# ON THE NATURE OF THE COMPONENTS OF THE POTENTIAL COMPLEX INDUCED BY ELECTRIC STIMULATION ON ANODONTA NERVE

# E. LÁBOS and I. VARANKA

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

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In preliminary experiments by electric stimulation of the cerebrovisceral connective (CVc) of the fresh-water mussel Anodonta cygnea L. we dwelt on the stimulus-parameter-dependence of the action potential (SALÁNKI et al. 1964), on the demonstration of the morphological and electrophysiological heterogeneity of the nerve (LÁBOS et al. 1963), on the pharmacological behaviour of the nerve (LÁBOS et al. 1966) and on the analysis of the effects of some methodical conditions (LÁBOS 1965). The experiments unequivocally indicated that the evoked complex potential of the nerve consists of a part more sensitive to chemical influences and of a more resistant part. The present studies are related to the characters of the complete and resistant rest potential. The complete action potential is the action potential of the nerve activated with sufficiently great stimulation while the rest potential is the response to be led off after the block of the conduction (e. g. tetracaine or procaine treatment).

A substantial part of the previous leadings and purposefully also the present ones were conducted under conditions where one of the electrodes of the exciting and leading off circuit is common so that also the local response of the nerve was recorded (BURES et al. 1960). It is necessary to elucidate the relationship of the rest-potential and local potential to each other. In connection with the analysis of other features of these potentials we dwelt also on the issue of the decrement of the *Anodonta*-CVc described under various methodical conditions (ZHUKOV 1946; KAHN and KUSNEZOV 1938). BULLOCK (1965) believes the cause of the decremental conduction to be found in the conditions dwelt on by SCHLOTE (1955).

## Method

The nerve during excitation and conduction was in paraffin oil. Excitation was carried out by DISA Multistim stimulator, recordind with the DISA 51BO1 (1M $\Omega$ , 100 pF) DC amplifier. Among the stimulating and recording electrodes one was a common and at the same time grounded electorede. The upwards directed deflection signifies an increase in positivity of the area below the active (not grounded) leading off electrode as compared with the potential of the area below the ground electrode. Silver wire and plate electrodes were used. For reproducibility of the electrode layout the distance between the stimulating electrode and the proximal edge of the ground plate (s), the length of the ground plate (g) and the distance between the (different) recording electrode and the other marginal point of the ground plate (r) are given. Under the given conditions at distances of 1 mm minimum the potential with maximum amplitude is obtained at the sequence of values 1-10-3 mm s-g-r. We refer to ground positive stimulation when the common ground electrode at the time of the employed square-impulses is the anode, while the other stimulating electrode compared with it is the negative one (cathode). The case of the stimulation of reversed polarity is called ground-negative one.

# Results

# 1. The difference between the response of the fresh and blocked nerve

The CVc responds after application of effectively blocking pharmacons in the present case tetracaine — to the electric excitation with a prolonged, one-component "rest potential".

In Fig 1. in the cases A, C, E a ground-negative excitation, in the cases B, D, F a ground-positive excitation was employed. The non-blocked nerve retains the direction of its response with the change of the polarity of the stimulus at the given parameters of excitation but we obtain a lesser response to ground positive excitation. From Fig. 1 it appears that after tetracaine block (C, D, E, F) we obtain a response turning with the polarity of excitation.

On this basis we can distinguish a resistant polarity-dependent and polarity-independent comparatively rapid wave group which is substantially more sensitive to chemical influences. The response at the fresh nerve contains both. To the turn of this polarity-dependent part is ascribed the reduction of the response of the fresh nerve with the employment of ground-positive excitation.

It should be noted that the deflection begins after the 10 ms square wave impulse employed subsequently to its ending. Thus the rest-potential does not correspond to the stimulus-artefact but is a substantially slower procedure. Using a longer stimulus (Figs 1E and 1F) it becomes visible that a more inert phenomenon is involved which continues irrespective of the ending of the excitation. As pointed out previously (LáBos et al. 1966) similar phenomenon can be induced on dead nerve or thread wetted with electrolyte. The slow phenomenon goes also with the reaction of the living nerve, and can be led off at the layout using the three electrodes. The living nerve, besides, gives a polarity-independent response, while the blocked and dead excitation exhibits only polarity-dependent phenomena. Under the given methodical conditions, besides, the stimulus-artefact appears both on living and blocked nerve.

#### 2. The response of the nerve to ground-positive excitation.

If the nerve sector below the ground-electrode is the anode, then depending on the voltage and period of the stimulation subsequently to the ending of the latter, downwards directed signals of various size are obtained. On Fig. 2 we employed ground-positive excitations of short period and of various tensions. Subsequently to the wave directed downwards after various periods we observe a wave of opposite direction. The latter is the polarity-independent



Fig. 1. Explanation in the text. (A-C-E: ground negative, B-D-F: ground positive stimulation

1. ábra Magyarázat a szövegben. (A-C-E: földnegatív, B-D-F: földpozitív ingerlés.)

response appearing during the period of the anelectrotone but after the ending of the stimulus signal. Since this is directed upwards, its appearance causes the potential to rise.

The beginning of the wave directed upwards takes place depending on the velocity of the processes of opposite trend sooner or later; therefore the real period of latency can not be exactly determined. Although the period until the



*Fig.* 2. Ground positive stimulation voltage is changing. Electrode layout r-g-s/3-10-1 mm; DC-recording 2. *ábra* Földpozitív ingerlés. Ingerfeszültség változik. Elektróda elrendezés: r-g-s/3-10-1 mm; DC-elvezetés.



Fig. 3. Ground positive stimulation. Impulse-duration changing. Electrode layout 3-10-1 mm; DC recording; stimulus voltage 5 V 3. ábra Földpozitív ingerlés. Impulzusszélesség változik. Elektródaelrendezés 3-10-1 mm; DC elvezetés; ingerfeszültség 5 V.

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turn increases both on the increase of voltage and impulse duration (see *Figs* 2 and 3), on account of the picture of composed character the beginning of the action potential can not be exactly identified with the moment of the turn. Still it undoubtedly appears from *Fig.* 3 that the polarity-independent action potential begins at the ending of the stimulus and constantly lags behind with the increase of the stimulus duration.



Fig. 4. A) Components; B) Passive nerve equivalent on the sector "r"; C) Electrod<sup>e</sup> ayout; D) Impulse prolonging circuit

4. ábra A – Komponensek, B – Passziv idegekvivalens az "r" szakaszon. C – Elektródaelrendezés D – Impulzusnyújtó kapcsolás

Summarizing the facts it appears (Fig. 4a) that the potential condition can be broken down to three phenomena in the course of ground-positive and negative stimulation:

1. stimulus-artefact, which is a polarity-dependent, differentiated square impulse (S)

2. polarity-dependent slow potential (P)

3. polarity-independent action potential (A)

From all these it appears that the direction of the polarity-independent action potential is, irrespective of the trend of the excitation signal, always such that the positivity of the different recording electrode or the negativity of the ground electrode respectively is seen to increase. Since the nerve sector in excitement is negative as compared with that in rest, therefore the comparative increase of negativity of the ground electrode as compared with the different electrode can only signify the excitement of the area below the ground electrode. Thus the place of origin of the signal recorded is the ground electrode. The time of origin of the action potential falls to the period after the cessation of the anelectrotone induced in the ground-electrode.



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Fig. 5. The response of CVc at various voltages. Impulse duration 5 ms; r-g-s/3-10-1 mm; DC-recording; ground negative stimulation
5. ábra A CVc válasza különböző ingerfeszültségek mellett. Impulzusszélesség 5 ms; r-g-s/3-10-1 mm; DC – elvezetés; földnegatív inger.

The process is initiated by the differentiated excitation signal which according to our measurements under the given conditions (the upper limit of the amplifier is 100 kcp (a 1/100-1/1000 part of the amplitude of the excitation signal, the relation between impulse duration and time constant  $d/\tau \sim 100$ ; e. g. upon 5V - 3 ms excitation with optimum electrode layout  $\pm 20$  mV amplitude and about 50  $\mu$  sec time constant can be observed.

# 3. The effect of ground-negative excitation

In this case the direction of the polarity-independent potential coincides with the direction of the slow potential. At an 8 ms impulse width with 0.1 - 0.4 V voltage only the slow potential can be observed (*Fig. 5*). Further increas-



Fig. 6. A) Volt age-dependence of passive (P), complete (A + P) and active (A) potentia component. The curve P was recorded after the novocaine blocking of the nerve.
B) Response amplitude increase (fibre "activation") pertaining to the unit increase in voltage. Considerable activation takes place only below 2 V.

6. ábra A. — A passzív (P), teljes (A + P) és aktív (A) potenciálkomponens feszültségfüggése. A P görbét az ideg novokain-blokkja után vettük fel. B. — Egységnyi ingerfeszültségfokozáshoz tartozó válaszamplitúdó-növekedés (rostaktiválás). Jelentős aktiválás csak 2 V ingerfeszültség alatt van.

ing the voltage there appears the first polarity-independent component practically with "all or nothing" character. Since on the CVc previous authors (KAHN and KUSNEZOV 1938; ZHUKOV 1949; LÁBOS et al. 1963; SALÁNKI and LÁBOS 1964) stated that it conducts the excitation with decrement and the "all or nothing" character is no property of the responses of structures conducting with decrement, we will dwell on the demonstration of the appearance of response with a threshold in detail. As CVc is a complex nerve, its discrete response appears not at a definite intensity of stimulus but in a stimulus voltage interval. It is seen (Fig. 6 A) that upon the increase of the voltage by 0.2 V (from 0.3 V to 0.5 V) a considerable amount of fibre is activated. The further increase of voltage is accompanied by a great increase of the amplitude  $\Delta$  (A+P)  $\Delta$  V high; Fig. 6 B). It appears from Fig. 6 B illustrating the voltage dependence of fibre activation that at 1 V, 4 msec under the given conditions the fibre activation is minimal. According to measurements conducted for the first active component a stimulus of 1.5-2 V is already supermaximal.

From previous investigations (LÁBOS 1965) it is evident that the electrode removal in the stimulation circuit may increase the above value several times. Therefore, without indicating methodical conditions e. g. electrode parameters the reproduction of this data is not possible even apart from the individual dispersion.

The voltage-dependence curve of the active wave group (as measured at the first peak) (Fig. 6 A) is in our assumption combined out of the corresponding curve of the passive polarity — dependent potential and the first polarity-independent component. Thus the A-curve indicates the corrected voltage dependence.

In our previous studies owing to the AC recording it was difficult to evaluate the slow components. From Fig. 5 it appears that the potential maximum is at the 40, 80, 220 and 720 msec moments as measured from the start of the stimulus signal. Accordingly, there is about 20-fold difference between the velocity of the most rapid and the slowest process. The afterpotential indicating the positivity of the ground-electrode is present, however, also with DC-recording (see Fig. 5, at 1 V), but this corresponds only partly to a true after-potential and is on the other hand the consequence of a rather high degree of asymmetry in the conduction. In such sense it may be brought in connection with spreading.

# 4. The effect of the change in electrode distance

According to previous examinations small electrode displacements substantially influence size and shape of the recorded action potential (LABOS 1965).

At the empoyment of the leading off seen in Fig. 4 C and of groundnegative stimulation the removal of the (different) leading electrode from the ground electrode leads to the following changes:

- 1. with the increase of the distance r the height of the greatest component increases and then diminishes (Figs 7 and 8)
- increases and then diminishes (Figs 7 and 6)
- 2. the components become indistinct
- 3. as measured on the basis of time at the peak of first component the velocity of this component depends on the assumed path-way of conduction; this relation subsists irrespective of whether we assume the site

of origin of the excitement to be at the possible two extreme points.

When conceiving the action potential recorded as a spreading excitation, we can refer to conduction with increment and decrement. But then we must raise the question of the place of origin of the excitement to measure the distance of the way covered. On Fig. 9. we represented the dependence on



Fig. 7. Change of the action potential at the "r" sector of 1-28 mm length Stimulus parameters: 3 V, 3 msec; DC-recording; g = 10 mm, s = 1 mm
7. ábra Az akciós potenciál változása 1-28 mm hosszúságú "r" szakasz mellett. Ingerparaméterek: 3 V, 3 msec; DC-elvezetés; g = 10 mm, s = 1 mm.

the way of the assumed velocity of the conduction considering two extreme hypotheses namely whether the excitement originated in points 1 or 2, respectively. From the *Figure* it appears that the hypothesis of the leading off conducted potential goes with the consequence that the velocity has an increment. This increment is of a lesser degree if the excitement would arise in the distant point 2.





 ábra A 7. ábrán látható válasz maximális amplitúdójának függése az "r" szakasz nagyságától.



Fig. 9. Explanation in the text; S = stimulator; A = amplifier9. *ábra* Magyarázat a szövegben; S = ingerlő; A = erősítő

# 5. On the characters of the potential of passive origin

The period of the passive polarity-dependent potential generally exceeds substantially the period of the excitation signal. When employing long excitations it shows a release effect, a breaking point. This phenomenon begins



Fig. 10. The voltage dependence of the value of the passive component at various duration of impulse. Ground positive and ground negative stimulation

10. ábra A passzív komponens nagyságának feszültség függése különböző impulzusszélességek mellett. Földpozitív és földnegatív ingerlés.

to appear in excitations longer than 100 msec (Fig. 3). Also with DC recording a slow overshoot can be observed which with high stimulus parameters amounts to 5-10 per cent of the main phase.

The dependence of this potential on the voltage (Fig. 10) at small impulse duration is linear. Consequently it differs mainly here from the similar dependence of the action potential. With increasing impulse duration the curve somewhat fattens. With optimum electrode layout (1-10-3 mm) and with impulses of 1-100 msec duration the peak value of the passive potential attains a  $5.10^{-3}-10^{-4}$  part of the stimuli-voltage. The size of the response directed downwards and upwards on blocked nerve is uniform, but a period of several times 10 sec is needed to elicit a reaction true to form and of the original size. The impulse duration dependence of the amplitude of the potential between 1-10 ms steeply rises to flatten subsequently.

In some cases the passive response obtained on the ground-negative and ground-positive stimulation differs to the benefit of the former. The basis of this asymmetrical behaviour can not be sought in the given electrode display, deviation of stimulating current density, conduction with decrement, inhibiting effect of anode zone, and asymmetrical reaction of amplifier. Consequently it must be ascribed either to the injurious effect of the long-term excitations or to the fact that the depolarisation of the blocked nerve takes place more readily than its hyperpolarization.

## Discussion

In analysing the phenomena examined let us deal first of all with the passive polarity-dependent potential. Since thread and dead nerve also exhibit similar phenomena, the term passive response is justified. Naturally the passive reaction different from each other of thread, dead nerve and living nerve reflects also the differences of electrochemical processes taking place in these objects under the influence of electric voltage difference. With extracellular recording it is not possible to decide whether in the living nerve the local potential is only of electrolysis (SEGAL 1958) or another phenomenon. The intracellular recording clearly points to membrane potential changes (HODGKIN, and HUXLEY 1945). The analysis of this, however, exceeds our fixed purpose.

The quadripole, which most closely imitates the time course of the passive response is the impulse stretching circuit (TARNAY 1962). Besides the linear circuits some RCL circuits near limit damping also give similar response if upon their input we give a square pulse. They are not satisfactory, however, for other reasons.

The other important character of the polarity-dependent passive response is that it appears also in subthreshold excitations. As to this feature it corresponds to the subthreshold response of HODGKIN (1938). But even over the supermaximal voltage the increase of passive response could be observed.

Its relative resistance to blocking substances justifies the denomination as rest potential.

Its character of local response, local potential follows from the mode of recording (BURES 1962). It is remarkable that the synaptic potential which is formally similar to the passive potential also shows the features enumerated (TAKEUCHI and TAKEUCHI 1962, ECCLES 1957). Thus, both the natural and artificially arising excitement is introduced by a phenomenon concordant in several features. Of course beside the similarities referred to there are also substantial differences the discussion of which exceeds our purpose.

The passive potential obviously possesses such characteristics on the basis of which it may be named electrotonic potential. To this the fact is pointing that the cessation of its positivity leads to excitement.

We regard as the place of origin of the polarity-independent potential the ground electrode because its direction points to the relative negativity of the ground electrode. In this sense we recorded also the polarity-independent potential as a local phenomenon. It is evident that this does not contradict to its spreading but it can not be regarded as a signal of active change under the different electrode, when it is directed upwards. The downwards directed and the shunt of opposite direction exceeding even the zero line (see Fig. 5, at 1V) may be the consequence of the action potential spread below the different electrode because it points to the increase of negativity of the area below this electrode.

Thus it can be established that we lead off the passive and active response originated under the ground electrode. The local changes taking place under the ground electrode interfere with the waves directed downwards and develop as a consequence of spreading. The excitement originates where the passive response appears as a negativity. Consequently the nerve behaves so that it always responds to a change of ascending direction of the square excitation: we have lead off cathode-on and anode-off responses. In this respect the reaction of the CVc agrees with the response of vertebrate nerves. At groundpositive stimulus the conduction of the excitement developed below the negative stimulating electrode is inhibited by the developed anodic zone. Thus the responding system behaves so as if it would react to a differentiated signal and leaves without answer the positive phase.

In judging the origin of increment and decrement observed in the course of electrode removal we must reckon with the following possibilities:

1. The measurement of the spreading velocity is not correct because the site of measurement (that is the peak of the action potential) is shifting for different reasons.

2. If we assume the fact of spreading for the explanation of the phenomenon demonstrated in Figs 7 and 8 then the increment can be conceived as a separation phenomenon. In the course of bipolar recording the removal of the conducting electrodes may lead to increased amplitude of the originating wave if the velocity of spreading and the rising velocity of the spreading wave are in a definite relation. But then we ought to observe the increase of the amplitude of the wave spread below the different electrode which, however, is not observed.

3. Increment and decrement can be conceived as a consequence of the passive electric properties on the basis of the following simple cable model. Let us assume that the equivalent of the nervous signal source is a generator causing longitudinal polarisation between the different recording electrode conduction and the ground electrode which has an ohmic resistance and capacity depending on the length. To the reality of the assumption of capacity the differentiation of the square signal points directly. This equivalent (see F ig. 4 B) contains these two elements in a parallel bond.

Then, according to the 1. law of KIRCHOFF:

$$\mathbf{I}_{\Sigma} = I_A + I_R + I_C$$

where the sum of the currents flowing through the elements R, C and the amplifier A constitute the total current. The current flowing on the amplifier on the input resistance causes the voltage corresponding to the recorded signal.

From the former equation

$$I_A = I_{\Sigma} - (I_R + I_C) = I - \left[ U \frac{1}{R} + j \omega C \right]$$

where  $I_{\Sigma}$  is the short-circuit current which in the case of steady excitation is constant, U is the voltage drop on the parallel RC- member.

The voltage drop on the input of the amplifier is

$$E_A = R_A \bigg[ I_{\Sigma} - U \bigg( \frac{1}{R} + j \, \omega \, C \bigg) \bigg]$$

Let the values of R and C be proportional with the inter-electrodal distance r. Then

$$E_A = K_A - UR_A igg[ rac{1}{k_{
m R}r} + j \ \omega \ k_{
m C}r igg]$$

From the model employed it follows (see Fig. 11):



Fig. 11. Explanation in the text 11. *ábra* Magyarázat a szövegben.

1. On account of the growth of capacity proportional with the length a linearly increasing member  $(k_C r)$ , on account of the growth of resistance a hyperbolically decreasing member  $(1/k_R r)$  is substracted from the tension dropping on the instrument. Thus from the electromotoric force constant in the case of constant stimulus on account of the inner impedance of the signal source the losses are deducted. The dependence of the value of the voltage drop on the amplifier is determined by these factors. Also the role of the shuntresistances can not be neglected (e. g. liquid layers in the nerve; see Fig. 4 B). The r-dependence assumes the shape observed in the experiment.

2. In view of the presce of the capacity its signal consuming effect will be more explicit for the rapid components and therefore the dominance of

the slow phenomena can be expected at high r values. This is what the experiments show in reality.

3. The phase of the components of different frequency must show a shift as compared to each other owing to the capacitive member.

It appears that the model used, the correctness of which must be controlled with concrete longitudinal impedance measurements, can readily be employed for the case examined of the electrode removal. Thus in the realization of the decrement observed the role of the passive electric properties can not be neglected. It is remarkable that the slow and according to literature decrementally spreading local response (see the handbook of BURES 1962, p. 243) does not exhibit an explicit decrement. This also stresses the correctness of our model exacting the decrement of lower grade and of methodical origin of the slower components.

The issue of the decrement of the response spreading forth is another problem. According to the model employed a decremental conduction is possible but it must not be assumed for the observed reduction of amplitude. Since it exhibits "all or nothing" properties, it is probable that it has no real decrement.

# Summary

The response induced with electric stimulation of the cerebrovisceral connective (CVc) of the fresh-water mussel (Anodonta cygnea L.) was examined.

The experiments were conducted with the common grounding of the stimulating and measuring circuit. It was established that

1. The response is divided into a polarity dependent, to chemical influences less sensible passive and a polarity-independent blockable component.

2. The excitement is caused by the increased negativity of the site of its origin. The ground-positive excitation gives an off response. The site of origin of the response recorded is the ground plate.

3 During the polarity independent action potential the negativity of the ground electrode increases, that is in this sense it is accompanied by the change of relative positivity of the different leading-off electrode. Positive "after potential" can be observed also with DC-recording.

4. The increment and decrement observed in the course of the removal of the different leading-off electrode as well as filtering and phase-shift can be explained by the change of the complex admittance of nerve sector in the measuring circuit (r) without the assumption of the recording of the spreading wave.

5. One of the most simple non-linear models of the passive response is an impulse prolonging circuit.

## REFERENCES

 BURES, J., M. PETRAN, J. ZACHAR (1960): Electrophysiological Methods in Biological. Research. Publishing House of the Czechoslovak Academy of Sciences, Prague.
 BULLOCK, T. H., G. A. HORRIDGE (1965): Structure and Function in the Nervous Systems

of Intervertebrates. W. H. FREEMAN and Company, San Francisco London. Vol.. II. Chapter 24. p. 1405. and Chapter 23, p. 1307.

ECCLES, J. C. (1964): The physiology of synapses. – Springer Verlag, Berlin. HODGKIN, A. L. (1938): The subthreshold potentials in crustacean nerve fibre. – Proc. Roy. Soc. Ser. B. 126, 87-121.

HODGKIN, A. L., A. F. HUXLEY (1945): Resting and action potentials in single nerve fibres. - J. Physiol. 104, 175-195.

KAHN, J. L., D. P. KUSNEZOV (1938): Decremental conduction of excitation in non-medullated nerve commissure of Anodonta. - Bull. Biol. Med. Exp. 6, 3-5.

LÁBOS, E., I. ZS. -NAGY, K. BENKŐ, J. SALÁNKI (1963): Electrophysiological and electro-microscopic studies on the fibre composition of the crebrovisceral connective of Anodonta cygnea L. - Annal. Biol. Tihany 30, 59-65.
 LÁBOS, E. (1965): The effect of the change of electrode dimensions and distance on the

action potential induced by electric excitation of the unmyelinated nerve Anodonta cygnea L. - Annal. Biol. Tihany 32, 17-27.
 LÁBOS, E., J. SALÁNKI, I. PINKER (1966): Pharmacological analysis of local potential

in unmyelinated nerve. - Acta Biol. Hung .(in press).

SALÁNKI, J., E. LÁBOS, I. NÁN (1964): Electrophysiological properties of the cerebrovisceral connective of the fresh-water mussel (Anodonta cygnea L.). - Annal. Biol. Tihany 31, 133-145.

SEGAL, J. (1958): Die Erregbarkeit der lebenden Materie. VEB. G. Fischer Verlag, Jena. Schlote, F. W. (1955): Die Erregungsleitung im Gastropodennerven und ihr histo-logisches Substrat. – Zeitschrift f. vergleich. Physiol. 37, 373-415.

TAKEUCHI, A., N. TAKEUCHI (1962): Electrical changes in pre- and postsynaptic axons of the giant synapse of Loligo. – J. gen. Physiol. 45, 1181–93. TARNAY, K. (1963): Elektronikus mérések. – (Electronic Measurements). – Műszaki

Kiadó, Budapest.

Zникоv, JE. К. (1964) Жуков. Я. К, Некоторые закономерности эволюции возбуждения. Ж. общ. биол. 7, 435-453.

# AZ ELEKTROMOS INGERREL KIVÁLTOTT POTENCIÁLKOMPLEXUM KOMPONENSEINEK TERMÉSZETÉRŐL, ANODONTA IDEGEN

#### Lábos Elemér és Varanka István

# Összefoglalás

Edesvízi kagyló (Anodonta cygnea L.) cerebroviscerális connectivumának (CVc) elektromos ingerrel kiváltott válaszát vizsgáltuk.

A kísérletek az ingerlő és mérő-áramkör közös földelése mellett történtek. Megállapítható, hogy:

1. A válasz polaritásfüggő, kémiai behatásokra érzéketlen passzív, és polaritásfüggetlen, blokkolható komponensre oszlik.

2 Az ingerületet az ingerület keletkezési helyének negativitás-növekedése okozza. Így földpozitív inger nyitási választ ad. Az elvezetett válasz keletkezési helye a földlemez.

3. A polaritás-független akciós potenciál tartama alatt a föld-elektród negativitása nő, azaz ilyen értelemben a differens elvezető elektród pozitivitásváltozása kíséri. Pozitív "utópotenciál" DC-elvezetés mellett is észlelhető.

4. A differens elvezető elektród távolítása során észlelt inkrement és dekrement, valamint szűrés és fáziseltolódás a mérőköri idegszakasz (r) komplex admittanciájának változásával, a terjedő hullám elvezetésenek feltételezése nélkül magyarázható.

5. A passzív válasz egyik legegyszerűbb modellje az impulzusnyújtókapcsolás.

# О ХАРАКТЕРЕ КОМПОНЕНТОВ НЕРВНОГО ИМПУЛЬСА, ВЫЗВАННОГО ЭЛЕКТРИЧЕСКИМ РАЗДРАЖЕНИЕМ В НЕРВЕ БЕЗЗУБКИ

## Элэмер Лабош и Иштван Варанка

1. Изучали реакцию церебровисцерального коннектива беззубки на электрическое раздражение.

 Опыты проводили в условиях общего заземления отводящего и раздражающего электродов.

3. В реакции различимы две составляющие. Одна зависит от полярности и нечувствительна к химическим воздействиям, другая не зависит от полярности и состоит из компонентов, блокируемых при химических воздействиях.

4. Возбуждение возникает при увеличении местной негативности. В этом случае при замыкании возникает импульс под заземляющей пластинкой.

5. В течение потенциала действия, независимого от полярности, увеличивается негативность под земляным электродом, иначе говоря происходит изменение позитивности под дифферентным отводящим электродом. Положительное последействие наблюдается и при использовании усилителя постоянного тока.

6. Инкремент и декремент, наблюдаемые при смещении дифферентного отводящего электрода, фильтрация и сдвиг фаз объясняются изменением полной проводимости участка нерва в измерительной цепи; нет необходимости предполагать, что при этом имеет место изменение распространяющейся волны возбуждения.

7. Самая простая модель пассивного ответа обсуждена.

Dates in the state of the second states in the