse series causing relaxation, or tonic contraction was caused by mechanical stimulation of the mantle as it was described earlier (SALÁNKI and LÁBOS, 1963). The parameters of the electrical stimulation were: 20 volts, 4 msec (duration of the impulse), 8 cps frequency and 30 or 60 sec (duration of the stimulation).

*The following drugs were used:* acetylcholine chloride (ACh) (Sandoz); nicotine-H-tartrate (BDH); atropine sulphate (Fluka); d-tubocurarine-HCl (dTC) (Schuchardt); hexamethonium iodide (Schuchardt); tetraethyl ammonium chloride (TEA) (BDH); tetramethyl ammonium bromide (TMA) (Fluka); eserine salicylate (Merck); neostigmine bromide (Merck); mytolon-HCl (Winthrop Ltd); L-adrenaline-D-H-tartrate (EGA); L-noradrenaline bitartrate (Serva); dopamine-HCl (Sigma); DL-isoproterenole-HCl (IPNA) (Fluka); dibenamine-HCl; dichloro-isoproterenole-HCl (DCI) (Eli et Co. Ltd); ergotamine-H-tartrate (BDH); bromo-d-lysergic acid diethylamide (BOL-148) (Sandoz); serotonin creatinine sulphate (5HT) (Sandoz).

The doses used refer to the whole of the compound (salts).

Each drug was tested at least five times.

## Results

In most of the cases the posterior adductor of *Anodonta* relaxes spontaneously after the preparation is ready. This spontaneous relaxation comes about comparatively faster and more frequently in summer than in winter time. We carried out experiments mainly on muscles in relaxed state. A part of the muscles having remained in tonic contraction after preparation relaxed after injection of the physiological saline, others showed relaxation only to the effect of drug-injection. Independent of treatment the muscles performed usually rhythmic contractions. The level of tonus was different taking each individually.

### 1. Control

Intramuscular injection of physiological saline caused the fast contraction of the adductor followed by an immediate relaxation. The length of the whole cycle has taken about 2—5 minutes. As this length of time is not constant, in every case a control was necessary. After the control injection the background activity usually did not change, in several cases, however, a temporary increase or decrease in the frequency was observed. This was taken into account in every case at the evaluation of the experiment.



## 2. Effects of ACh and cholinergic pharmacons

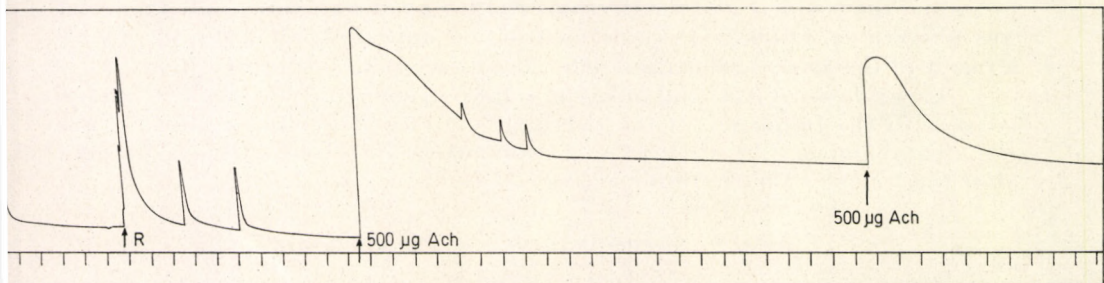
The effects caused by these substances are summarized in *Table I*. Four main effects are emphasized: increase of the tonus level, decrease of the tonus level, increase of the frequency of the phasic contractions, and decrease of the frequency of the phasic contractions. The latter two refer to the frequency of the rhythmic activity.

*Table I*

The effects of cholinergic drugs

	Dose ( $\mu$ g)	Number of experi- ments	Increase of tone	Decrease of tone	Increase of rhythm	Decrease of rhythm	No effect
ACh	100	10	5				5
ACh	500	5	5				
Nicotine	100	5	5			5	
TMA	10	6	6			5	
TMA	50	5	5			5	
TMA	100	10	10			10	
TMA	500	5	5			5	
TEA	10	5			2		3
TEA	100	5	1		4		1
Mytolon	100	10	9		3		1
Mytolon	500	12	11		12		
Atropine	100	7			1		6
Atropine	500	10			3		7
dTC	100	5			1		4
dTC	500	5	1		3		1
Hexamethonium	100	10	4		2	1	6
Eserine	100	10	1		1	4	4
Eserine	500	10	3			1	6
Prostigmine	100	10					10
Prostigmine	500	10					10

It was found, that 100—500  $\mu$ g dose of the ACh cause a temporary tonic response. The degree and duration of this effect increased with the quantity of the ACh. After ACh injection some immediate relaxation occurs, but afterwards the remaining tonic contraction decreases very slowly (at times lingering on for 10 minutes). Repeated ACh injection evoked a less effect (*Fig. 1*). Simultaneously the decrease of the rhythmic activity was observable.



*Fig. 1.* Effect of ACh on the spontaneous activity of the posterior adductor.

R — injection of physiological solution:  $\uparrow$  — 500  $\mu$ g ACh

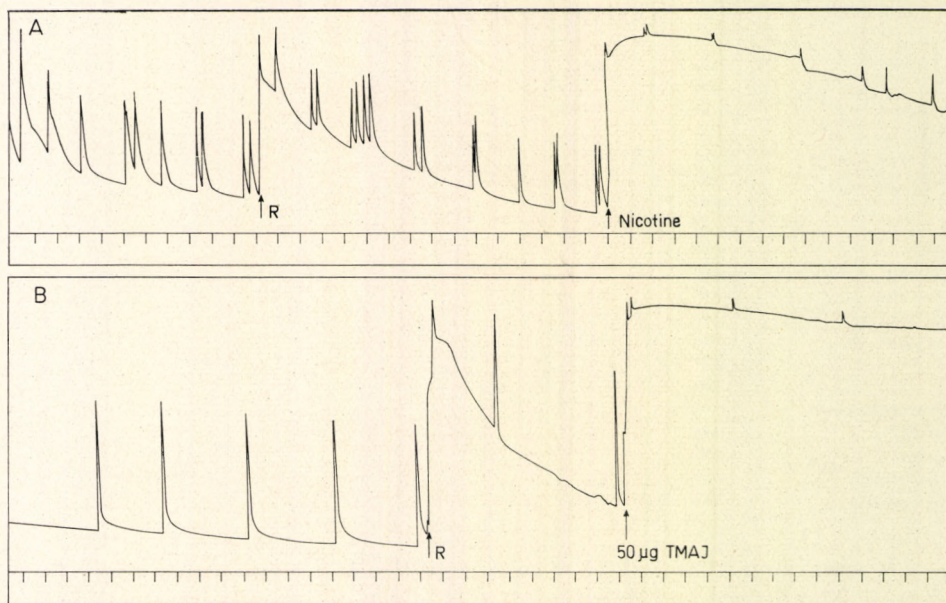
Time scale — 60 sec



Nicotine caused tonic contraction already in 50–100  $\mu\text{g}$  amount. This effect appears very rapidly and no subsequent relaxation was noticeable. After 5–10 minutes plateau a slow decrease of the tonus occurred, but it remained constant at a new level (*Fig. 2*). The frequency of the rhythmic activity usually decrease and the amplitudes of the fast contractions in consequence of the high level of tonus are lowered.

TMA increased the tonus very effectively, already in 10  $\mu\text{g}$  dose. The tonic contraction lasted long, only insignificant relaxation could be observed even in 1–2 hours. The previous rhythmic activity may remain untouched (*Fig. 2B*).

TEA in 100  $\mu\text{g}$  amount caused increase in the rhythmic activity.



*Fig. 2.* A — effect of 50  $\mu\text{g}$  nicotine;  
B — effect of 50  $\mu\text{g}$  TMA.

100–500  $\mu\text{g}$  mytolon enhanced in most of the cases both the level of the tonus and the frequency of the rhythm (*Fig. 3A*), but sometimes only the latter was observable (*Fig. 3B*). Tonic contraction appeared not instantly but as a result of decreasing relaxation after successive phasic contractions.

Large doses of dTC and atropine caused in some of the cases a moderate increase in the frequency of the rhythmic activity. The effect of eserine was not unambiguous. Prostigmine and hexamethonium (100–500  $\mu\text{g}$ ) did not alter the tonus or the rhythmic activity.

### 3. Effects of adrenergic agonists and antagonists

Adrenaline in 10–100  $\mu\text{g}$  amount enhanced the level of tonus, and in most of the cases also increased rhythmic activity (*Table II*; *Fig. 4A*). Nor-adrenaline injection caused similar effect (*Fig. 4B*). The evoked tonic contrac-

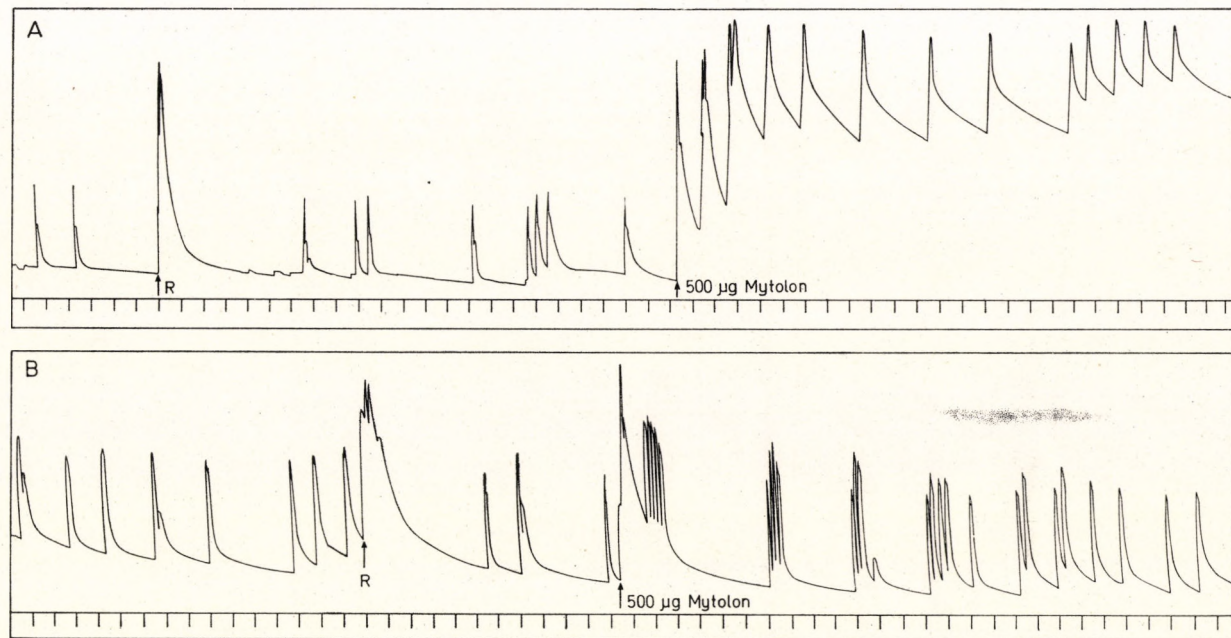


Fig. 3. Effect of 500 µg mytolon.  
 A — increase of tone and rhythm;  
 B — increase of rhythm



Table II

	Dose ( $\mu$ g)	Number of experiments	Increase of tone	Decrease of tone	Increase of rhythm	Decrease of rhythm	No effect
Adrenaline	10	7	5		4		1
Adrenaline	100	10	8		5		2
Noradrenaline	10	6	4		3		2
Noradrenaline	100	12	5		5		4
Dopamine	10	12		1	9		3
Dopamine	100	10	3	2	2		5
Dopamine	500	10		7	8		1
Tyramine	100	9		9	3		1
Tyramine	250	6		6	1		
IPNA	100	5	3		4		2
Dibenzamine	100	10	1		1		9
Dibenzamine	500	10	8		8		2
DCI	100	6	2				4
Ergotamine	100	5			2		3
5HT	10	4			4		
5HT	50	5		5		4	
Tryptamine	100	5		4	3		1
Ergometrine	1	5			5		
Ergometrine	10	5			4		1
Ergometrine	100	5	2		5		
BOL-148	10	4	2				2
BOL-148	100	7	3		5		1

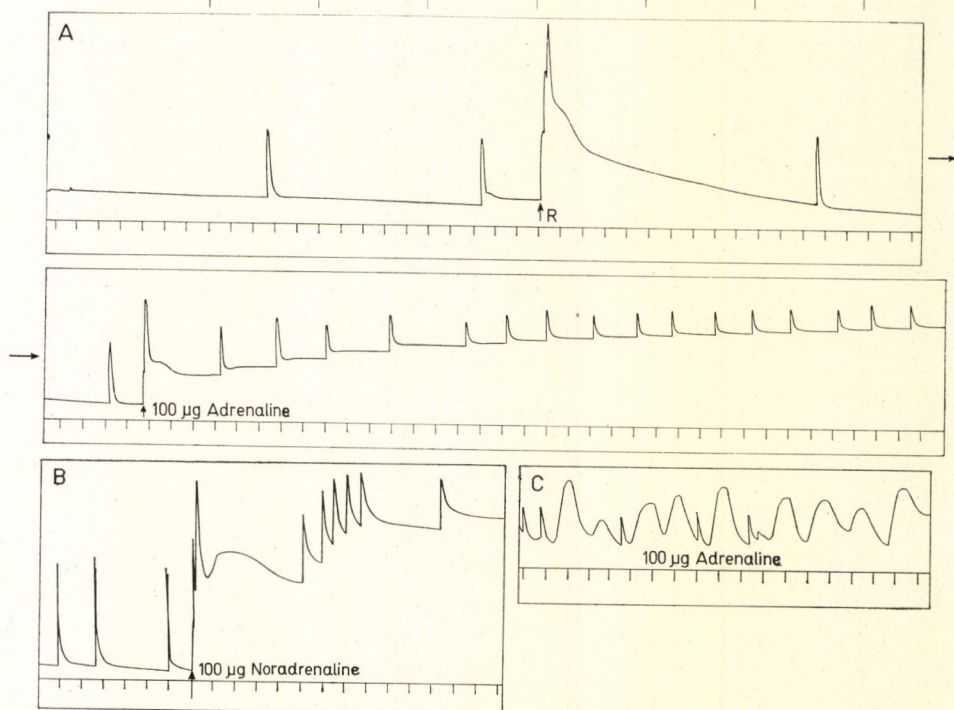
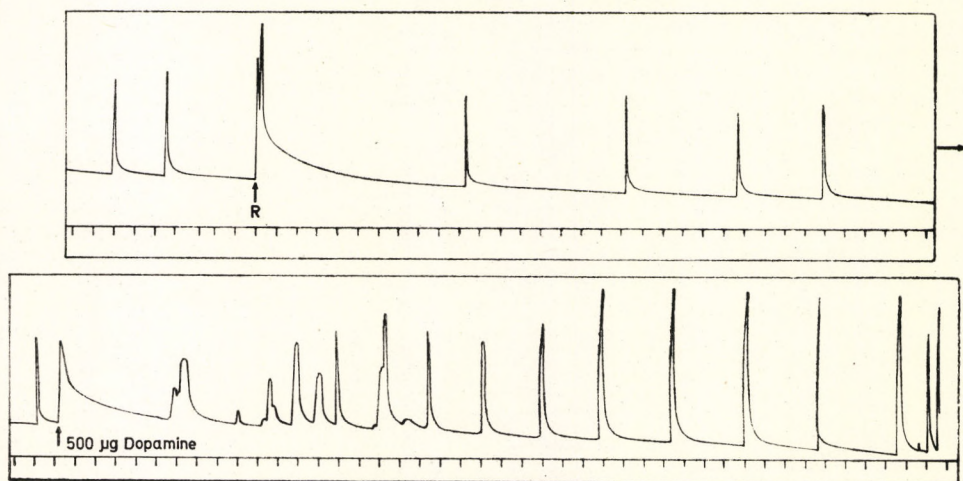


Fig. 4. Effects of 100  $\mu$ g adrenaline (A) and 100  $\mu$ g noradrenaline (B); C — slow waving after 100  $\mu$ g noradrenaline

tion lasted in both cases for a long time, and also the relaxation and rhythmic activity of the foot was observable. Sometimes a slow waving occurred in the level of tonus (*Fig. 4C*).

The effect of IPNA was similar to that of the noradrenaline.

Dopamine (100–500  $\mu\text{g}$ ) increased the rhythm and augmented the amplitudes of the phasic contractions. In *Fig. 5*, demonstrating the effect of the dopamine the phasic contractions have two components, and dopamine influences the second one. 500  $\mu\text{g}$  dopamine decreased the tonus.



*Fig. 5.* Effect of 500  $\mu\text{g}$  dopamine. The lower curve is the immediate continuation of the upper one

Tyramine in 100–250  $\mu\text{g}$  amount decreased the tonus, in some cases, however, an increase in the rhythm was observed.

Large amount of dibenamine (500  $\mu\text{g}$ ) increased temporarily both rhythmic activity and tonus level.

The effect of DCI (100  $\mu\text{g}$ ) was insignificant. Also ergotamine proved to be ineffective.

#### 4. Effects of 5HT, tryptamine, BOL-148 and ergometrine

5HT caused in a few minutes a significant relaxation already in 10  $\mu\text{g}$  amount, and also decreased the frequency of the rhythmic activity (*Fig. 6A*). Tryptamine similarly caused a decrease in the tonus, but in many cases increased the rhythm (*Fig. 6B*). BOL-148 often increased the rhythmic activity, and seldom did it enhance the tonus (*Fig. 6C*).

Small doses of ergometrine increased the rhythm significantly (*Fig. 7A, B, C*). The increase of the frequency appears immediately after the injection. Later on parallel with the damping of the increased frequency (*Fig. 8*.) the augmentation of the amplitudes was observable.



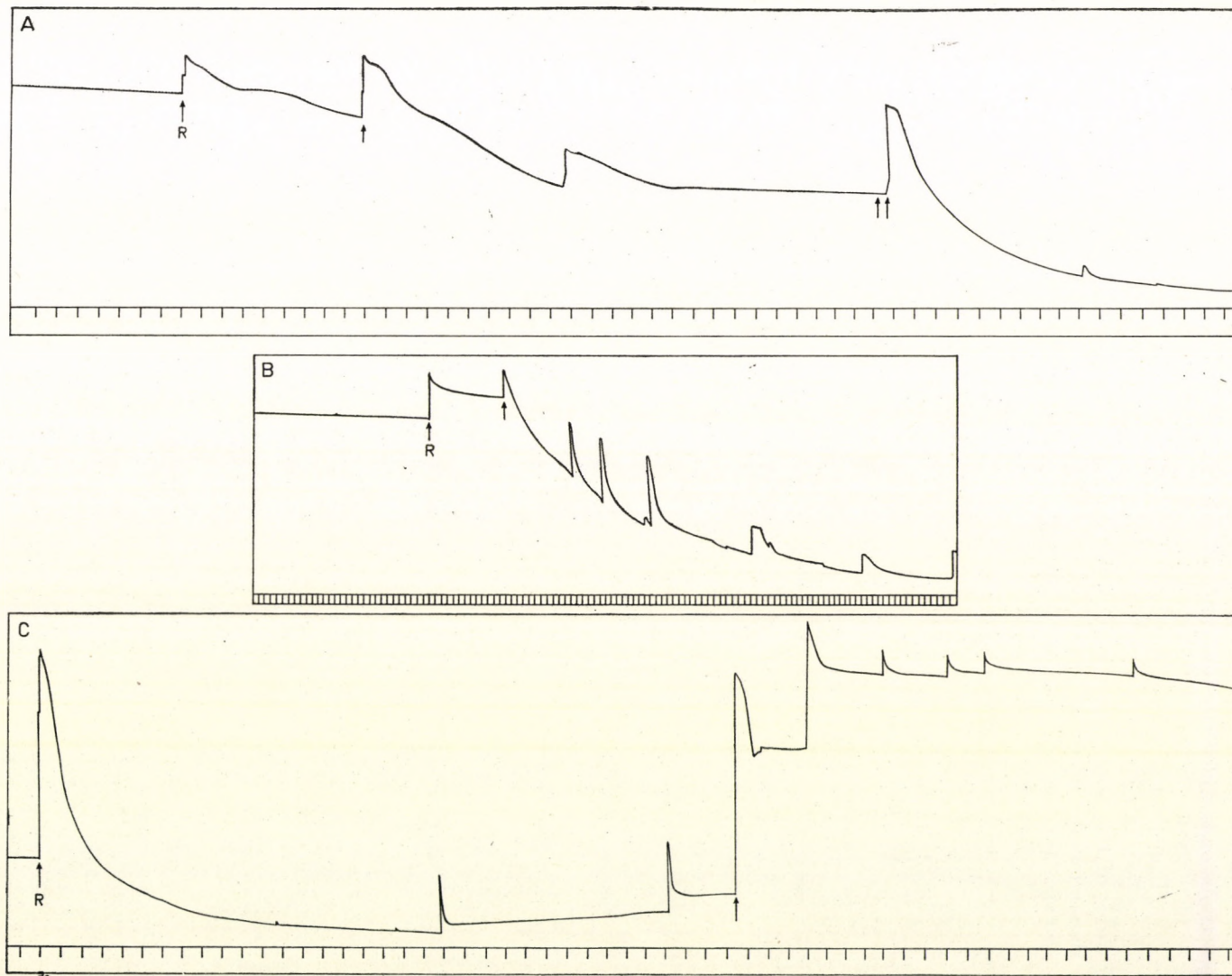


Fig. 6. A — effect of 5HT;  $\uparrow$  — 10  $\mu$ g;  $\uparrow\uparrow$  — 50  $\mu$ g; B — effect of 100  $\mu$ g tryptamine; C — effect of 100  $\mu$ g BOL



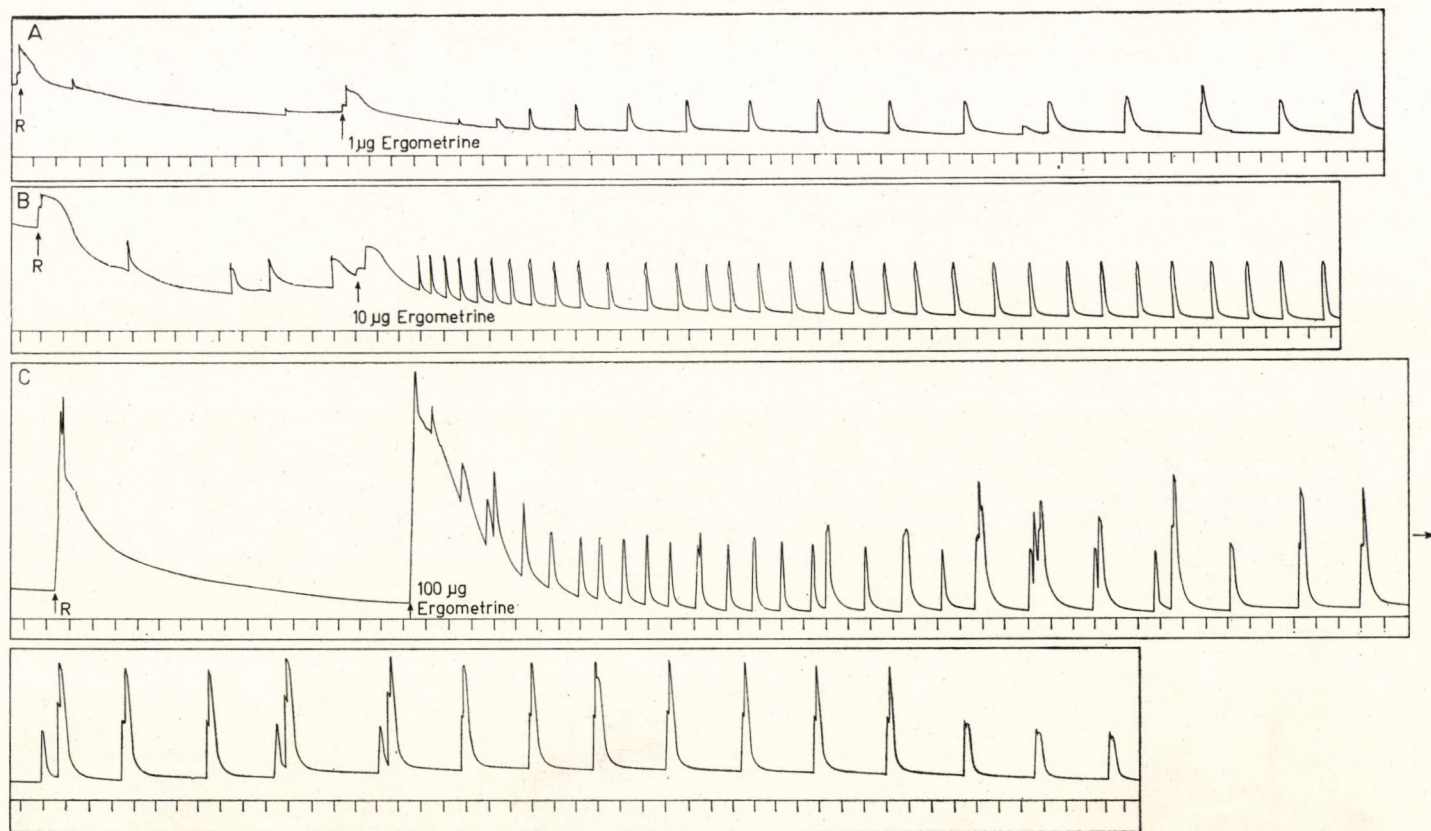


Fig. 7. Effect of ergometrine: A — 1 µg; B — 10 µg; C — 100 µg;



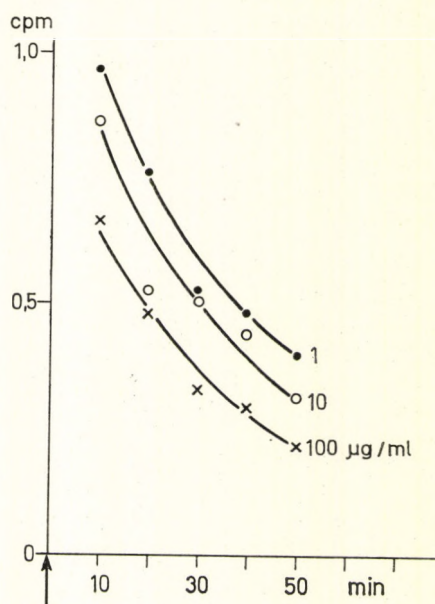


Fig. 8. Change in the frequency of the rhythmic contractions evoked by ergometrine during the first 50 minutes

#### 5. Effect of drugs on the muscle response evoked by electrical stimulation of the CVc

With suitable series of impulse applied to the CVc the contraction and subsequent relaxation of the posterior adductor may be effected (SALÁNKI and LÁBOS, 1963). Significant differences were found whether stimulation takes place before or after drug injection. In most of the cases a decrease in the amplitude of the evoked response was observable. In many instances the specificity of this effect is dubious, because the response itself depends to a great extent on the previous stimulations and on the actual level of the tonus. Therefore conclusions were drawn only in cases when other phenomena also occurred.

The increased tonus caused by ACh could only be relaxed very poorly as compared to the control, however, with repeated stimulation the tonic contraction diminished by a considerable degree (Fig. 9).

The tonic contraction caused by nicotine and TMA could be relaxed in a less degree (Fig. 10). The rate of relaxation depends on the dose of the drug used.

#### 6. Combined drug effects

The increase of tonus caused by 500 µg ACh was not potentiated by 100 µg eserine or prostigmine.

Previous atropine injection (100 µg) prevented the effect of ACh, while 100 µg dTC proved to be ineffective in similar situation.

Both ACh and nicotine responses were smaller than usual, if they were evoked after the injection of 100 µg mytolon.



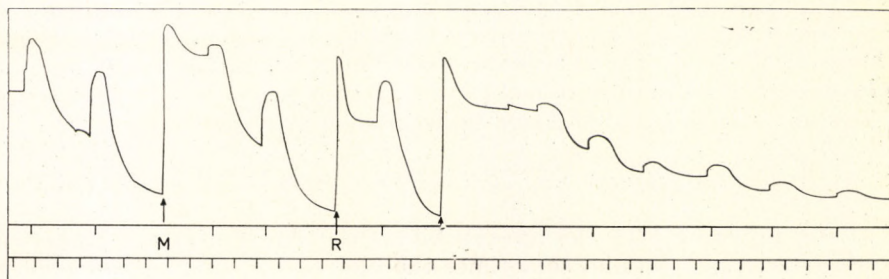


Fig. 9. Effect of stimulation of the CVc before and after ACh treatment. Middle curve — signals of the electrical stimulation. M — mechanical stimulation of the mantle; R — control injection;  $\uparrow$  — 500  $\mu$ g ACh

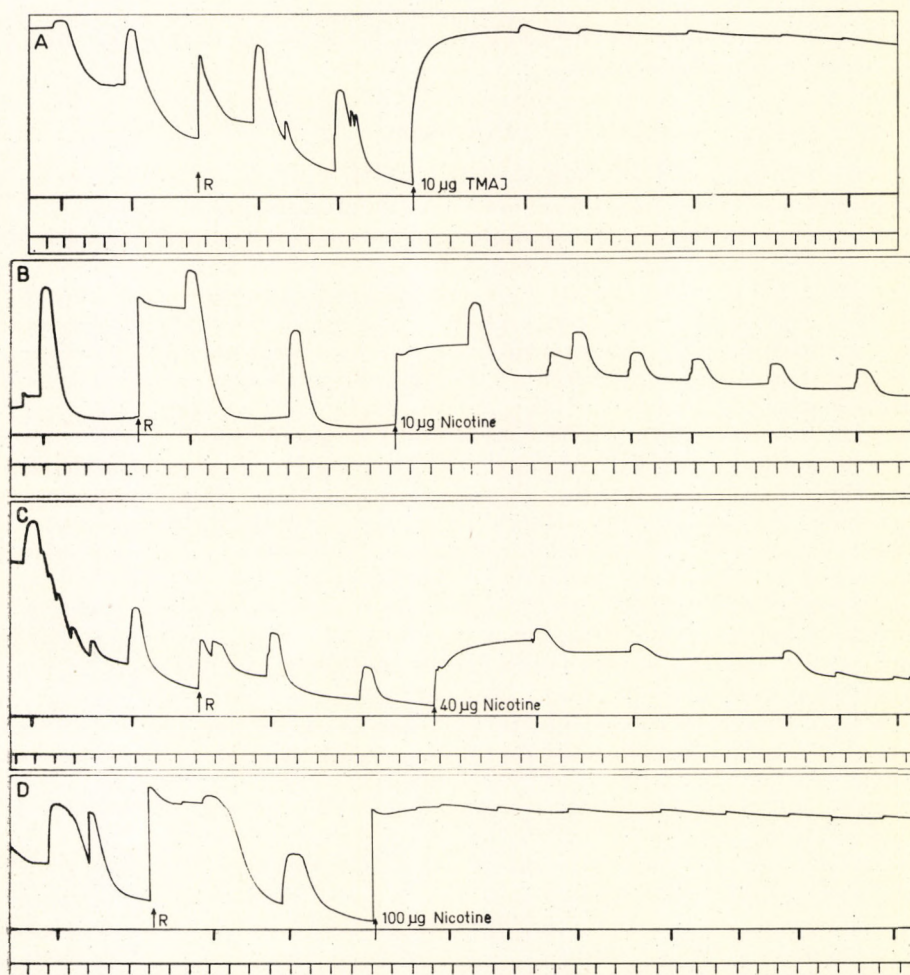


Fig. 10. Effect of nicotine and TMA when CVc was stimulated  
A — 10  $\mu$ g TMA; B — 10  $\mu$ g nicotine; C — 40  $\mu$ g nicotine; D — 100  $\mu$ g nicotine



Combined injection of 5HT and adrenaline caused immediate increase of the tonus, followed by a considerably rapid relaxation. At the same time an increase of the rhythmic activity was observable. In one case (*Fig. 11A*) the increase of the tonus, in others (*Fig. 11B*) the increase of the frequency of the rhythm was dominant. After large doses the relaxation was prevalent (*Fig. 11C*).

We could not observe any similar effects after applying 5HT and ACh together.

After injecting 5HT the nicotine tonus was either very temporary or it was absent completely, and sometimes the increase of the rhythm occurred.

In case of injecting 10  $\mu\text{g}$  5HT and 100  $\mu\text{g}$  BOL-148 together, the effect of 5HT was dominant. Increasing the dose of the BOL (500  $\mu\text{g}$ ), besides the relaxation a considerable increase in the frequency of the rhythmic activity appeared.

Combined application of adrenaline and dibenamine (200–200  $\mu\text{g}$ ) resulted in the decrease of the level of tonus and the increase of the rhythmic activity in most of the cases.

### Discussion

On the basis of the results obtained some conclusions can be drawn for the presence of cholinergic, adrenergic and tryptaminergic mechanisms. There are significant differences, as adrenaline, noradrenaline and 5HT were effective in low doses, while ACh acted only in high concentrations.

ACh, TMA, nicotine, mytolon, adrenaline, noradrenaline, dibenamine and BOL-148 caused tonic contraction of the adductor. In contrary to this 5HT, tryptamine, tyramine and in large dose also dopamine evoked considerable decrease of the adductor tone. The rhythmic activity was increased by catecholamines, ergometrine, dibenamine, BOL, mytolon and TEA.

The tonus-inhibiting effect of 5HT is in accordance with the results obtained for the ABRM of *Mytilus* (TWAROG, 1967). As after stimulation of the CVc causing the relaxation of the adductors the 5TH content increases in the muscle (SALÁNKI and HIRIPI, 1969), the natural relaxing role of 5HT seems very probable. BOL did not antagonize the relaxing effect of 10  $\mu\text{g}$  5HT even in 500  $\mu\text{g}$  amount, nevertheless increased the rhythmic activity.

Our results on the effect of the ACh are in agreement with other data so far that it increased the tonus in high doses. However, the sensitivity was significantly less than it was found for the ABRM and on Gastropoda preparations (TWAROG, 1960; JAEGER, 1962; BURNSTOCK et al. 1967). The effects of TMA and nicotine correspond to that described for the ABRM (TWAROG, 1954, 1959). In contrary to this, mytolon and ACh did not cause antagonistic effects, distinguishing the *Anodonta* adductor from the ABRM of *Mytilus* (TWAROG, 1960). JAEGER (1962) reported also the ACh-potentiating effect of the mytolon.

Adrenaline is considered to be a less potent relaxant on ABRM as 5HT is (HOYLE, 1964), while according to JAEGER (1963) adrenaline is an effective tonus-increasing and poorer rhythm-increasing agent on penis retractor. GEIGER (1929) found on *Anodonta* that adrenaline increased the tonus and the rhythmic activity when added to the whole animal, and this effect could be prevented by ergotamine.



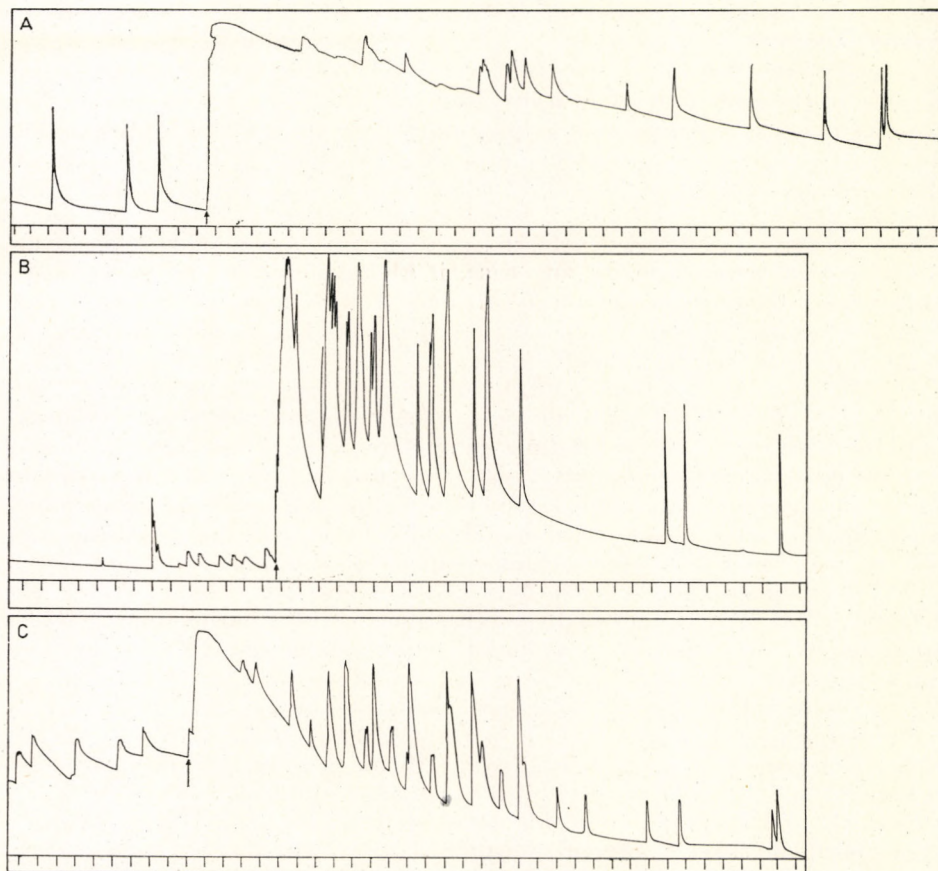


Fig. 11. Effect of 5HT and adrenaline injected together  
 A and B — 10–10  $\mu\text{g}$   
 C — 100–100  $\mu\text{g}$

In our case both adrenaline and noradrenaline resulted in the increase of the level of tonus and of the rhythmic activity.

When 5HT and adrenaline were injected together there was in the rhythmic activity a high and long lasting, while in the tonic contraction only a moderate and temporary increase, referring to the partial antagonism of these substances. 5HT decreases tonus and under such circumstances the rhythm-increasing effect of the adrenaline becomes prominent. Similar effect was demonstrated on ABRM of *Mytilus* by TWAROG (1954) to the combined application of ACh and 5HT, while on the penis retractor of snails JAEGER (1963) described the decrease of the tonic and the increase of the phasic responses when tryptamine and adrenaline were used together.

On the basis of our experiments we suppose that in the adductors of *Anodonta* an adrenergic-tryptaminergic antagonism exists. Consequently, the pharmacology of the *Anodonta* adductor differs from both the ABRM of *Mytilus* and the radula protractor of *Busycon* and *Buccinum* where ACh-5HT



antagonism was demonstrated (TWAROG, 1954; HILL, 1958; FÄNGE and MATTISSON, 1958).

The physiological role of a cholinergic system remains questionable because of the large dose of ACh necessary to evoke any definite effect, however, it cannot be excluded completely. As the combined effect of ACh and eserine does not differ significantly from that of the ACh, the relatively high cholinesterase activity of the adductor (SALÁNKI et al. 1967) may not be responsible for the ACh insensitivity. The effects of nicotine and TMA may be considered as a result of direct depolarization occurring on non-cholinergic receptor of the muscle membrane. In any case, if a cholinergic system does exist, it differs from the customary, maybe in such a way, that the mediator is not ACh. Among cholinolytics only atropine prevented in some cases the effect of ACh, dTC proved to be ineffective.

The shape of the tonic contractions caused by ACh, nicotine and TMA differs from that caused by adrenaline and noradrenaline. The development of the latter resemble the catch-tone characteristic in physiological conditions introduced by rhythmic contractions. This may indicate, however, that the site of the action of adrenaline and noradrenaline is not the muscle membrane itself but they play a role in the mobilization of a tonus increasing substance or they are triggering a molecular mechanism causing tonic contraction.

Agonistic-antagonistic relations were not unequivocal among adrenergic drugs, e.g. both adrenaline and dibenamine increased the muscle-tone. However, applying 100—100  $\mu$ g adrenaline and dibenamine together, the decrease of the tonus-level is observed.

Comparing our results with those found in the glochidia of *Anodonta* it is interesting to note that the lack of the effect of cholinergic drugs on these latter is more expressed, even TMA and nicotine were ineffective on the larvae (LÁBOS et al. 1964). At the same time there is a similarity in the presence of adrenergic and tryptaminergic regulation (LÁBOS et al. 1964; LÁBOS, 1966). In respect of tryptaminergic substances some difference exists between adult mussels and larvae: in the former both 5HT and tryptamine were effective relaxants while in the latter the rhythm was influenced only by tryptamine.

The effect of BOL-148, increasing both rhythm and tone, may be interpreted with the antiserotonin character of the lysergic acid derivatives. This may be valid also for the ergometrine, however, the direct effect of the latter cannot be excluded either. It is interesting to note, that ergometrine proved to be a very potent excitator of rhythm also on the neurones of the *Helix aspersa* (WALKER, 1968).

### Summary

The spontaneous activity as well as the evoked responses of the posterior adductor of *Anodonta cygnea* were investigated after intramuscular injection of cholinergic, adrenergic and tryptaminergic substances. We found:

1. Ach in large doses, TMA and nicotine in low concentrations cause tonic contraction. Mytolon and TEAC increase the frequency of the spontaneous phasic contractions. Prostigmine, eserine, curare, hexamethonium and atropine are ineffective or act indefinitely.



2. Adrenaline, noradrenaline, and IPNA cause tonic contraction and increase the rhythmic activity. Dopamine and tyramine in large doses increase the rhythm but inhibit the tone. Dibenamine in large dose acts similarly to adrenaline. Ergotamine and DCI are ineffective.
  3. 5HT inhibits both tone and rhythm, tryptamine decreases tone but enhances rhythm. BOL-148 increases both tone and rhythm, while ergometrine results an increase in the rhythm.
  4. With stimulation of the cerebro-visceral connective the tonic contraction caused by ACh could be relaxed to some extent while the TMA and nicotine tonus remained nearly intact.
- It is supposed, that in the regulation of the adductor activity in the fresh water mussel an adrenergic-tryptaminergic antagonism exists.

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## KOLINERG, ADRENERG ÉS TRIPTAMINERG ANYAGOK SZEREPE TÓNUSOS MOLLUSCA-IZOM (*ANODONTA CYGNEA* L.) SZABÁLYOZÁSÁBAN

Salánki János és Lábos Elemér

### Összefoglalás

*Anodonta cygnea* hátsó záróizmába adott intramuszkuláris injekciókkal vizsgáltuk az izom tónusos és ritmusos működését és a cerebrovisceralis konnektívum (CVc) ingerlésével kiváltott válasz befolyásolhatóságát. Azt találtuk, hogy

1. ACH csak nagy dózisban, a TMA és nikotin kis koncentrációban is tónusfokozó. Ritmusfokozó a mytolon és a TEAC. Hatástalan, ill. nem egyértelmű hatásúak a prosztigmin, ezerin, dTC, hexamethonium és atropin.

2. Az adrenalin, noradrenalin, IPNA tónus és ritmusfokozóak. A dopamin és tyramin nagy dózisban ritmusfokozó és tónusgátló. A dibenamin nagy koncentrációban ritmus és tónusfokozó, ergotamin, DCI hatástalan.

3. Az 5HT tónus- és ritmusgátló, a tryptamin tónusgátló és ritmusfokozó, a BOL tónus- és ritmusfokozó, az ergometrin igen kifejezett ritmusfokozó.

4. A CVc ingerlésével a TMA és nikotin-tónus nem, az ACH-tónus viszonylag jól ernyeszthető.

A záróizomműködés szabályozásában feltehetően adrenerg-serotoninerg antagónizmus játszik szerepet.



РОЛЬ ХОЛИНЕРГИЧЕСКИХ, АДРЕНЕРГИЧЕСКИХ И  
ТРИПТАМИНЕРГИЧЕСКИХ ВЕЩЕСТВ В РЕГУЛЯЦИИ ТОНИЧЕСКОЙ  
МЫШЦЫ БЕЗЗУБКИ

*Я. Шаланки и Э. Лабош*

Внутримышечным введением веществ в заднюю запирающую мышцу беззубки были изучены тоническая и ритмическая реакции мышцы, а также видоизменение ответа, вызванного раздражением церебро-висцерального коннектива (ЦВК). Было установлено, что:

1. ТМА и никотин в низких концентрациях, а ацетилхолин в высоких дозах вызывают усиление тонуса. Митолон и ТЕАС увеличивают тонус. Простигмин, эзерин, д-тубокурарин, гексаметоний и атропин являются неэффективными, вернее их эффект неоднозначный.

2. Адреналин, норадреналин, изо-пропил-норадреналин увеличивают и тонус и ритм. Дофамин в высоких концентрациях увеличивает ритм и угнетает тонус. Дибенамин в высоких концентрациях является усилителем ритма и тонуса. Эрготамин и ДЦИ неэффективны.

3. 50Т тормозит ритм и тонус, а БОЛ увеличивает оба процесса. Эргометрин значительно увеличивает ритм.

4. Раздражением ЦВК, тонус вызванный ацетилхолином, почти полностью ослабляется, но эффект ТМА и никотина остаются без изменения.

В регуляции деятельности запирающей мышцы по всей вероятности имеет значение адренергический-серотонинергический антагонизм.