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MAKE AND BREAK RESPONSES OF *ANODONTA* NERVE EVOKED BY DIRECT CURRENT STIMULATION

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The cathodal origin of the nerve-impulse and the failure to appear or nevertheless sometimes the emergence of an action potential with a decreased amplitude when the anode is proximal to the recording electrodes, are known as the basic principles of electrophysiology (PFLÜGER; 1859; BURES, 1960). This latter phenomenon, that can be observed mainly on isolated nerves at special conditions of the stimulation has been explained in the old literature (BIEDERMANN, 1895) by the supposition of the so called virtual cathode claiming that it would be responsible for the anode-make and cathode-break excitations. LORENTE de NO (1947) explained such virtual cathode-phenomena on isolated nerves by the irregularities of the interpolar nerve-segment. LORENTE de NO has concluded that the anode-excitation is not originating from a virtual cathode yet exists when the stimulating current is very low and/or the nerve is near to its unstable state.

The aim of our experiments was to describe and interpret the laws of direct current excitation for the cerebrovisceral connectives (CVc) of *Anodonta cygnea* L., at a constant arrangement of the electrodes. It will be pointed out that the PFLÜGER's laws, the WALLER's formula and the supposition of the virtual cathode represent a simplification, can not explain the facts and are not describing unequivocally the behaviour of CVc.

Methods

The isolated cerebrovisceral connectives (CVc) of *Anodonta cygnea* L. were kept in physiological solution of MARCZYNSKY (1959) and later during the leading off, the nerve was lifted into paraffin oil (SALÁNKI et al. 1964). Only such samples of paraffin oil were suitable which do not contain more volatile hydrocarbons (LÁBOS, unpublished). Four silver-electrodes were applied. Among them the stimulatory electrode situated proximally to the recording ones, was an earthed silver plate of 10 mm, the others were made from silver wire of 0,2 mm diameter *(Fig. 1)*. The action potential of some mV was amplified by a symmetric RC-amplifier (DISA, 14COO2, 200 MΩ, 24 pF; 1,6—500 cps). For stimulation the constant voltage output of a DISA Multistim equipment was applied.

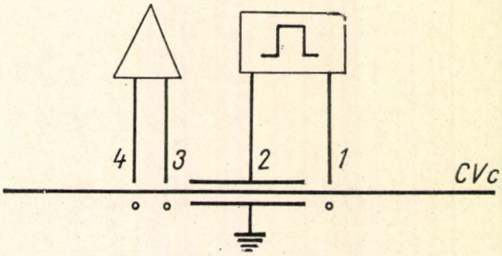

Fig. 1. Experimental arrangement. The 1st electrode is 1 mm away from the proximal edge of the 2nd electrode of 10 mm. Distance between the 2nd and 3rd electrodes is also 1 mm. Between the 3rd and 4th electrodes it is 10 mm.

Passive components (LÁBOS and VARANKA, 1966) owing to the special leading off and amplification have not been observed up to 1,6 V of stimulatory voltage. Between 1,6 and 2,0 V, it increased the amplitude by a value representing not more than 10 per cent. As it is a systematic error, it did not trouble the comparisons. The amplitudes of action potentials were measured peak to peak at the maximal component. The designations of the responses are the following:

1. cathode-make response — CC
2. cathode-break response — CO
3. anode-make response — AC
4. anode-break response — AO

In all cases the marking of the polarity had reference to the larger, earthed and stimulatory electrode, proximal to the leading off pair.

The temperature was 25—28 °C.

Results

1. *Polarity-dependence of the amplitude-voltage characteristics at short pulses*

Fig. 2 shows that in general the amplitude of the response is higher, if the electrode proximal to the recording ones, — otherwise always earthed — is used as anode. Thus, the voltages necessary to activate to 50 per cent, using pulses of 3 msec, are 0,8 and 1,2V, stimulating by pulses of 10 msec are 0,42 and 0.82V, respectively, according to polarity whether it is earth-positive or earth-negative. Therefore it can be seen, that the anode-proximal excitation is dominating.

2. *Amplitude-voltage diagrams when applying pulses of 1 sec*

In general the on- and off-responses begin to separate above 100 msec duration of the stimulatory pulses. Already during a stimulus of 1 sec, this separation takes place entirely. As one can notice in *Fig. 3* both make and break responses can originate under the influence of cathode (earth-negative) or anode (earth-positive) stimulation. Furthermore, the amplitude of the responses can be arranged in diverse sequences depending on the stimulatory voltage. Almost all possible sequences exist well reproducibly.

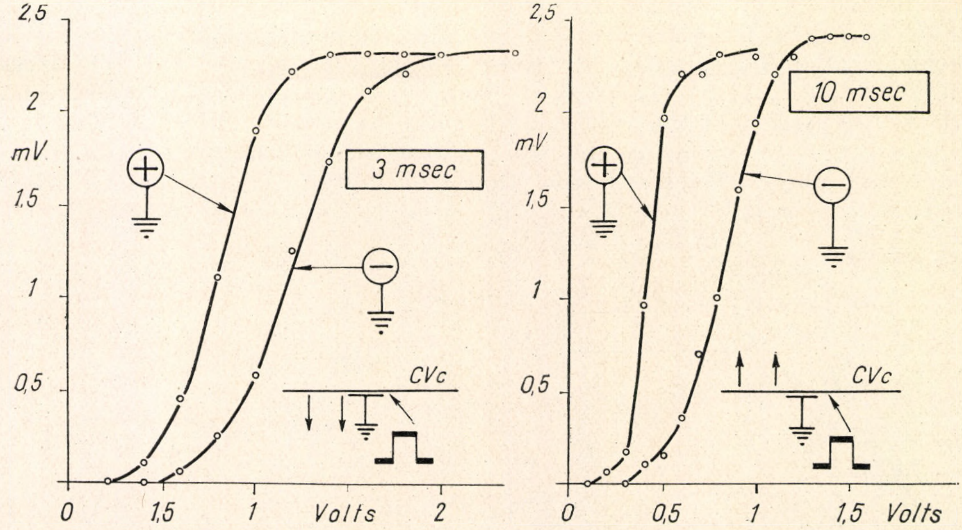

Fig. 2. Amplitude-voltage diagrams at 3 and 10 msec pulses. Earth-positive and earth-negative stimulations

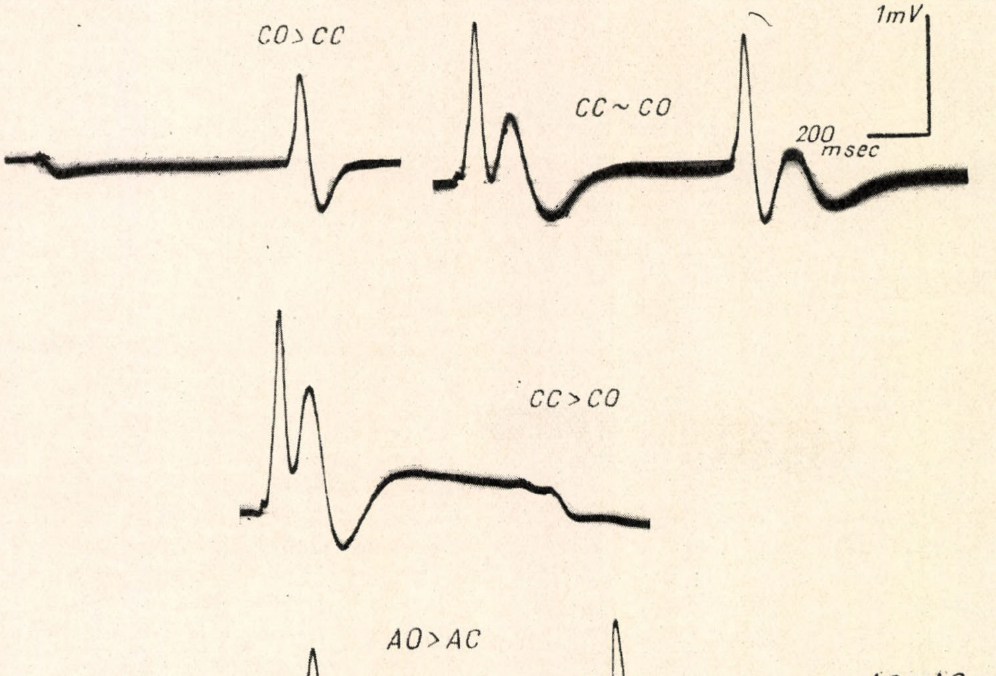

Fig. 3. Different sequences of anode and cathode on and off responses. Designations see in the text

In *Fig. 4/A* the average of amplitude voltage diagrams of 15 nerves is demonstrated. The standard deviations of the CC, AC, CO and AO curves are 12,5 ± 9,7; 21,2 ± 12,2; 25,4 ± 9,6; 25,4 ± 15,2 per cent respectively. It is observable that the values of CC curve have the minimal uncertainty. The standard deviations of the remaining ones is higher by 1,5—2. The differences are statistically significant. Thus $0{,}05 > P > 0{,}02$ ($f = 38$; $t = 2{,}14$) is valid for the differences of the coefficients of variation in the cases of CC and AC curves. It is noticeable that the dispersions of the low amplitudes are higher and the standard deviation in a sense follows the course of the averages *(Fig. 5)*.

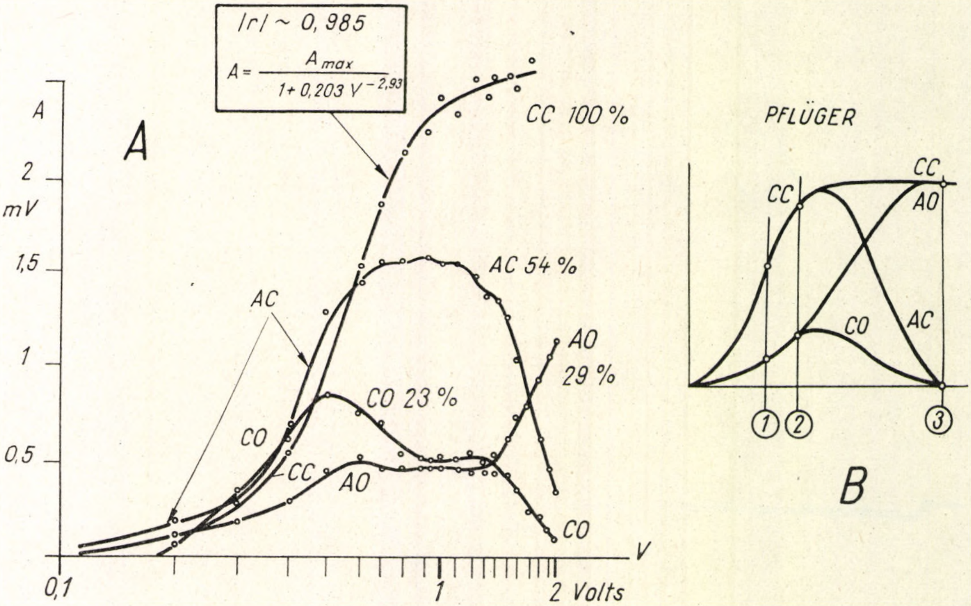

Fig. 4. A — Amplitude-voltage curves of 15 nerves at the 4 kinds of excitation. B — The ensemble of curves expected according to PFLÜGER's laws. Data in per cent design the ratios of surfaces up to 2 Volts.
Empiric equation for CC is also demonstrated. Duration is 1 sec.

In *Fig. 4* a deviation of the four curves can be well observed. The CC-response has always an S-shaped curve. The value of saturation is 2,53 ± 0,66 mV. The voltage evoking the half-maximum is 0,45 ± 0,49V. The AC-curve starts a little more steeply than the CC, later by a lower amplitude (1.56 ± 0,82 mV) it reaches to a maximum of plateau and finally at about 2—2.5 V V of stimulatory voltage disappears. The CO one has two maxima at 0.5 and 1,2V. Their values are 0,85 ± 0,89 mV and 0,54 ± 0,39 mV resp. The CO diagram also starts more steeply than the CC one, and it vanishes at 2V. The AO-curve starts least abruptly of all and culminates broadly at a low value (0,54 ± 0,64 mV), but from 1,25 V it begins newly to increase. Its steady-state value is about 1,5 mV. The ratios of the surfaces under the curves represent a typical sequence, if the summation is carried out to the steady-state values:

CC > AC > AO > CO and finally
CC > AO > AC > CO

The four curves form a complicated system of intersection points. The number of intersections of not random type is in average 4—5, but in extremities is 0—10. The 4—5 observed intersections imply the same number of changes in the sequences of amplitude. In the demonstrated case the sequences are the following:

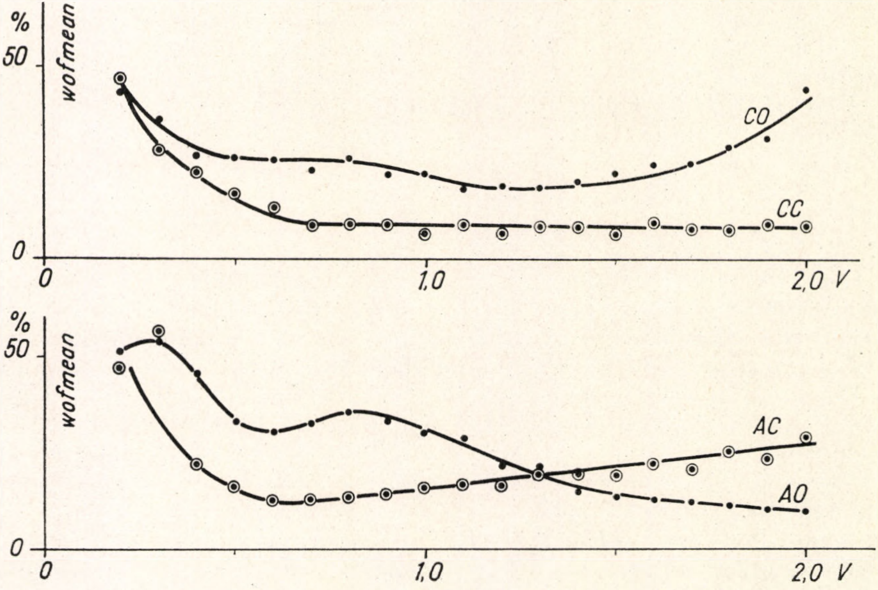

Fig. 5. Variation coefficients of averages plotted against voltage for CC—AC—AO—CO responses (belong to the data of *Fig. 4)*

1. AC > CO > CC > AO   if 0 < V < 0,45 V
2. AC > CC > CO > AO   if 0,45 < V < 0,65
3. CC > AC > CO > AO   if 0,65 < V < 1,35
4. CC > AC > AO > CO   if 1,35 < V < 1,68
5. CC > AO > AC > CO   if 1,68 < V <

Among these, the 4th corresponds to the physiological contraction-sequence of Waller. Referring to the lst (different) stimulatory electrode the 5 sequences are

1. $CC_1 > AO_1 > AC_1 > CO_1$
2. $CC_1 > AC_1 > AO_1 > CO_1$
3. $AC_1 > CC_1 > AO_1 > CO_1$
4. $AC_1 > CC_1 > CO_1 > AO_1$
5. $AC_1 > CO_1 > CC_1 > AO_1$

Also in this case, the Waller-formula is not valid but for a very short interval.

The statistical significance of the differences in amplitudes of the 5 given sequences have to be tested only at low voltage values, as the changes of the 3rd-5th sequences correspond to very high differences. For the average-diagrams the significance of the deviations does not subsist. The cause of this lies in the fact that the range of AC > CC occurs at different intervals duty increasing the dispersion. But the normalization of the curves is problematic. After all, the range of AC > CC has been found in fact in 11 cases out of 15 and in these cases the CC-response may be 5 times higher than AC *(Fig. 6)*. In 4 cases CC > AC is valid. The relation of CO > CC can be observable in half of the cases, of similar dispersing range.

3. *Types of responses*

The differences among some characteristic types of nerve get lost in the course of averaging. These types merit a special discussion. Here it must be stressed that the pecularities in the sequences may not issue from the conditions of the measurement when speaking about CC—CO or AC—AO response-pairs, because they are separated just by the direct current of 1 sec, the effect of which is examined. But the AC—CC, AO—CO, AC—CO, AO—CO relations must be compared to each other more carefully because they were not evoked by the same pulses. Applying a suitable set of measurements and controls, we can eliminate this difficulty.

One of the types is when the CO response is entirely absent. In this case the system of intersections is simple. In other cases, when the CO-response is not too high and the CC-dominance is absolute, the relations of curves are also simple *(Figs. 6A* and *6B)*.

On the contrary, if both peaks of both on-response curves (AO and CO) are explicit *(Fig. 7A)*, the intersections are numerous. In such a case one can observe that the first maxima run together and the breaking down of the 2nd maximum in the CO-curve, the 2nd increase of AO at the saturation manifest themselves at about the same voltages as the breaking down of AC which possibly is of two-phase *(Figs. 7A* and *7B)*.

It occurs accidentally, that the AO response is dominating, mainly when AC is of low value and its maximum is not wide *(Fig. 8.)*.

20 out of 24 possible orders have been observed. However, some of these show themselves only when activating certain nerves. In the table, the numbers of intervals are listed of which a given sequence was found to be characteristic.

Data obtained for the site of intersections are the following (examined on 15 nerves):

1. CC · CO	7	intersections	0,54 ± 0,17	Volt
2. CC · AO	6		0,57 ± 0,22	
3. CC · AC	11		0,55 ± 0,29	
4. AC · AO	15		1,72 ± 0,73	
5. AC · CO	13		1,05 ± 0,57	
6. AO · CO	17		1,19 ± 0,52	(average ± s.d.)

It can be seen that the 3 first points of intersections between 0.5 and 0.6 Volt coincide, forming an initial and unstable system of intersections. They occur in a half of the cases and are found near to the half-saturation value of the CC curve. The found interaction do not represent a system so far uniform.

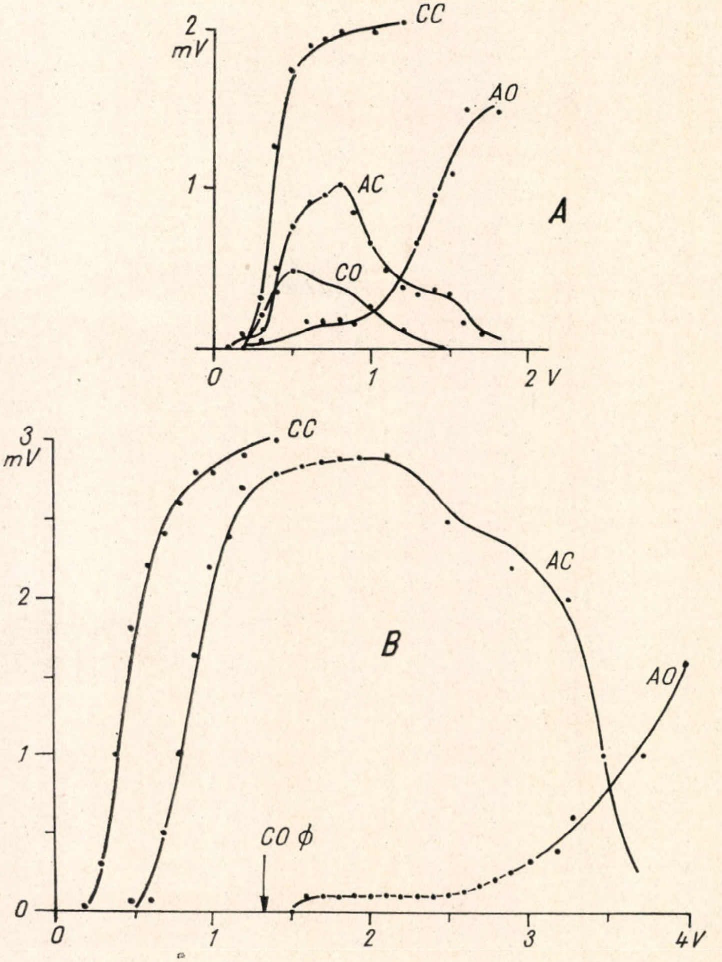

Fig. 6. Extreme types of response, when CO response is low or absent

The sites of AC × AO and AC × CO points deviate significantly ($f = 26$; $t = 2{,}74$; $0{,}02 > P > 0{,}01$). The difference between the AC × AO and AO ×. AO × CO points is significant as well ($f = 30$; $t = 2{,}41$; $0{,}05 > P > 0{,}02$) But the deviation between AC × CO and AO × CO points is not significant statistically ($P > 0{,}05$).

Thus the 6 possible intersections group in the vicinity of 3 values of stimulus-strength.

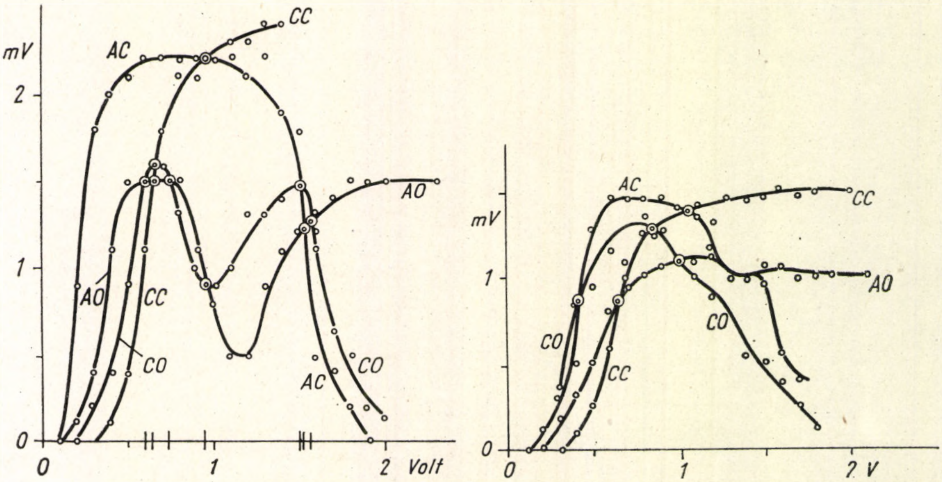

Fig. 7. Extreme types of response, when amplitudes of AC, CO and AO are high

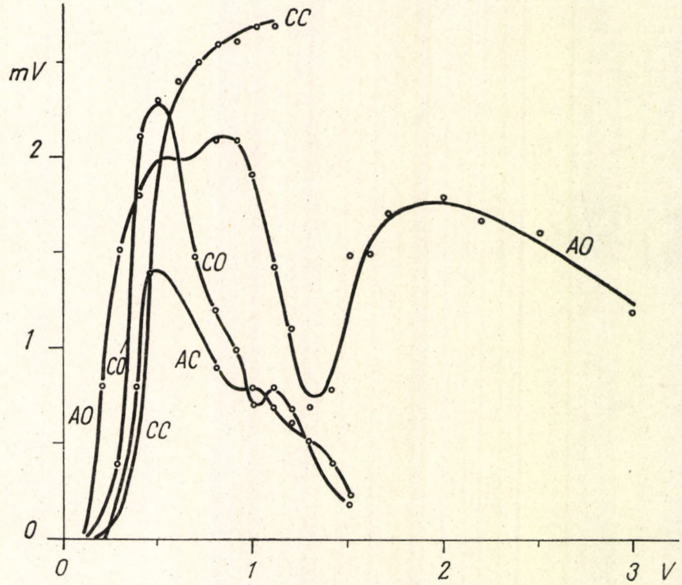

Fig. 8. Anomalous case with AO dominance

4. *The slope of CC-curves at different d durations of pulses*

Only the CC out of the four curves could be approached simply. The approximation was carried out by the following way. The quantities log $\frac{\mathrm{A}}{\mathrm{A}_{\max}-\mathrm{A}}$ was calculated from the maximal and actual values of amplitude. These were plotted against log V, when we obtained a line *(Fig. 9)*.

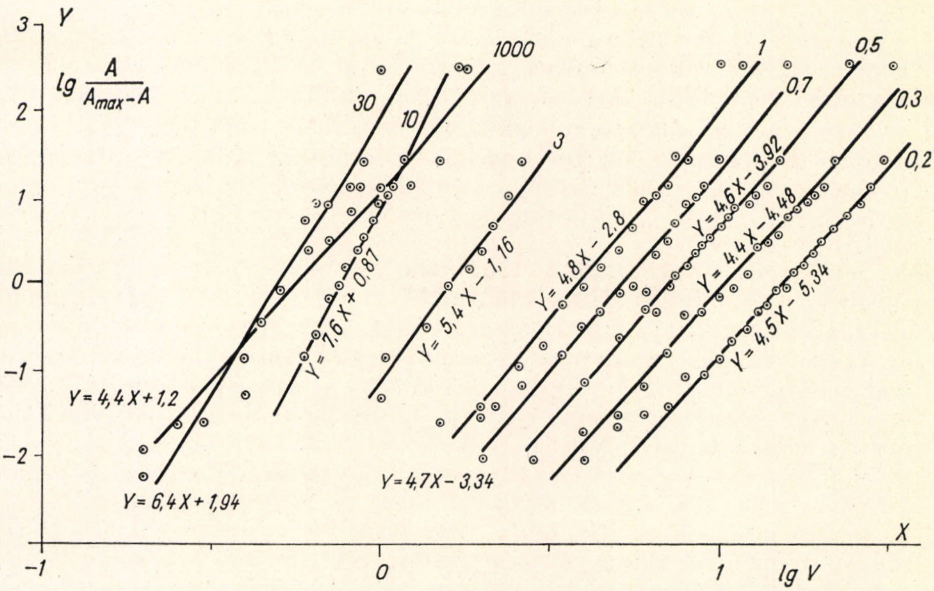

Fig. 9. Linearization of the amplitude-voltage curves. Duration was changed between 0,2 and 1000 msec. Explanation in the text.

From this

$$\log \frac{A}{A_{max}-A} = \alpha \log V + \delta$$

and

$$A = \frac{A_{max}}{1+\beta V_Z^{-\alpha}} \sim \frac{A_{max}}{1+(V_{0,5}/V_Z)^{\alpha}}$$

where $-\log\beta = \delta$. The α-constant is about 4,5 for short pulses. At medium values (3—30 msec) it is 5,5—7,5 and finally for d = 1 sec, the slope decreases newly, $\alpha = 2{,}9 - 4{,}5$. The value of β is much more dependent on d. If for $Z = \frac{A}{A_{max}}$ degree of the activation the strength-duration relation is $V_Z(d)$, then $\beta = \left(\frac{1}{Z} - 1\right) V_Z^{\alpha}(d)$ or $\beta^{-1/\alpha} = V_{0,5}(d)$.

Discussion

For an acceptable interpretation of the observed phenomena it is necessary to take into account the following factors:

1. the character of excitation
2. the site of origin of the responses
3. the condition of the zone influencing the excitation during its propagation (electrotonus, accomodation, refracterity)
4. the different character of stimulatory electrode
5. the fact that the CVc is a complex nerve (Zhukov, 1946; Lábos et al. 1963; Gupta et al. 1969).

Talking of these we have some preliminary suppositions.

ad 1 and 2. — Both opening and closing excitations exist. Threshold of the latter is higher when stimulating by pulses of long duration (**Hill**, 1936; **Werigo**, 1883, 1901). According to **Pflüger** (1859) the make-excitation originates at the cathode, and the break one comes from the anode. In his opinion the make- and cathode-excitations are more intensive. According to the old literature the virtual cathode-phenomena contradict **Pflüger**'s laws only apparently, according to **Lorente** de **No** (1947) they contradict them in reality.

ad 3. — According to **Pflüger** (1859), the cathode-zone is facilitatory the anode-zone is inhibitory. **Hill** (1936) and **Werigo** (1189, 1901) have claimed just the opposite. The attention to this seeming contradiction has been directed by **Naszonov** (1958). Both opinions are well explained by the accomodation and the dynamics of subthreshold-excitation. But, for example, the cathode-effect is inhibitory and that of the anode is facilitatory when the nerve has been treated by KCl (**Woronzov**, 1924, 1925).

ad 4. — In our case the electrode (2) proximal to the recording pair is larger, for this reason it is less different.

ad 5. — Measurements of the amplitudes have been carried out always at the lst component, this is why the influence of the 2nd one is negligible.

In *Fig. 4B*, the postulates of **Pflüger**'s laws and the contraction-sequence of **Waller** are schematically demonstrated. In our case the earth-negative stimulus is descending, the earth-positive is ascending relating to the indicator (leading off electrodes). *Fig. 4B* was drawn after a usual description of the phenomena in recent text-books (**Lissák**, 1961). We like to underline that the decrease of CO excitation is thought to be an unstable phenomenon and **Werigo**'s depressive cathode-effect is supposed to be elicite by the decrease.

Summing up our experimental results it can be claimed unequivocally that **Pflüger-Waller** laws are highly simplified. One of the causes explaining this situation may be that the laws in question are laws for contraction. In this study the excitation is indicated by an action potential and this is why the details are more finely reflected.

The classical interpretation (**Pflüger**, 1859), that the make-excitation is dominating and excitation generally is evoked by cathode-make (CC) or by anode-break (AO), gives the following explanation. The CC and AC-responses come from the earth electrode and the AC and CO ones originate at the different electrode. The CC response spreads without disturbs to the leading off, but the AC one travels coming from a farther point troubled by the intermediate anode-zone which goes from strength to strength. Therefore, its value at saturation must be lower and depressed at higher voltages.

The threshold of the off-responses is higher, this is why AO $<$ CC (both come from the earth-electrode). The CO excitation is the anode-off response of the different electrode, therefore, CO $<$ AC. The disappearance of the CO phenomenon is due to the depressive cathode-effect (**Werigo**, 1889, 1901). The intermediate cathode-zone is namely accomodated. The breaking down of CO is an obligatory phenomenon, contrary to common knowledge.

In our opinion, the AC response stands higher than CC after a short pulse and often even following a pulse of 1 sec, because the effect of higher current-density at the different electrode cannot be surpassed by the intermediate and yet weak anode-zone. In the given case the condition indicated by Lorente de No (1947), i.e. the weak stimulus cannot show clearly the cause. At the AC × CC intersection the inhibitory effect of the anode zone just excels this effect of the different electrode. But after short pulses *(Fig. 2)* an anode-zone capable to inhibit the response could not have been formed yet. Such a short stimulus which can evoke a maximal response does not represent a weak stimulus.

The sequences of average-curve *(Fig. 4A)* referring to the adequate electrodes are the following:

1. $CC_1 > AO_1 > CO_2 > AO_2$ different electrode is dominating
2. $CC_1 > CC_2 > AO_1 > AO_2$
3. $CC_2 > CC_1 > AO_1 > AO_2$ closing-dominance
4. $CC_2 > CC_1 > AO_2 > AO_1$
5. $CC_2 > AO_2 > CC_1 > AO_1$ closing and proximal dominance

This explanation, in fact, corresponds to the Pflüger's laws and takes into account the accomodation as well. The cathode-depressive-effect is consequent. Waller' formul is not valid steadily referring to either of the electrodes.

Therefore the CC or AO responses, which become saturated, originate proximally and the CO or AC ones are of distal origin troubled during their propagation. This is supported by the following observation. In *Fig. 3*, in the case of the response, where both CO and CC-species are visible, there is a delay of about 60 msec between the two comopnents of both responses. This may correspond to a real difference of travelling way. The supposition of a virtual cathode is not required.

However, the explicit two maxima of CO, AC and AO curves require further explanation. We think that this is just the phenomenon expressing mostly the complicated determination of the response-ensemble. Essentially the problem consists in a decision. Whether the sites of origin for the two maxima are same or not, i.e. whether true CO and AC exist excitations or not? Whether the 6 parts of the AC, AO and CO curves and 1 or perhaps 2 sections of CC correspond to the theoretically possible 8 kinds of excitation (CC, AC, AO, CO or distal and proximal)?

A contribution of the two components cannot be led to the two maxima because of the way of measurement. The saturation of the 2nd maximum of AO also speaks against such a supposition. Furthermore, it would be contradictory that the maxima and the points of inflexion are intimately connected, e.g. the 2nd increase of AO is correlated to the breaking down of CO and AC. When the first maximum is reached, both components increase and after both decrease, and finally, both increase again.

We do not think it likely — contrary to Lorente de No's opinion (1947) — that true cathode-off and anode-on excitations exist under physiological conditions, therefore, we search the cause of curves with two maxima and inflections (CO, AC, AO) in other factors. It may be supposed that the process itself under the intermediate electrodes disturbing the spreading is of two-phase and this shows itself in the two maxima of the amplitude-voltage curves. The different determinations of the curves are shown clearly by the uncertainty *(Fig. 5)* of the CC-curve which is not the same as that of the remaining three (CO, AC, AO). When several rivalling factors are responsible for a given value

Table 1

Sequences

Sequence >				Number of observed intervals	Remarks
CC	AC	AO	CO	10	At high voltage; it is not at the saturation (between 1—2 Volt)
CC	AC	CO	AO	14	Mediocre voltage (1 Volt)
CC	AO	AC	CO	15	At saturation is regular (above 2 Volt)
CC	AO	CO	AC	6	
CC	CO	AC	AO	6	
CC	CO	AO	AC	5	
AC	CC	AO	CO	5	
AC	CC	CO	AO	6	
AC	AO	CC	CO	2	At long duration and low voltage transient or at high voltage
AC	AO	CO	CC	2	At short pulses is consequent
AC	CO	CC	AO	3	*(Fig. 2)*
AC	CO	AO	CC	3	
AO	CC	AC	CO	0	Were not observed
AO	CC	CO	AC	0	
AO	AC	CC	CO	0	
AO	AC	CO	CC	0	
AO	CO	CC	AC	1	Anomalous *(Fig. 8)*
AO	CO	AC	CC	1	Anomalous *(Fig. 8)*
CO	CC	AO	AO	1	
CO	CC	AO	AC	2	More seldom at low voltage (below 0.6 V)
CO	AC	CC	AO	2	
CO	AC	AO	CC	1	
CO	AO	CC	AC	1	
CO	AO	AC	CC	1	

of the amplitude, the standard deviation could be significant. This is just the case of the CO, AO, AC curves, having break and/or distal origin.

Concerning the examples of response-types extremely deviating from each other we think of the variability of accomodation to be important. Some values of accomodation-constant may represent an increase of excitability (LÁBOS and FAZEKAS, unpublished). Probably LORENTE de No's comment (1947) on the connection existing between the dominance of anode- or off-responses and the instability of the nerve is related to this phenomenon mentioned before.

The duration-dependence of the slope of CC-curves — in our opinion — is related to the progressive separation of the on- and off-responses. When stimulating by short pulses (0,2—1 msec), only one response contributes to the amplitude. But between 3 and 30 msec, where the curves are steeper *(Fig. 9)*, both the make- and break-responses participate in the amplitude. The slope is newly decreased ($\alpha = 3-4,5$) at a stimulus of 1 sec, where the separation is entire and only the CC response is measured. The on or off character of the responses to short stimuli ($d <$ msec) is questionable, though their usual interpretation is of on-type (HILL, 1936). This is supported also by the similarity of α-values for the short and 1 sec stimuli.

The behaviour of the single-axon preparations (Tasaki, 1951; Hodgkin, 1965) under the effect of direct current can not be compared directly with the responses of CVc, mainly because of their ,,all or nothing" character. For this reason a discussion of the related literature may not be absolutely necessary. Considering the response of an axon, it can be stated that there are not similar amplitude-voltage characteristics or they are of incomparably steeper. In spite of the complexity of CVc, its similar diagrams, already contain very high exponents ($\alpha = 3-7$). Such high exponents can issue not only because of the narrow band of fibre-histogram (Lábos et al. 1963), but they can be related to the high exponents for Na^+ and K^+ conductance in the Hodgkin-Huxley equations as well (Hodgkin and Huxley, 1952; Hodgkin, 1965; Moore, 1968).

Summary

The laws of direct current stimulation were studied on the cerebro-visceral connectives of *Anodonta cygnea* L. at a given arrangement of the electrodes. The indicator of the excitation was the action potential.

It has been established, that all possible responses (cathode, anode, closing, opening) and almost all of their possible sequences exist. The voltage-dependences of the responses are different. All of these diagrams but the cathode-on curve, are of two-phase. The cathode-on and anode-off responses show a saturation.

The 4 curves intersect one another at 4—5 points in an average. The intersections form a regular system. They are grouping near to 3—4 different values of stimulus-strength.

The order of the responses depends on the voltage. At least 5 regular sequences are observable. The steady-state sequence is not identical with the Waller's formula. It is (designation see in the text):

$$CC > AO > AC > CO \quad \text{that is} \quad CC_2 > AO_2 > CC_1 > AO_1$$

Depending on the condition of the nerve the off-responses may be very high or they may be entirely absent.

CC-curves were approached at several durations of pulses. Their formul is $A = A_{\max}[1 + \beta V^{-\alpha}]^{-1}$, where α and β are dependent on the pulse-duration; $\alpha \sim 3-7$ and $\beta^{-1/\alpha} = V_{0,5}\,(d)$.

The empiric equation expressing the whole (V,d)-function is

$$A_Z = \frac{A_{\max}}{1 + [V_{0,5}(d)/V_Z(d)]^{\alpha}}$$

where the $V_Z(d)$ curves represent strength-duration relations belonging to Z degree of activation ($0 < Z < 1$).

Stimulated by short pulses, at the given electrodes, the anode-proximal excitation is always higher.

In our opinion both on and off excitations take place at both of the stimulating electrodes. Their relation is determined by their ab ovo different thresholds, by accomodation, spreading, size and arrangement of electrodes. The existence of true cathode-off and anode-on excitations are not probable. A supposition of the virtual cathode is not required.

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ANODONTA IDEG ZÁRÁSI ÉS NYITÁSI INGERÜLETE EGYENÁRAMÚ INGERLÉS HATÁSÁRA

Lábos Elemér

Összefoglalás

Anodonta cygnea L. cerebroviscerális connectivumán vizsgáltuk adott elektródarendszer mellett az egyenáramú ingerlés törvényszerűségeit. Az ingerület indikátora akciós potenciál volt.

Megállapítottuk, hogy minden lehetséges válasz (katód, anód, zárási, nyitási) és közöttük csaknem minden amplitúdó sorrend létezik. A válaszok ingerfeszültségfüggése eltér. A görbék a katódzárási válasz kivételével kétfázisúak. A katódzárási és anódnyitási válasz telítési jellegű.

A 4 görbe átlagosan 4—5 helyen metszi egymást. A metszéspontok törvényszerű rendszert képeznek. 3—4 eltérő ingerintenzitás körül csoportosulnak.

A válaszok sorrendje feszültségfüggő. Legalább 5 törvényszerű sorrend létezik. Az egyensúlyi sorrend nem azonos a Waller-formulával, hanem

$$CC > AO > AC > CO, \text{ azaz } CC_2 > AO_2 > CC_1 > AO_1$$

Az ideg állapotától függően a nyitási válaszok igen nagyok lehetnek vagy teljesen hiányozhatnak.

A CC-görbéket különböző impulzusszélességeknél közelítettük. Ennek alakja $A = A_{max} (1 + \beta V^{-\alpha})^{-1}$, ahol α és β impulzusszélességfüggő; $\alpha \sim 3-7$.

Az amplitúdó teljes (V, d)-függését kifejező empirikus egyenlet

$$A_Z = \frac{A_{max}}{1 + [V_{0,5}(d)/V_Z(d)]^{\alpha}}$$

ahol a V_Z (d) görbék a Z aktiválásához ($0 < Z < 1$) tartozó ingerintenzitás-időtartam-összefüggések.

Rövid időtartamú ingereknél az adott elektródák mellett mindig az anód-proximális ingerület nagyobb.

Véleményünk szerint mindkét ingerlő elektródnál keletkezik zárási és nyitási ingerület. Ezek viszonyát ab ovo eltérő küszöbük, az akkomodáció, a terjedés és az elektródméret ill. elrendezés szabja meg. Valódi katódnyitási és anódzárási ingerület valószínűtlen. Ezek a folyamatok a másik elektródnál kezdődnek. Virtuális katód feltételezésére nincs szükség.

ВОЗБУЖДЕНИЯ ЗАМЫКАНИЯ И РАЗМЫКАНИЯ НЕРВА БЕЗЗУБКИ ПОД ВЛИЯНИЕМ ПОСТОЯННОГО ТОКА

Э. Лабош

Были изучены закономерности возбуждения при помощи постоянного тока применением данной системы электродов к церебровисцервальному коннективу беззубки.

Было установлено, что существуют все возможные реакции: (реакция на катод анод, размыкания и замыкания) и между ними обнаруживаются все возможные порядки амплитуд. Зависимость ответов от напряжения раздражения разная. Кривые, за исключением реакции на размыкание катода, являются двухфазными. Реакции размыкания катода и замыкания анода носят насыщнный характер.

В среднем 4 кривых пересекают друг друга в 4—5 пунктах. Места пересечений создают закономерную систему. Они появляются при 3—4 различной интенсивности возбуждения.

Порядок ответа зависит от напряжения. Существуют по крайней мере 5 закономерных порядков. Порядок равновесия не соответствует формуле Валлера, а $CC > A_0 > AC > CO$ т. е. $CC_2 > AO_2 > CC_1 > AO_1$. В зависимости от состояния нерва реакции на, размыкание могут быть огромными или полностью отсутсвуют.

Приближение кривых *C* осуществлялось при помощи импульсов разной продолжительности. Это имело следующий вид:

$$A = A_{max}(1 + \beta V^{-\alpha})^{-1}$$

где α и β зависят от продолжительности импульса: $\alpha \sim 3—7$. Полная зависимость амплитуды (V, d) выражается по следующему эмпирическому уравнению:

$$A_z = \frac{A_{max}}{1 + [V_{0,5}(d) V_z(d)]^{\alpha}}$$

где кривые V_z(d) относятся к активности z($0 < z < 1$) и выражают зависимость интенсивности и продольжительности возбуждения. При данной системе электродов после кратковременного раздражения проксимальное возбуждение анода всегда выше.

По нашему мнению, возбуждение замыкания и размыкания возникает под обоим раздражающим электродом. Их отношения определяются различным порогом аккомодации, распространения а также размером и расположением электродов. Подлинного возбуждения размыкания катода и замыкания анода не существует. Эти процессы берут свое начало под другим электродом. Нет надобности предположения виртуального катода.