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Physiology. — J. W. LANGELAAN on: *"Further investigations on muscle-tone."* (Abstract). (Communicated by Prof. T. PLACE).

On the assumption of a muscle-reflex arc on which the muscle-tone depends, it was proved in a previous series of experiments [1]), that there is a logarithmic relation between the value of the successive tonicity-quotients and the corresponding increments of the charge. The distensibility was taken as measure of the muscle-tone. From this the analytical expression was derived, which represents the increase in length of the not visibly contracting muscle as function of the increase of the charge.

For this relation was found:

$$l = Ap + Bp \; lgn. \; p,$$

and it was pointed out that this held good only for the interval of the increase of the charge, over which the experiment ranged.

These experiments made on frogs, were afterwards extended to cats, whose spinal cord was cut at a high level. The m. triceps surae was chosen to record distention curves, according to the method shortly described in my previous communication. The operations were done under ether narcosis, but as soon as the medulla was cut, no more narcotic was given. The severing was always followed by spinal shock, but within a few hours the muscles proved, at least partly, to regain their tonicity.

Also in this case the distention curve appeared to be represented by the same analytical expression, but the variation of charge during the experiment was far more considerable. As an illustration we subjoin four tables, representing the measurements of four curves.

1) Proc. Kon. Akad. van Wetensch. Amsterdam, Sept. 29th 1900.

Experiment of 6/XII 1900.

TABLE I. 12th curve.

$A = 74.6 \times 10^{-6}$ $B = -2.6 \times 10^{-6}$		
p	l. meas.	l. calc.
0.0 c_1	0.0 c_2	0.0 c_2
6.2	13	10.7
12.6	19	23
19.0	34.5	(34.5)
25.4	45.5	45.1
38.2	67	66.7
45.6	79	(79)
$P = 38$ $p = 127.6$ $c_1 = 2.80$ $c_2 = 10^{-3}$		

TABLE II. 14th curve.

$A = 100.5 \times 10^{-6}$ $B = -7.8 \times 10^{-6}$		
p	l. meas.	l. calc.
0.0 c_1	0.0 c_2	0.0 c_2
6.2	12.5	13.5
12.6	25	25.5
25.4	48	(48)
38.2	69.5	68
51.0	87.5	87.7
51.9	89	(89)
$P = 38$ $p = 143.8$ $c_1 = 2.77$ $c_2 = 10^{-3}$		

Experiment of 4/XII 1900.

TABLE III. 7th curve.

$A = 104.5 \times 10^{-6}$ $B = -6.2 \times 10^{-6}$		
p	l. meas.	l. calc.
0.0 c_1	0.0 c_2	0.0 c_2
6.2	14	16.6
12.6	29.5	31.9
19.0	46	46.7
25.4	61	(61)
38.2	92	88.7
46.2	105.5	(105.5)
$P = 38$ $p = 143.1$ $c_1 = 3.10$ $c_2 = 10^{-3}$		

TABLE IV. 8th curve.

$A = 103.9 \times 10^{-6}$ $B = -6.3 \times 10^{-6}$		
p	l. meas.	l. calc.
0.0 c_1	0.0 c_2	0.0 c_2
6.2	13	15.3
12.6	28	29.4
19.0	43	(43)
25.4	55.5	56.2
38.2	83	81.7
51.4	107	(107)
$P = 38$ $p = 147.3$ $c_1 = 2.87$ $c_2 = 10^{-3}$		

The number of tracings I have measured amounts to 22 derived from three cats. It appears from these measurements, that within the given interval of the increase of the charge, the deviations between the measured values and those calculated by means of the given formula are not more considerable than was to be expected in connection with the accuracy of the method. But already in the tables given in my previous communication and also in the tables of these measurements it is clear, that the deviations of the beginning of the curve are most considerable and that they decrease rapidly with increasing charge. All these deviations fall in the same direction. It is therefore probable, that they are due to a definite cause, and in my opinion, it is to be found in the law of FECHNER, which according to its deduction is to be considered only as a "loi limite". I hope to return to this point in a following series of experiments.

Then I directed my attention to the two constants A and B, which occur in the formula representing the distention curve.

It was proved by the experiments, that when a distention-curve was recorded during the period of shock or with intact medulla in deep narcosis, a straight line was found within a certain interval of time and increase of charge. In a case where the shock was very severe, the rectilinear part of the curve was found to cover an interval of the increase of charge not exceeding 130 grs. This increment of charge took place in 50 sec., the initial charge amounting to 38 grs. Other muscles gave other values which however deviated but little. If the experiment was extended over a greater interval of time and increase of charge, the elastic after-phenomena modified the shape of the curve in a considerable way.

As we know, that under shock and deep narcosis the efferent (motor) part of the muscle-reflex arc (e.g. from the pyramidal tract) remains irritable, while it appeared at the same time that when the shock was disappearing, the linear curve passed into the curve which we know as characteristic for the tonic muscle, we had an indication of the way in which to proceed with the analysis; for the given formula of the distention curve leads to a linear curve for $B = 0$. It is therefore obvious to consider the term $Bp\ lgn.\ p$ as the representation of the influence of the afferent (sensible) part of the muscle reflex arc on the distention curve. It is difficult to decide, whether the linear distention-curve $l = Ap$ is to be considered as typical for a muscle when only under influence of its efferent nerves, or whether this formula is only to be taken as a first approximation, implicitly implied in the law of FECHNER which served us as starting point. For even if in this case the initial linear part was followed by a parabolic distention-curve, as was found for frog-muscles, yet this part of the curve must be modified by the influence of the elastic after-phenomenon. As now this elastic after-phenomenon is not to be eliminated under the conditions of the experiment, the question which we have raised, must be left undecided for the present.

The curves were recorded in sets of three, while the time between the successive curves was noted down. The curves of a same set, which may be indicated as 1st, 2nd and 3rd, according to their succession in time, may be mutually compared; but what took place between the successive sets of three curves was not noted down. The values of A and B, as they are determined from the distention-curves follow in three tables.

TABLE V.

Experiment of 6/XII 1900.						
		9	12.	15.	18.	21.
Ist curves	$A \times 10^5$	87.3	74.6	84 8	69.9	62 5
	$B \times 10^5$	—5 1	—2.6	—5.5	—2.7	—2.7
		11.	14.	17.	20.	23
IInd curves	$A \times 10^5$	97.5	100.5	84 6	78.1	84.1
	$B \times 10^5$	—6 8	—7.8	—5.8	—5.3	—6 1

TABLE VI.

Experiment of 4/XII 1900.						
		7.	13.	19.	22.	
IInd curves	$A \times 10^5$	104 5	107	95.7	127.5	
	$B \times 10^5$	—6 2	—8.1	—6 0	—10 9	
		8.			23	26.
IIIrd curves	$A \times 10^5$	103.9			120.1	118 8
	$B \times 10^5$	—6 3			—10.9	—8.9

TABLE VII.

Experiment of 11/XII 1900.

Ist curves		6	9.
	$A \times 10^5$	163.9	135.0
	$B \times 10^5$	−6.7	−7.9
IInd curves			10.
	$A \times 10^5$		191.0
	$B \times 10^5$		−19.6
IIIrd curves		8.	
	$A \times 10^5$	150.4	
	$B \times 10^5$	−9.9	

It appears from these values in connection with the time-notation, that if the interval of time between two successive distention-curves is shorter than three minutes, the constant B in a succeeding curve is considerably greater. With B the value of A increases. Among the values mentioned there are three cases, viz. Table V curves 15 and 17, Table VI curves 7 and 8, and curves 22 and 23, for which nearly identical constants are found, and in these three cases the interval between two successive curves was always longer than five minutes. In further experiments I hope to return to this last phenomenon, which if generally correct, seems very important to me.

If the conception of a muscle-reflex arc is correct and if it is also true, that B represents the coefficient added to the term, which is the analytical expression of the influence of the afferent part of this muscle-reflex arc on the shape of the distention-curve, then the increment of B caused by a shortly preceding distention, is only a special case of the physiological rule, which is generally less accurately formulated as follows: "shortly after every stimulation the nerve is more irritable." But then the increase of the coefficient A together with the increase of B is not accidental. From the two subjoined tables:

TABLE VIII.

Experiment of 13/XII 1900.

		4.	7.	10.	13.	16.	19.	25.
IInd curves	$A \times 10^5$	76.5	71 6	65.6	76.8	69.4	69 9	56.9
	$B \times 10^5$	0 0	0 0	0.0	0.0	0.0	0 0	0 0

TABLE IX.

Experiment of 18/XII 1900.

		4.	10.	13.	16.	19.	25.
Ist curves	$A \times 10^5$	79.6	76.2	72.5	79.8	79 1	64.1
	$B \times 10^5$	0.0	0 0	0 0	0.0	0.0	0.0

which represent the value of the coefficient A in two sets of experiments, where the cat had not recovered from the shock, it appears that in this case the coefficient A according to its value will join those cases where the coefficient B has the smallest value which can occur in connection with the accuracy of the method. The mutual differences of these coefficients A in the two tables are greater than was to be expected from the method, and the successive deviations are distributed over the series of experiments in such a way, that they can certainly not be brought under a simple rule.

In connection with the discontinuous tonus-tracings I have already pointed out these irregularities which appear after the muscle-reflex arc has been interrupted.

The distention-curves obtained from cats with intact spinal cord and under very slight narcosis are quite different from those which occurred when the medulla was cut at a high level. Ether was used as narcotic. The shape of these curves is in appearance perfectly accordant with the curves obtained by Mosso and BENEDICENTI for men, with their myotonometer. In this case the measurements gave for most curves increasing tonicity-quotients with increment of charge, within the interval over which the experiment ranged. Under some circumstances these curves show a point of inflection. The place of this inflection-point depends greatly upon the depth of the narcosis, and the extent of the increase of the charge. The tonicity-quotient, which is very low at first, rises quickly, then slowly with increase of charge, reaches its maximum at the inflection-point and begins then to decrease. For this last part of the curve, where decreasing tonicity-quotients correspond with increase of charge, the law of FECHNER proved by approximation, to connect the increase of the charge with its effect, the corresponding value of the tonicity quotient.

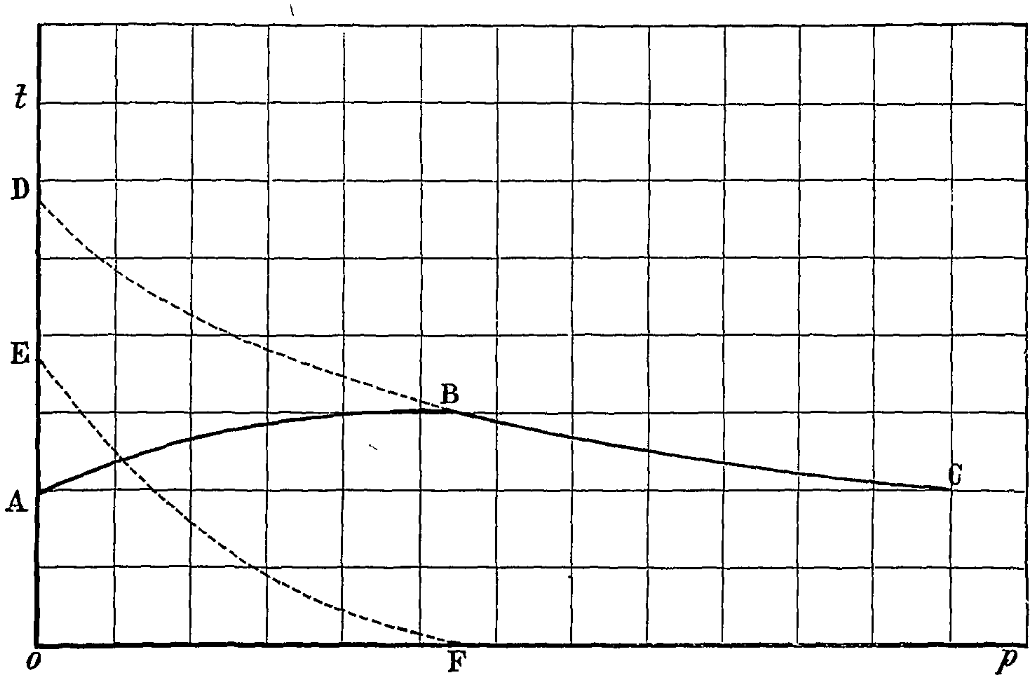
Starting from the well-known fact, that a high section of the medulla, after the shock is passed, gives rise to increase of muscle-tone and that therefore a physiological inhibition seems to disappear, the analysis of these curves was attempted in the following way.

The stimulus, originating by extension in the terminations of the afferent nerves of the muscle, ascends along afferent paths and arrived in the spinal cord, it is directly transferred along a short path to the efferent part of the primary muscle-reflex arc. About this we know that the law of FECHNER connects stimulus and its effect. But this same stimulus, ascending along the long path, which as secondary muscle-reflex arc is built upon the first, brings about a change which may be composed by addition with the change in the primary muscle-reflex arc. The supposition of the simple addition of the two influences on the muscle, has been stated very clearly, i. a. by SHERRINGTON. But if the law of FECHNER holds true for that part of the curve which lies beyond the inflection-point, and this part is therefore not different from those tracings, recorded when the stimulus can only pass the primary reflex arc, then the physiological meaning of the inflection-point is this: the inflection-point in the curve appears at the moment, when the influence of the secondary muscle-reflex arc on the primary disappears. But knowing also that in these tonus-curves, the tone is at first very low, that it reaches its maximum at the inflection-point, at which moment the influence of the secondary on the primary muscle-reflex arc ceases, we have also to assume, that the stimulus passing through this secondary muscle-reflex arc, brings about a change in it, the effect of which is seen as the disappearance of a tone-inhibition. We assume now as second supposition that here too the law of FECHNER brings relation between the effect and its cause, the stimulus.

The analysis is now possible in the following way. For a certain increase of charge the corresponding extent of the variation of tone is determined from the segment of the curve which lies beyond the inflection point. This is the basis for the further calculation as from this a series of successive tonicity-quotients is extrapolated according to the law of FECHNER. So this series of tonicity-quotients represents the probable value of the muscle-tone, corresponding to a group of successive increases of charge, if the stimulus had only passed through the primary muscle-reflex arc. Then the inflection point in the curve is determined as accurately as possible. At this point the inhibiting influence which is exerted by the secondary on the primary muscle-reflex arc is zero. Also the real value of the tonicity-quotient for a certain increase of the charge is known from the measurements of the curve. But if by means of the before-mentioned extrapolation the probable value of the tonicity-quotient can be calculated, exclusively depending on the primary muscle-reflex arc and by direct measurements the tonicity-quotient under simultaneous influence of the two muscle-reflex arcs can be determined, and if the premise of the simple addition of these quantities is correct, it is possible to determine by simple subtraction of these quantities the value of the inhibiting influence exerted by the secondary muscle-reflex arc. But if for two given charges the value of this influence is known, it is possible, to interpolate a number of terms by means of the second premise. For this, terms were chosen corresponding to those for which the value of the tonicity-quotient was calculated, when the muscle was only under the influence of its primary muscle-reflex arc. The difference between these tonicity-quotients must then be identical with the tonicity-quotient, determined directly from the curves. We shall elucidate this method by a scheme. Let the curve A B C represent the value of the tonicity-quotients as function of the increase of the charge. In B a maximum is reached and this point coincides with the inflection-point on the distention-curve. Accordingly the influence of the secondary muscle-reflex arc on the primary disappears at point B. Consequently F is the final-point of the curve representing the extent of the tone-inhibition of the secondary muscle-reflex arc on the primary. The portion between B and C represents therefore the value of the tonicity-quotient as function of the increase of the charge, when the muscle is exclusively under the influence of its primary muscle-refleo arc. Extrapolating according to the law of FECHNER, BD is obtained, and curve D C becomes then the graphical representation of the value of the tonicity-quotient as function of the increase of charge, if the muscle had been only under the influence of its primary muscle-reflex arc all through the course of the experiment. O A is the value of the tonicity-quotient under influence of the

2

two muscle-reflex arcs, as it is really measured, but then $OE = OD - OA$ is the value of the tone-inhibiting influence exerted by the secondary muscle-reflex arc. This determines point E and construing curve EF between the two points according to the law of FECHNER, this curve becomes the graphical representation of the tone-inhibiting influence exerted by the secondary muscle-reflex arc. Over the interval of the charge OF the difference of the ordinates determined by the two curves DB and EF must now at any moment be equal to the ordinates determined by the curve AB.



It appears clearly from this graphical representation, that there can only be question of a definite problem in these cases, where the curve shows an inflection point and that the possibility of this analysis depends on this.

The result of the measurement and of the calculation of the tonicity-quotients performed on this basis is given for four curves.

Experiment of 30/XI 1900.

TABLE X. 20th curve.

p	Tonicity-quotient meas.	cal.
0.0 c_1		
3.0	3.1 c_3	(3 1 c_3)
6.2	3.7	3.8
12.6	4.5	(4.5)
25.4	3.5	(3.5)
51.0	?	2.5
62.4	2.7	2.3

$P = 38$ $c_1 = 2.88$

$c_3 = 0.00035$

infl. point at 12.6.

Experiment of 24/XI 1900.

TABLE XII. 35th curve.

p	Tonicity-quotient meas.	cal.
0.0 c_1		
3.0	2.7 c_3	(2.7 c_3)
6.2	3.2	3.7
12.6	4.5	(4.5)
19.0	4.1	3.7
25.4	3.1	(3.1)
30.0	3	2.8

$P = 45$ $c_1 = 2.58$

$c_3 = 0.00037$

infl. point at 12.6.

Experiment of 30/XI 1900.

TABLE XI. 2nd curve.

p	Tonicity-quotient meas.	cal.
0.0 c_1		
3.0	2.2 c_3	(2.2 c_3)
6.2	2.5	2.7
12.6	3.2	3.2
25.4	3.6	3.7
38.2	3.9	(3.9)
47.7	3	(3)

$P = 38$ $c_1 = 2.92$

$c_3 = 0.00034$

infl. point at 38.2.

Experiment of 24/XI 1900.

TABLE XIII. 29th curve.

p	Tonicity-quotient meas	cal.
0.0 c_1		
3.0	4.9 c_3	(4.9 c_3)
6.2	6.7	6.5
12.6	6 6	(6.6)
19.0	5	5.4
25.4	4.6	(4.6)

$P = 45$ $c_1 = 2.73$

$c_3 = 0.00035$

infl. point at 9.5.

2*

In order to examine whether this analysis might be applicable to curves obtained for men by MOSSO, I have measured one of them [1]).

TABLE XIV.

Tonicity-quotient p	meas.	cal.
0.0×7.2 c_1		
6.25	3 c_3	(3 c_3)
12.5	5.5	5
21.9	6.5	(6.5)
25.0	3.5	(3 5)

$P=800 \quad p=2200 \quad c_1=\frac{2200}{800}$

$$c_3=\frac{180}{500\times 2200}$$

infl point at 21.9.

It seems to me that we may conclude from the values given, that the analysis of the tonus-curves with intact medulla is possible with the aid of the two premises, or inversely we may conclude to the probability of the two premises from the concordance between the measured and the calculated values.

These experiments were made in the physiological laboratory of the medical school of Harvard University at Boston where I enjoyed the hospitality of Professor H. P. BOWDITCH.

Amsterdam, May 1901.

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[1]) Arch. Ital. de biologie 1896 T. XXV p. 356 fig. 3.