

**REFLEX INFLUENCES ON THE ACTIVITY OF ADDUCTORS
OF FRESH WATER MUSSEL (*ANODONTA CYGNEA* L.)
BY STIMULI APPLIED TO THE HEART**

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It has been demonstrated in earlier investigations (KOCH 1917, WOORTMANN 1926, BUDDENBROCK 1960, PÉCSI and SALÁNKI 1964) that a correlation exists between the open or closed condition of valves and the frequency of heartbeat, which may be of importance in the regulation of the circulation of haemolymph (KOSHTOYANTS 1957a). Several factors as the periodic and rhythmic movement of valves (ZIKS and BOGDANOV 1956) and the hydrostatic pressure of mantle cavity which is related to the former (TRUEMAN 1954), the haemolymph movement produced by the movement of foot (BRÜCKE 1925) and various extero- and interoceptive stimuli are of importance in the frequency changes of cardiac action. It has been established in previous studies that the relationship between the condition of the valves and the frequency of heartbeat cannot be explained by mechanical stimuli only. It was assumed that the adductors may in the course of periodic activity influence cardiac action also by reflexes *i.e.* the visceral ganglion may when regulating the activity of posterior adductor also inhibit or accelerate simultaneously cardiac action (PÉCSI and SALÁNKI 1964).

In cognizance of the relationship existing between cardiac action and the conditions of valves whether open or closed *i.e.* the functional condition of adductors, further on basis of the assumption that there may exist a reflex connection between the adductors and the heart, the question arises whether the stimulation of the heart by various (chemical, mechanical and electric) stimuli may react on the functional condition and activity (tonic contraction, rhythmic activity) of adductors.

The anterior adductor receives its nerves from the cerebral ganglion, the posterior one from the visceral ganglion and the heart also is innervated by the visceral ganglion (SPLITTSTÖSSER 1913). This fact poses the interesting problem, whether the reflex responses of adductors that may perhaps be produced by the stimulation of the heart will take place simultaneously in both adductors, or perhaps there is a phase shift between the activity of the two adductors just because they are innervated by two different ganglia. To obtain answer to this question investigations were performed not only on animals with intact valves but also on animals whose valves were completely intersected whereby the activity of the two adductors was made mechanically completely independent from each other.

Methods

The experiments were performed in situ in the winter months (January—February) on 13—14 cm long specimens of freshwater mussel (*Anodonta cygnea* L.) originating from the back-water of river Rábca. Previous to experimental use the animals were kept in aquarium in streaming Balaton-water at a room temperature of 18—20°C. The preparation of animals for the examination was made as follows. The part over the heart of one valve — on an area corresponding to the size of the heart — was removed with a tooth-drill. The other valve of the animal was fastened into the trough placed into a vessel containing about 1 litre Balaton-water. Care was taken that the water should not reach the aperture above the heart. The heart was set free by cutting up the mantle and pericardium along the longitudinal axis of the heart and the ventricle of the heart was connected with a lever.

Because the contraction and relaxation of adductors result in closures and openings of valves respectively it is possible to record the activity of the adductors by reproducing the movement of the valve in such a manner that the valve is connected with a lever.

If the experiments are conducted on animals with intact valves it is not possible to determine whether the two adductors take part with simultaneous action (contraction and relaxation) in the movement of valves or perhaps there is a time shift between the activity of the two adductors. To elucidate this question experiments were performed on animals the one valve of which was sawed across along the dorso-ventral axis of the animal whereby the activity of anterior and posterior adductor was by mechanical means rendered completely independent.

In this intersection of valve and ligamentum care was taken that possibly both adductors should dispose of equal portion of ligamentum.

Connecting the heart and the two valves separately with a lever it was possible to record simultaneously but independently the movements of the two halves of the shell and cardiac action (*Fig. 1*). The levers were adjusted in such a way that their readings should fall exactly under each other on the smoked paper of the kymograph.

In order to estimate correctly the kymograms it is important to note that in case of systole the corresponding lever moved upwards whereas in case of contraction of adductor the levers recording the activity of muscles moved downwards.

In the course of experiments chemical stimuli were produced by the following substances: 5-hydroxytryptamine creatinine sulphate (5-HT) (Fluka), acetylcholine bromate (ACh) (Chinoïn), tryptamine-HCl (T. Schuchardt) and KCl (Reanal). These agents were added in physiological solution for mussels (MARCZYNSKI 1959). 5-HT was applied in 10^{-4} M, tryptamine and acetylcholine in 10^{-4} — 10^{-2} M and KCl in 0.5—4 M concentrations. The agents were applied to the heart and into the pericardial fluid in 0.2 ml quantities by means of a syringe. In the latter case it became about tenfold diluted. In some experiments a piece of filter paper soaked in the above substances was placed on the heart in such a way that these should act only on the wall of the ventricle. Mechanical stimuli were produced with a soft cotton-puff. Electric stimulation was made by means of a series of impulses (20 V, 1 msec, 100 Hz, 30 sec duration) provided by a square wave generator through a pair of silver electrodes.

Results

The functional condition of adductors may be

- a) lasting tonic contraction,
- b) period of relaxation, ready for quick phasic activity, when periods of contractions and relaxations are alternating rhythmically. When recording the

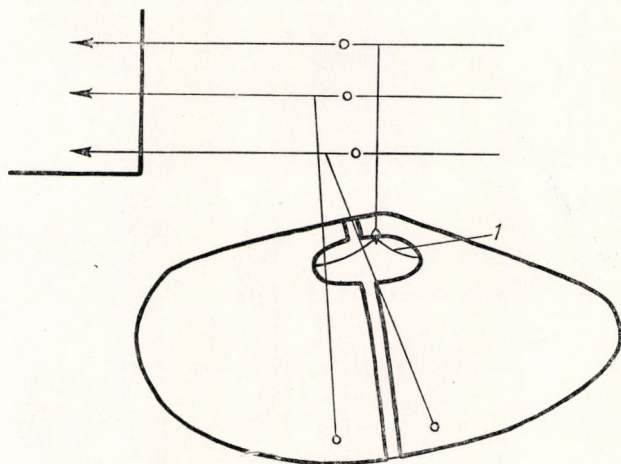


Figure 1. Method for simultaneous registration the activity of adductors and of the *in situ* heart. 1 = ventriculus. The order of levers downwards: heart, anterior adductor, posterior adductor

1. ábra. In situ kagylószív és a héjműködés egyidejű regisztrálódásának módszere. 1 = ventriculus. Az írókarok sorrendje felülről lefelé: szív, elülső záróizom, hátsó záróizom

activity of adductors separately it was observed occasionally that the posterior muscle displayed rhythmic activity whereas the anterior one was in the state of tonic contraction. In the course of investigations stimulation of the heart (pericardium and ventricle respectively) was carried out in both conditions of adductors for it was suggested that the heart would react differently in the two different functional conditions. 5-HT deserved special attention because a specific role is attributed in literature to this substance which is demonstrable in a considerable quantity in the heart tissue (WELSH and MOORHEAD 1959).

Influence of 5-HT applied to the heart on the activity of adductors

When 5-HT in 10^{-4} M concentration was applied to the heart or pericardium respectively during the state of relaxation of adductors performing rhythmic activity, changes were observable both in the rhythm of valve action and in the degree of contractions. The effect produced on the adductors subsequently to the application of 5-HT took place quickly and in certain cases after some minutes an increase in rhythmic activity was observable (Fig. 2A). This effect manifested itself in rapid contractions becoming gradually more pronounced and taking place in quick succession without considerable relaxation between the single contractions. This increase in tonicity lasted until the adductors became contracted to such a degree which corresponds to closure.

Subsequently to this, gradually increasing relaxations were observable between the single contractions and the adductors became in a relatively short time (some minutes) as relaxed as previously to the application of 5-HT, or in the majority of cases even more. Thus the application of 5-HT to the heart pro-

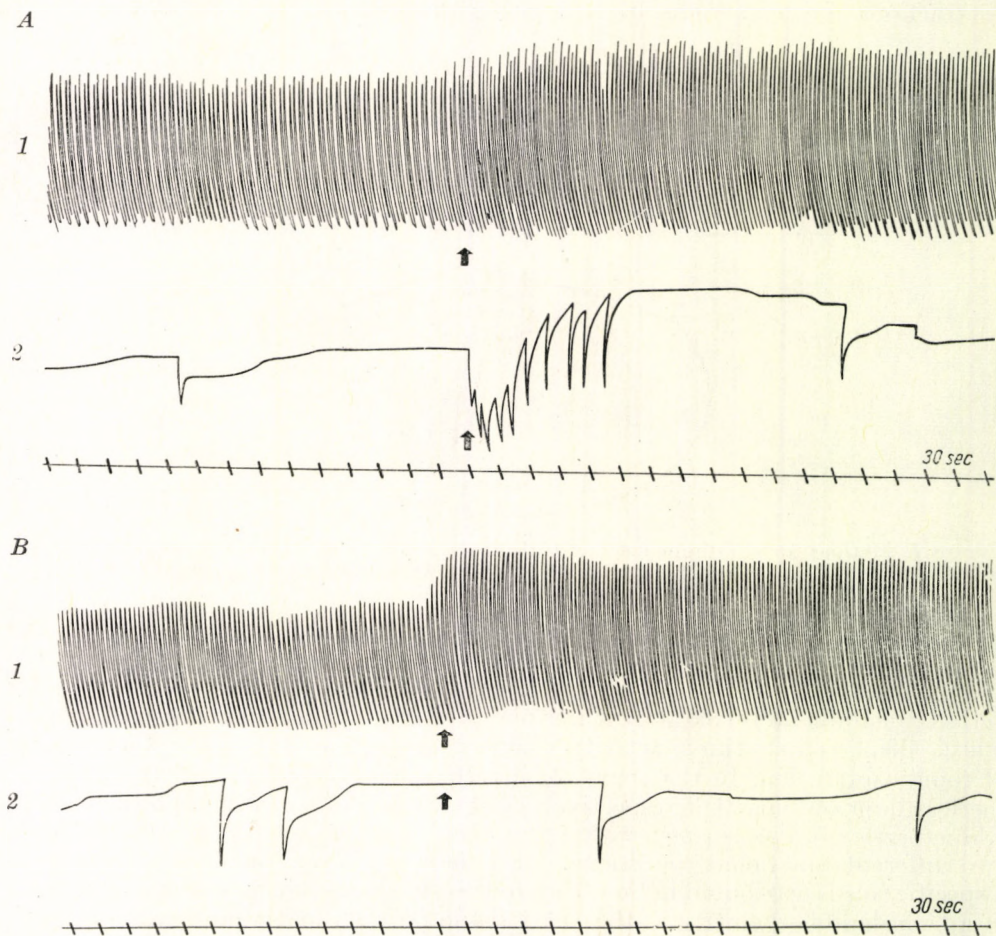


Figure 2. The influence of 5-HT applied to the heart on the reflex activity of animals with intact valves. *A* = when applied the first time; *B* = the same specimen 24 hours after the first application. *1* = registration of cardiac action; *2* = registration of the activity of valve

2. ábra. A szívre applikált 5-HT hatása a záróizmok reflexes működésére ép héjú állat esetén. *A* = először applikálva; *B* = ugyanaz a preparátum 24 óra múlva ismételt applikáláskor; *1* = szív működés regisztrálása; *2* = héjmozgás regisztrálása

duced an initial increase in the tonicity of adductor which was followed by a considerable decrease thereof. It is most remarkable that in no occasion was it possible to produce the same observed effect on the same animal, not even in the case when the stimulus produced by 5-HT was applied again repeatedly after 12–24 hours subsequently to the first effect (*Fig. 2B*).

Since 5-HT was applied to the heart and into the pericardial fluid, its direct influence on the heart manifested itself also immediately. The applied concentrations of 5-HT produced positive inotropic and chronotropic effects and increased also in most cases the tonicity of the heart. Under the given experimental conditions the heart — in contrast to the adductors — reacted to the introduction of new 5-HT solution in the same manner in all cases provided that sufficient time was left between the single applications for restoration to the previous level of activity.

When the experiments were conducted on animals with adductors isolated mechanically from each other and 5-HT was applied to the heart or to the pericardium, both adductors reacted with quick contraction to the stimulus produced on the heart in case the animals were in active condition *i.e.* in the state of lasting activity. Thereafter the tonicity and frequency of the posterior adductor increased as in the case of animals with intact valves and increased relaxation occurred only after 5–6 minutes, whereas the anterior adductor became to a great extent relaxed within the first minute (*Fig. 3*). It could be well observed that the increasing rhythmic action of the anterior half was always a little behind in time to the movement of the posterior half, *i.e.* the contractions and relaxations of posterior adductor preceded those of the anterior one.

If both adductors were in the state of tonic contraction at the application of 5-HT the first thing observed was a further increase in the tonicity of posterior adductor and the posterior halves became more linked up than usual *i.e.* they slid side by side in consequence to the increased abbreviation of muscle. Subsequently a relaxation took place followed by rhythmic activity of fairly high frequency and of great amplitude (*Fig. 4*).

Within some minutes after the moment that the posterior adductor began to relax the anterior adductor started also to relax. This relaxation was considerable and completely parallel with that of the posterior adductor, also on the anterior one rhythmic activity was observed. Thus, on the application of 5-HT to the heart the condition of tonic contraction of adductors ceased and a period of longer-shorter (occasionally several hours long) relaxed active condition took place.

In case the anterior half valve was closed completely whereas the posterior performed normal rhythmic activity the application of 10^{-4} M 5-HT to the heart produced an increase of rhythm in the posterior half and in 80% of cases opening of the anterior half occurred which displayed further on a rhythmic activity parallel with the posterior half (*Fig. 5*). The moment in which the anterior half opened did not coincide with the change in activity of the posterior half occurring just after the application of 5-HT but lagged some minutes behind.

The effect produced on the heart directly by 5-HT well conforms to the results obtained in previous experiments on intact valves. The computation of the averages of all experimental data shows that 5-HT in the concentration used produced a 15.7% and/or 35.0% increase in the frequency of heartbeat and in amplitude respectively.

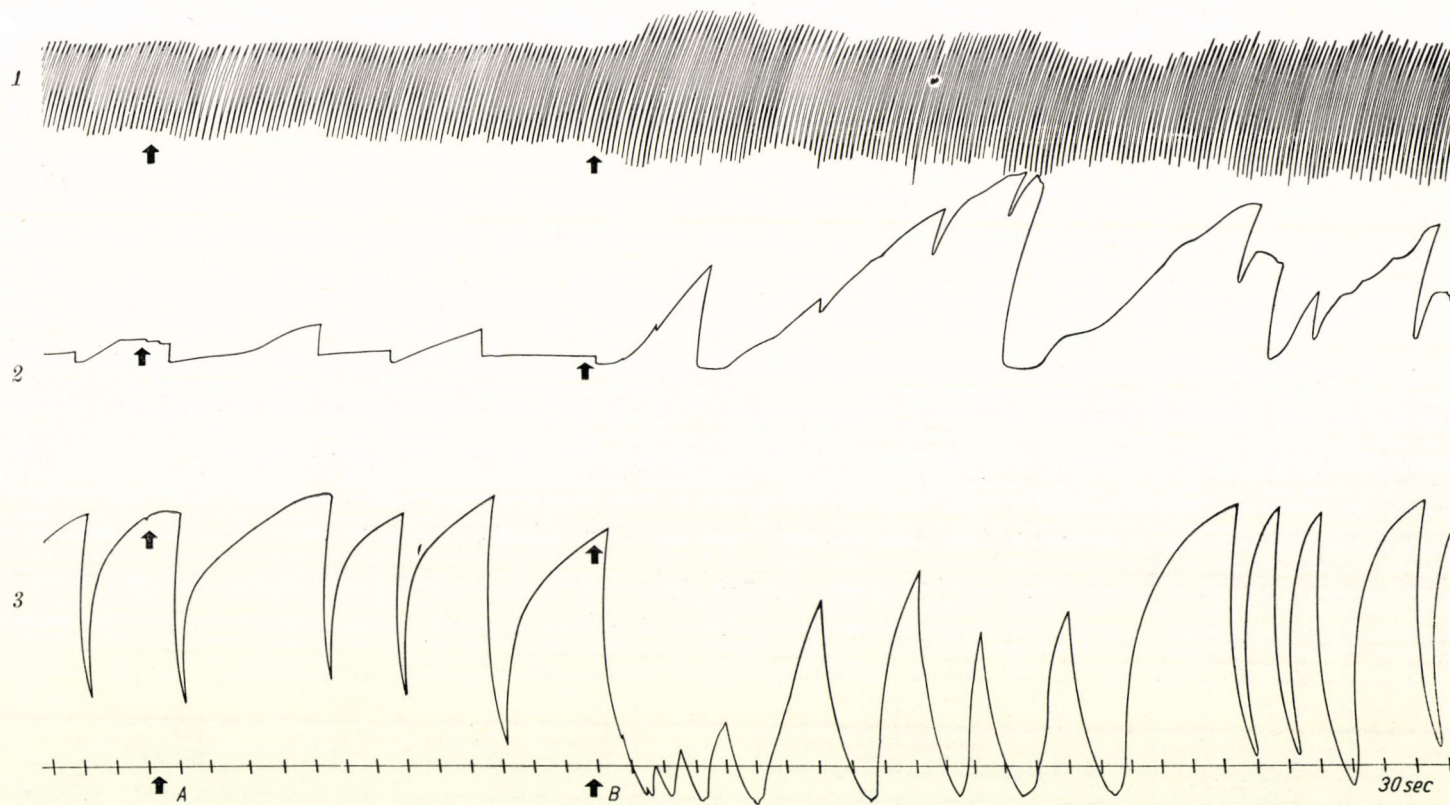


Figure 3. The influence of 5-HT in case of lasting activity. A = physiological solution; B = 5-HT. The order of recordings in this and in the other figures: 1 = cardiac action; 2 = anterior adductor; 3 = posterior adductor

3. ábra. 5-HT hatása tartós aktivitás esetén. A = kagylófiziológiás oldat; B = 5-HT. A regisztrátumok sorrendje itt és a következő ábrákon; 1 = szív működés, 2 = elülső záróizom, 3 = hátsó záróizom

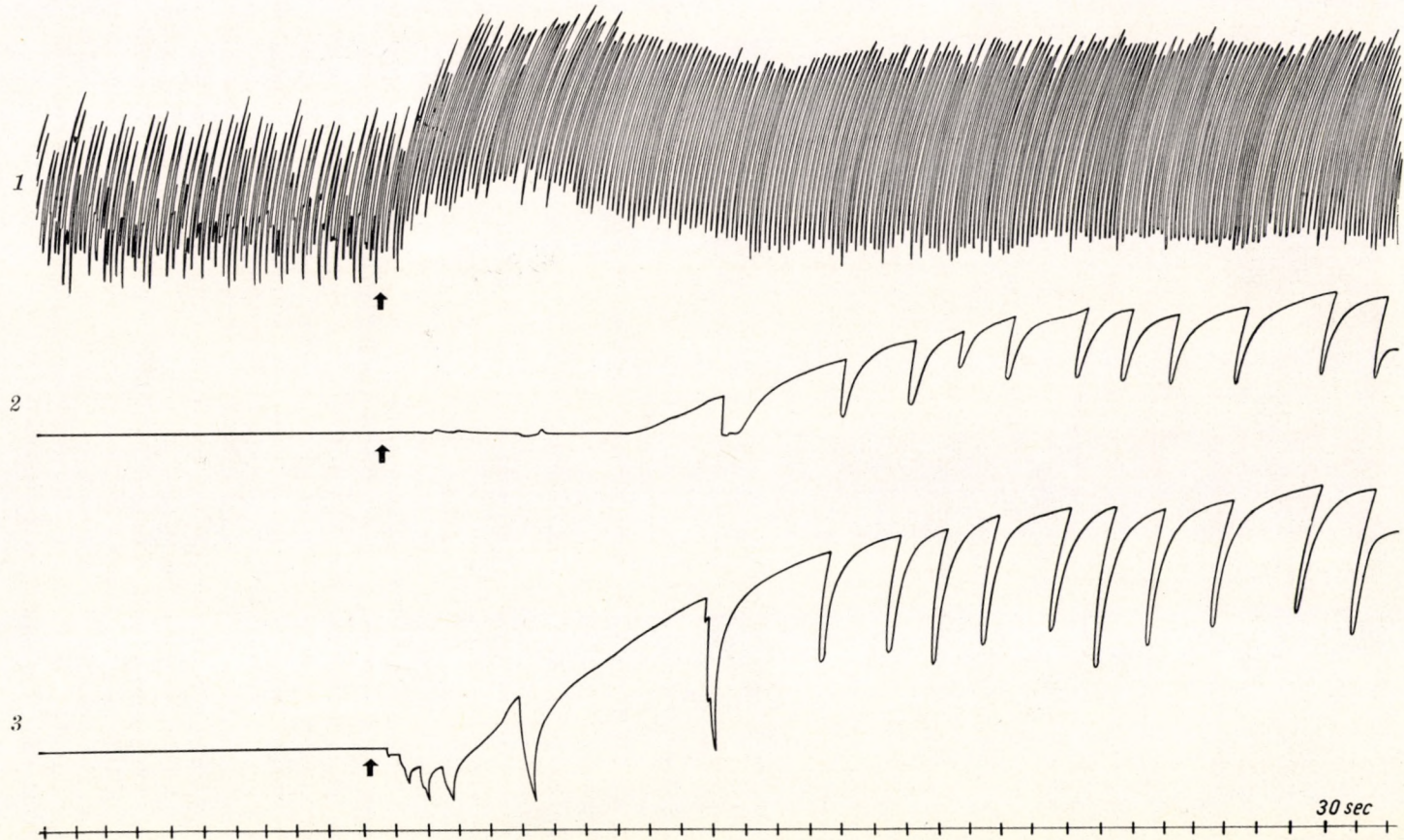


Figure 4. The influence of 5-HT in case of tonic contraction of the adductors
4. ábra. 5-HT hatása a záróizmok tartós tónusos kontrakciója esetén

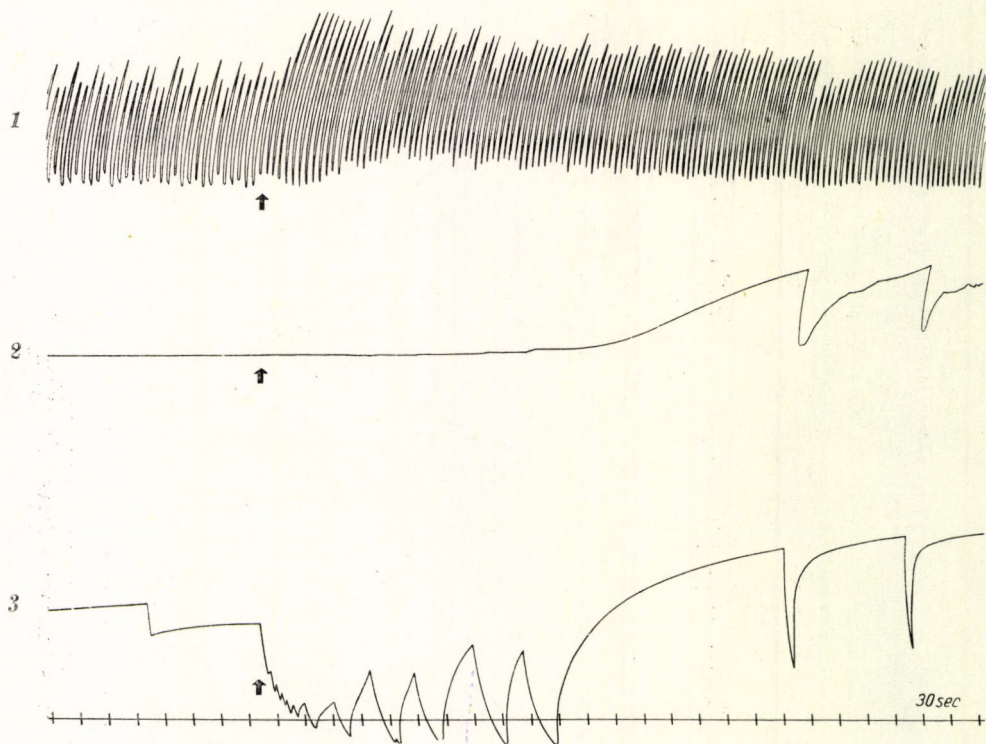


Figure 5. The influence of 5-HT in case of lasting tonic contraction of the anterior adductor

5. ábra. 5-HT hatása az elülső zárízom tartós tónusos kontrakciója esetén

Influence of other chemical agents (tryptamine, acetylcholine, KCl)

With regard to the fact that tryptamine related to 5-HT chemically influenced heartbeat in *in vitro* experiments in a similar way but to a lesser degree than 5-HT (GREENBERG 1960), further because this agent is able to influence also the activity of adductors centrally (SALÁNKI 1963) it was thought interesting to investigate whether it will be able when applied to the heart to produce by means of reflexes similar effects as 5-HT. It was found that in either case, when the shell of the animal was left intact or when the adductors were isolated from each other tryptamine produced similar to 5-HT an initial contraction of posterior adductor, and subsequently the relaxing of both posterior and anterior adductors. Nevertheless, to reach the same effect which was obtained by 5-HT, tryptamine had to be used at hundred times greater concentration, and it did not produce even then very explicit influence on the heart (Fig. 6).

According to published data (PUPPI 1963) the adductors are susceptible to ACh if this agent is applied to the ganglion. This agent has an inhibitory effect on the heart of *Anodonta cygnea* (TEN CATE and REESINCK 1954) and may presumably have, as an inhibitory mediator, an important role also physiologically (SAKHAROV and NISTRATOVA 1963).

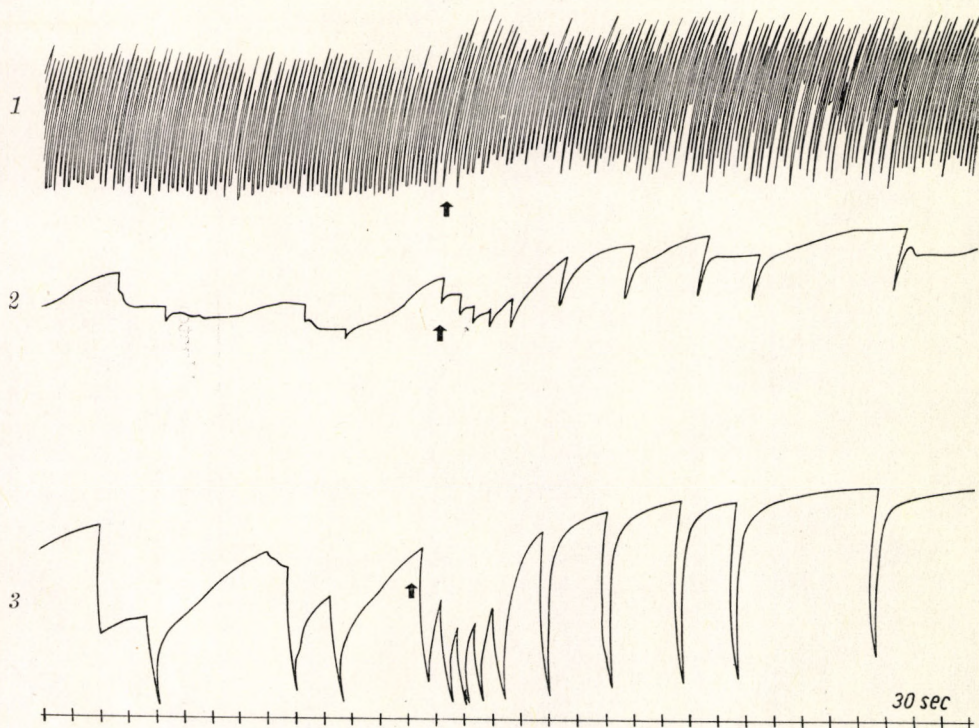


Figure 6. The influence of tryptamine on adductors being in the condition of lasting activity

6. ábra. Tryptamin hatása a záróizmok tartós aktivitása esetén

If 10^{-4} – 10^{-2} M ACh solutions were applied to the heart or into the pericardium no changes were observable in the activity or condition of the adductors whether they were in the state of rhythmic activity or in tonic contraction. It should be noted that the effect produced by the applied concentrations of ACh on the heart was not remarkable either, and only a small decrease in amplitude was observable occasionally.

The application of KCl to the heart produced reflex changes in the activity of adductors. If this agent was applied to the heart in the period of relaxation of adductors both the anterior and the posterior adductors reacted with very quick and strong contractions. The response of the posterior adductor was more pronounced. Lasting closure of valves (lasting tonic contraction), however, did not take place, and after an initial increase in tonicity the adductors began to relax and displayed rhythmic activity. Occasionally the previous level of relaxation was exceeded. If KCl was applied in the condition of tonic contraction to the heart relaxation took place as on the application of 5-HT (Fig. 7). KCl in 0,5–4 M concentrations (highly concentrated) yielded strong negative inotropic and chronotropic influences on the heart and increased, besides, the tonicity thereof almost to a maximum level. On occa-

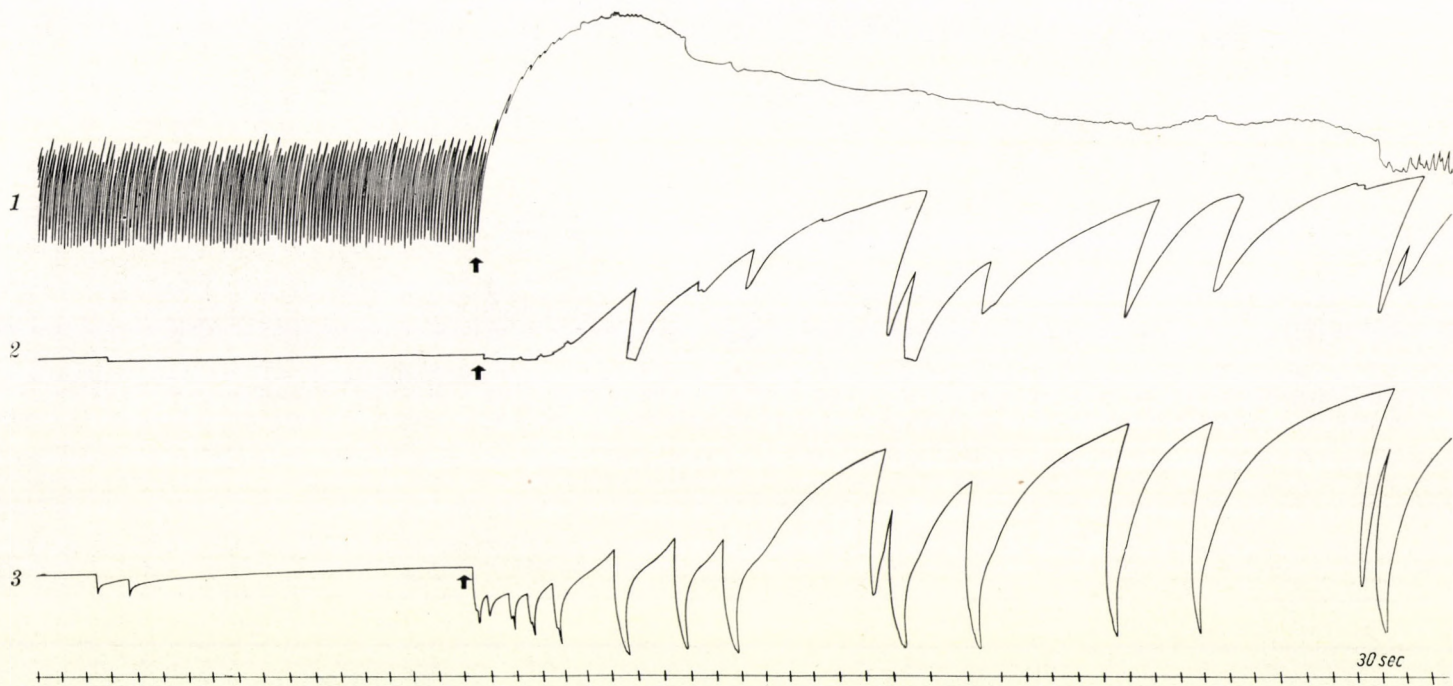


Figure 7. The effect of KCl in case of lasting tonic contraction of adductors
7. ábra. KCl hatása a záróizmok tartós tónusos kontrakciója esetén

sion even a systolic arrest was observed. In agreement with published data (JULLIEN ACOLAT, CARDOT, JOLY and BRIDE 1960) in situ heart was blocked by KCl, depending upon concentration.

Influences on the activity of adductors produced by mechanical and electrical stimulation of the heart

In connection with the chemical agents applied to the heart the question arises whether the changes in the activity of adductors are produced indeed only through the receptors of the heart and the pericardium, *i.e.* by means of reflexes, or one has to reckon also with the possibility that these agents may reach the adductors themselves by way of circulation or diffusion and influence them directly. For this reason it seemed important to attempt to excite the receptors of the heart with local stimuli as the mechanical and the electric one and to examine the responses of the adductors. The results obtained show, that if the adductors were in the condition of tonic contraction then the mechanical stimulation of the ventricle of the heart resulted in the majority of cases in relaxation after which a rhythmic activity of adductors followed for a longer period (*Fig. 8*). The tonic activity of the heart increased also simultaneously, and occasionally the magnitude of amplitude decreased from time to time to the half or to one third of the original without considerable changes taking place in frequency. The influence of a stimulation of 10–20 sec duration on the heart lasted for 4–5 minutes. Relaxation of adductors was well discernible only after some minutes subsequently to stimulation and the relaxation of the posterior adductor preceded in general by some minutes the relaxation of the anterior one.

It was possible to produce in many cases with the electric stimulation of the ventricle the opening of closed shells, *i.e.* the relaxation of tonically contracted adductors, after which their rhythmic activity was observable (*Fig. 9*). If, however, in the moment of the application of mechanical and electrical stimuli to the heart the adductors were in the condition of relaxation, a rapid contraction occurred, which was followed by other 2–3 deep contractions of the posterior adductor. This effect, however, was over within 1–2 minutes and thereafter the adductors continued their previous rhythmic activity.

Discussion

The possibility of influencing the activity of the adductors of various lamellibranchiates by reflexes has been evidenced in many respects. It is generally known that the exteroceptive stimuli, as the mechanical stimulation (touching) of mantle, of the area around the siphon and the foot results in the closure of valves (PAWLOW 1885, WOORTMANN 1926, NADORT 1943). Opening of the valves and changes in rhythmic activity were produced by ZIKS and BOGDANOV (1956) with the mechanical stimulation of the area around the heart. Opposed responses of adductors were described by WOORTMANN (1926) in the course of stimulating the mantle by O₂-rich or O₂-deficient water respectively. Characteristic muscle responses were registered by SALÁNKI (1961a, b) on the application of KCl and SH-inhibitors to the margin of the mantle, and he succeeded to produce specific changes in the rhythmic and

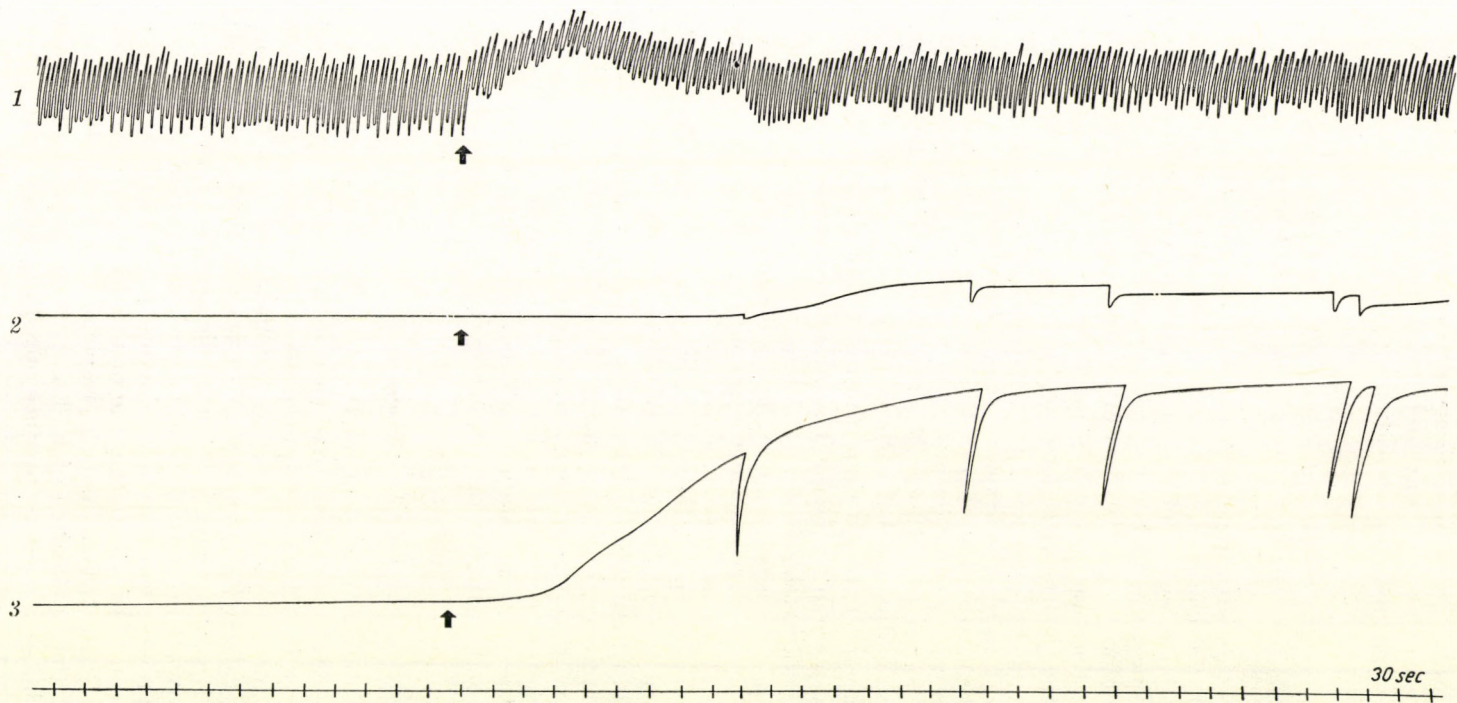


Figure 8. The influence of the mechanical stimulation of the heart on adductors being in lasting tonic contraction
8. ábra. A szív mechanikus ingerlésének hatása a tartós tónusos kontrakcióban levő záróizmokra

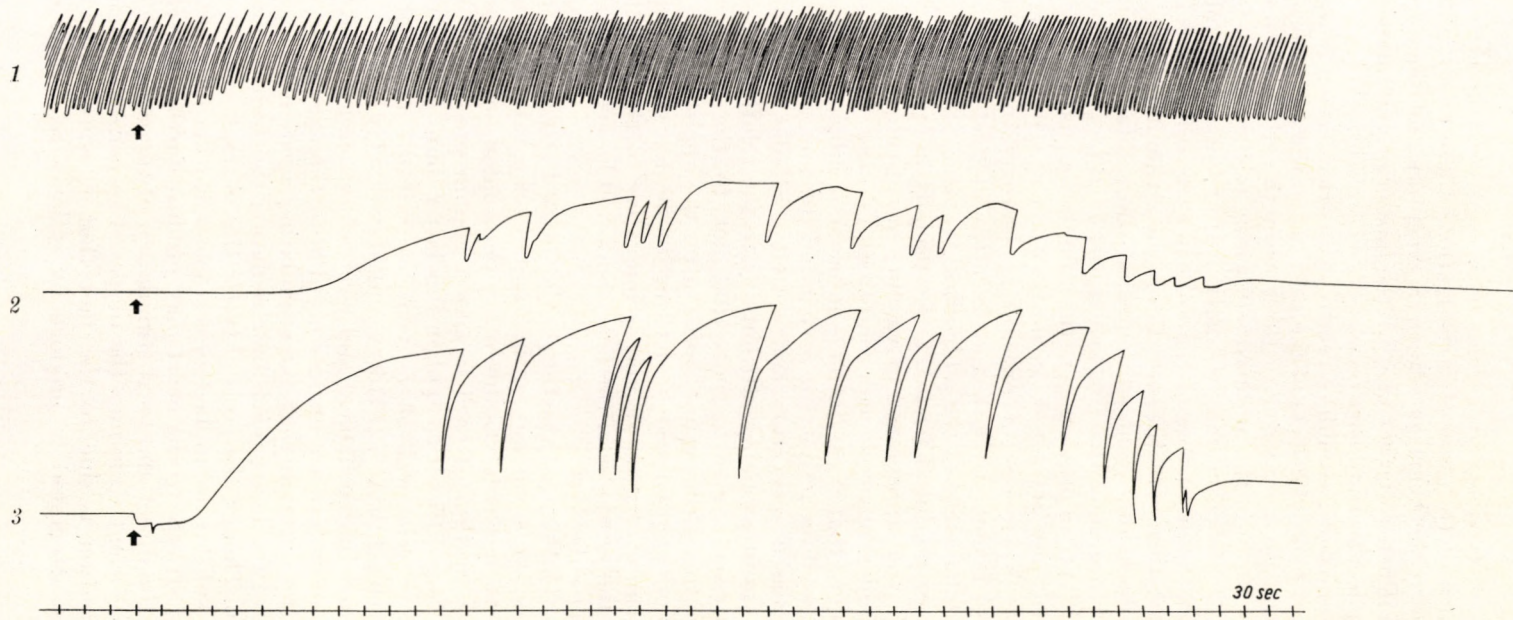


Figure 9. The influence of electric excitation of the heart on adductors being in lasting tonic contraction
 9. ábra. A szív elektromos ingerlésének hatása a tartós tónusos kontrakcióban levő záróizmokra

periodic activity of *Anodonta* by various interoceptive stimuli (SALÁNKI 1962). Upon the evidence of the present investigations there exists a direct, reflex connection between the heart as a zone of receptors and the adductors, and it is possible to influence the activity of the posterior and anterior adductors with stimuli applied to the heart.

As the results show, stimuli of relatively short duration (0.5—3 minutes) may produce most marked effects in the case, when the adductors are in tonic contraction. In the great majority of these cases the stimulation of the heart produces the relaxation of the adductors (opening of the valves) *i.e.* it induces the excitation of the mechanism of relaxation. If at the moment of the stimulation of the heart the adductors of the animal were in relaxation performing rhythmic activity, then on the effect of the stimulus some quick contractions were observable, and subsequently the adductors relaxed again. In some cases the degree of this relaxation was even higher (especially on the application of 5-HT) than previously to the stimulation, namely the mechanism of relaxation was more activated. In no occasion was it possible to produce tonic contraction by means of reflexes is, however, not out of question that stimuli of sufficient strength and duration applied to the heart would result in lasting tonic state of the adductors.

The influence produced by 5-HT is especially noteworthy, because one may reckon with the appearance of varying quantities of this substance in the heart also under physiological conditions (WELSH 1957, KOSHTOYANTS 1957b). This implies, that if cardiac action becomes subject to increased 5-HT effect in the course of its activity, it may induce by means of reflexes also the adductors to increased relaxation and activity. Similar influence produced by tryptamine is most probably attributable to the relationship between the chemical structures of the two agents and not to the influence of 5-HT metabolism, since the effect occurs shortly after the application.

The strong effect produced by KCl might be due to the depolarization role of this substance in general, and is indicative of the fact that reflexes originating from the receptors of the heart may well be activated also by such non-mediator type substance.

5-HT and KCl influenced also the rhythm of cardiac action simultaneously, namely exactly in the same way as in isolated preparations of the heart of mussels, whereas ACh which was inhibitory on isolated heart, was practically ineffective on the rhythm of cardiac action and in producing reflex effects on the adductor. It is difficult to explain this latter, but one may refer to data showing that the exterior wall of the ventricle full of fluid is also *in vitro* relatively less sensitive to ACh (FLOREY and MERWIN 1961).

Data obtained by mechanical and electrical stimulation prove that the responses of the adductors are exclusively due to the excitation of the heart and it is beside the question that the stimulating agent may by penetrating through the wall of the heart reach by circulation the adductor itself and influence it directly. Though the possibility for this is small even because of the small amounts of substances applied, nevertheless, the mechanical and electrical stimuli applied strictly to the heart may produce further evidences for the assumption that the direct and local stimulation of the receptors of the heart are completely sufficient to induce the observed responses of adductors.

Special attention is due to the fact that whenever, almost without exception, it was attempted to produce by reflexes relaxation of tonically

contracted adductors, the posterior adductor relaxed earlier than the anterior one. According to the assumptions in literature (PAWLOW 1885) the centre of relaxation is located in the cerebral ganglia and the cessation of tonicity of both adductors is regulated from there simultaneously. This implies further that the relaxation of adductors should be simultaneous or rather the relaxation of the anterior adductor should precede that of the posterior one. The data obtained contradict to this assumption, and it seems more likely that the relaxation of posterior adductor is the function of the visceral ganglion which innervates also the heart. On the other hand, the late relaxation of the anterior adductor is explainable by the assumption that the relaxing effect arising from the visceral ganglion towards the posterior adductor runs simultaneously also in the direction of the cerebral ganglia, where after proper summation of stimuli it produces the delayed relaxation of the anterior adductor. This fact naturally does not contradict the theory that the cerebral ganglia may under physiological conditions play an important role in the simultaneous, coordinated relaxation of anterior and posterior adductors. The idea, however, that the relaxing effect originates in case of both muscles exclusively from the cerebral ganglia should be rejected.

Summary

The responses of the anterior and posterior adductors of fresh water mussel to various stimuli were investigated. In the course of the experiment chemical (5-HT, tryptamine, ACh and KCl) mechanical and electric stimuli were applied.

The followings were established:

1. The local stimulation of the heart produces reactions not only on the heart itself, but influences also simultaneously the activity of the adductors. The effect on the adductors manifests itself in the activation of the mechanism of relaxation if the adductors are in tonic contraction. If, however, the adductors are in the condition of relaxation and show rhythmic activity at the application of the stimulus, then after some initial contraction increased relaxation takes place or there is a return to the original rhythm. Most pronounced relaxing effect was observable on the application of 5-HT to the heart.

2. When the activities of the two adductors were recorded separately it was observed, that the relaxation of the posterior adductor took place in general earlier than that of the anterior one. This implies, in contradiction to published data, that the central nervous elements responsible for the relaxation of adductors are not exclusively located in the cerebral ganglia.

3. The area of the heart is the receptor zone of the adductors and a close reflex relationship exists between the heart and the adductors.

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A TAVIKAGYLÓ (*ANODONTA CYGNEA* L.) ZÁRÓIZOMMŰKÖDÉSÉNEK
REFLEXES BEFOLYÁSOLÁSA SZÍVRE HATÓ INGEREKKEL

Összefoglalás

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Vizsgáltuk különböző ingerek szíven való alkalmazása esetén az elülső és hátsó záróizom válaszreakcióit tavi kagylón. A kísérletek során kémiai (5-HT, tryptamin, ACh, és KCl), mechanikai és elektromos ingereket alkalmaztunk. Megállapítást nyert, hogy

1. A szív lokális ingerlése nemcsak magán a szíven vált ki reakciót, hanem egyidejűleg a záróizomműködést is befolyásolja. A záróizmokon a hatás a relaxációs mechanizmus aktiválásában jut kifejezésre akkor, ha az izmok tónusos kontrakcióban voltak. Ha az inger alkalmazásakor a záróizmok ernyedtek, ritmusosan működő állapotban voltak, akkor kezdeti néhány kontrakció után ugyancsak fokozott relaxációt vagy az eredeti ritmusra való visszatérést észleltük. Legkifejezettebb relaxációs hatás az 5-HT szívre való applikálásakor volt megfigyelhető.

2. A két záróizom működésének egymástól független regisztrálásakor az volt megfigyelhető, hogy a hátsó záróizom ernyedése rendszerint hamarabb kezdődött, mint az elülső záróizomé. Ez irodalmi adatokkal ellentétben arra utal, hogy a záróizomok relaxációjáért felelős központi idegi elemek nem kizárólag a cerebrális ganglionokban helyezkednek el.

3. A szív területe a záróizmok receptorzónája, s a kettő között szoros reflexes kapcsolat áll fenn.

РЕФЛЕКТОРНЫЕ ИЗМЕНЕНИЯ ДЕЯТЕЛЬНОСТИ ЗАПИРАТЕЛЬНЫХ
МЫШЦ БЕЗЗУБКИ (*ANODONTA CYGNEA* L.) ПРИ РАЗДРАЖЕНИИ СЕРДЦА

Я. Шаланки и Т. Печи

Изучались ответные реакции передней и задней запирательных мышц беззубки в зависимости от применения разных стимулов на её сердце. В ходе экспериментов были применены химические (серотонин, триптамин, ацетилхолин, хлористый калий), механические и электрические раздражения. Было установлено, что

1. Местное раздражение сердца вызывает реакцию не только на самом сердце, но одновременно влияет и на деятельность запирательной мышцы. Эффект на запирательных мышцах выражается в активизации механизма расслабления, если мышцы были в состоянии тонического сокращения. Если в моменте раздражения запирательные мышцы находились в расслабленном, ритмически работающем состоянии, тогда через несколько начальных сокращений наблюдалось также повышение расслабления, или возобновление исходного ритма. Самым сильным расслабляющим эффектом обладал серотонин при его применении на сердце.

2. При регистрации деятельности двух запирательных мышц независимо друг от друга, было установлено, что расслабление задней запирательной мышцы наступает раньше расслабления передней запирательной мышцы. В отличие от литературных данных это факт указывает на то, что нервные элементы, ответственные за расслабление запирательных мышц локализируются не только в церебральных ганглиях.

3. Область сердца является рецепторной зоной запирательных мышц, и между сердцем и запирательными мышцами существует тесная рефлекторная взаимосвязь.