

ELECTRIC POTENTIAL AND ACTIVITY OF CHOLINE ESTERASE
IN THE ELECTRIC ORGAN OF ELECTROPHORUS
ELECTRICUS (LINNAEUS)

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(Received for publication, March 27, 1941)

INTRODUCTION

According to the theories of Loewi and of Dale acetylcholine (ACh) acts as the specific transmitter substance of nerve impulses to an effector organ or to a second neuron. Recent investigations suggest that the original theory must be altered to account for the ACh metabolism which closely parallels the electrical changes occurring everywhere at or near the neuronal surface (Nachmansohn and Meyerhof, 1941). This interpretation was necessary to explain the following observations.

1. A high concentration of choline esterase exists in strong electric organs (*Torpedo*, *Gymnotus electricus*). These organs can split in 60 minutes an amount of ACh equivalent to 1-3 times their own weight. The concentration of the enzyme is of the same order of magnitude as that estimated previously for motor end plates of muscle. The essential point is the fact that in these organs considerable amounts of ACh can be split during the refractory period which is of the order of milliseconds. This makes possible the assumption that ACh is closely connected with the discharge. The prerequisite for such an assumption is the possibility of a quick removal of the active substance. The existence of such a high concentration of the enzyme appears particularly significant in view of the high water (92 per cent) and low protein content (2-3 per cent) of the organs. In the weak electric organ of Ray the concentration is relatively low. If in the three species number of plates per centimeter and E.M.F. per centimeter are compared with the concentration of the enzyme a close parallelism is obtained (Nachmansohn, 1940). The observations on the concentration of choline esterase in electric organs, established during the years 1937 and 1938, and simultaneous and independent studies of Auger and Fessard on the discharge of electric organs under different conditions, especially after degeneration of the nerve, led to investigations on *Torpedo*

* This work was made possible by a grant of the Dazian Foundation.

marmorata carried out in Arcachon. There it was demonstrated that ACh is present in high amounts in the electric organ, that after nerve stimulation ACh is liberated in these organs, and that injection of ACh into the organ produces a discharge (Feldberg, Fessard, and Nachmansohn, 1940). These experiments support the view suggested by the previous experiments that the discharge is connected with the appearance of ACh.

2. Only a quantitative difference exists between the concentration of the enzyme in nerve fibers and that at synapses. This difference was interpreted as being related to a concentration of the enzyme at or near surfaces and therefore high at synaptic regions where the end arborization increases the surface (Couteaux and Nachmansohn (1940)). Direct evidence for this view was obtained with the giant fiber of squids in which it was found that practically all the enzyme is localized in the sheath and that only negligible amounts occur in the axoplasm (Boell and Nachmansohn, 1940).

The data on the concentration of choline esterase in the electric organ of *Electrophorus electricus* (Linnaeus) (= *Gymnotus electricus*) were incomplete and unsatisfactory. Only one specimen had been examined and only two determinations were made at that time.¹ Among all species the electric organ of *Electrophorus* has the greatest E.M.F. A detailed study of the enzyme concentration and distribution in relation to the E.M.F. appeared necessary. The present paper fills this gap and offers new evidence for the parallelism between number of plates per centimeter, E.M.F. per centimeter, and enzyme activity.

Methods

The activity of choline esterase was determined with the Barcroft-Warburg manometric method in the same way as described previously (Nachmansohn, 1939). Frog's Ringer solution with bicarbonate buffer was used as medium. The tissue was very thoroughly ground; for it is important to have a homogeneous suspension because of the high esterase activity of electric organs. Although the pieces of tissue taken for grinding were small, the suspension had to be diluted to a large volume, and the 3 cc. put into the Warburg vessel were only a small fraction of the total suspension. For instance 3 cc. of the suspension prepared from pieces of the electric organ of the smaller eel contained only about 0.5 mg. fresh tissue. The weights given in the tables indicate the fresh weight of tissue ground. As the amount actually put into the vessels was approximately the same in each series of experiments, that for each determination is not specified separately but is indicated only for each table. The balance used permits rapid and precise weighing which is necessary for such small amounts of fresh tissue. The balance has magnetic damping on both sides so that in about 15 seconds 0.1 mg. can be read on a scale directly and 0.01 mg. can be estimated. Generally only 4 manometric readings were made in intervals of 5 minutes

¹ This specimen died in October, 1938, in the Institut Océanographique in Paris and the enzyme activity was determined by one of us (D. N.) in the Laboratoire de Physiologie Générale de la Sorbonne.

after the substrate had been added to the enzyme suspension. The first 5 minute reading was not included in the calculation.

The protein determinations of the enzyme solutions were carried out gravimetrically. To 1 cc. of the enzyme solution in a 3 cc. centrifuge tube there was added 1 cc. of 40 per cent trichloroacetic acid. After 24 hours the precipitate was centrifuged for 30 minutes in a centrifuge at a rate of 4000 R.P.M. The precipitate was washed three times with distilled water. The centrifuged tube was put into a drying oven at 105°C. for several hours and the weight was then determined.

RESULTS

I. Electric Organ

The electric organs of two eels were examined. The first was medium sized and had a length of 120 cm., the second was small and only 67 cm. long.

The electric organ of the larger specimen had a length of 78 cm. Pieces were taken successively at five points from the head to the caudal end of the organ and the concentration of choline esterase was determined. The values obtained are given in Table I. The highest concentration of the enzyme is found in the region near the head end of the organ; it decreases continuously towards the caudal end. Fig. 1 shows the tentative curve of the change in enzyme concentration. The shape of this curve appears to be analogous to that which indicates the E.M.F. per centimeter and number of plates per centimeter determined on an eel of approximately the same size (Cox, Rosenblith, Cutler, Mathews, and Coates, 1940).

The number of sections (five) at which the enzyme concentration was determined and the number of determinations in each section were not sufficient for ascertaining the precise shape of the curve. In each section the concentration varies from one piece to the other: In the section 45 cm. from the snout four determinations were made, and the QCh. E. values were found to vary from 83-112. Such differences are not surprising. As the experiments quoted in the introduction suggest, choline esterase is concentrated at surfaces of neurons. The amount of active surface will vary from one piece to another. The greatest part will be presumably at the innervated side of the disc. It can be expected, therefore, that even in pieces taken from the same region the enzyme concentration will differ according to the amount of active surface although the number of plates per centimeter is equal. If a sufficient number of large pieces were taken these differences might become insignificant, and the value obtained would approach the average value of that section. But it is difficult to grind large pieces homogeneously and the error due to this difficulty may be as great as that due to the variations of active surface in small pieces.

In order to get more information about the variations which may occur in a given piece due to the uneven distribution of active surface, the enzyme concentration was determined in a series of slices cut with a freezing microtome. The results are given in Table II. Pieces I and II were taken about 60 cm.

TABLE I

Concentration of choline esterase in sections of the electric organ of *Electrophorus*, taken successively from the head to the caudal end. Length of animal 120 cm. *D* = distance of section from the snout in cm. *W* = mg. tissue ground. 2-5 mg. fresh tissue were taken per vessel. QCh.E. *s* = single determination, *a* = average.

<i>D</i>	Main organ			Organ of Hunter		
	<i>W</i>	QCh.E.		<i>W</i>	QCh.E.	
		<i>s</i>	<i>a</i>		<i>s</i>	<i>a</i>
30	66.0	134.0 118.0 123.0	125.0	73.0	93.5 93.5	93.5
	68.5	135.0 134.0	134.5	65.0	107.0 103.0	105.0
45	46.0	110.0 93.0 103.0	99.0	21.2	107.0	107.0
	48.7	110.0 111.0 116.0	112.0	28.0	140.0 125.0	132.5
	66.0	92.0 76.0 82.0	83.0			
	60.0	100.0 93.0	96.5			
60	47.0	50.0 50.0	50.0	44.5	79.0 73.7	76.5
	65.5	58.2 65.7	62.0	44.0	64.5 67.0	65.8
68	140.0	35.0 31.0	33.0	98.7	29.0 29.0	29.0
	165.0	38.0 42.0	40.0	76.0	27.0 28.0	27.5
102				41.0	37.5 41.5	39.5
108	71.0	36.5 42.5	39.5	45.0	42.5 42.0	42.5

from the snout of the eel described above. Piece III was cut out by biopsy from an eel of similar size and the region chosen was near to the head end of the organ. The values show how great the variations are from one slice to the other. Of special interest are the values obtained with piece I. It seems as if the values vary in a certain rhythm. This is demonstrated in Fig. 2. It may be assumed that this rhythmic change is not incidental but corresponds to a rhythmical change in active surface. This may be easily understood from the histological structure. It may appear only at a certain thickness of slices and when the slices are cut in a direction exactly parallel to the discs.

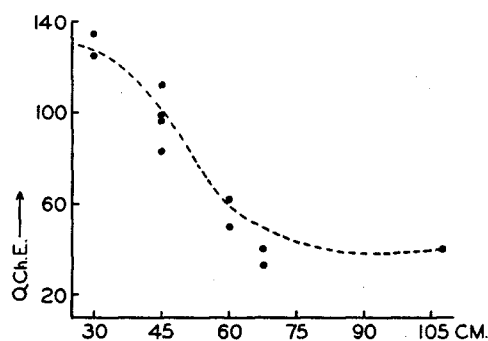


FIG. 1

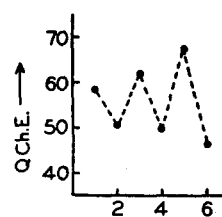


FIG. 2

FIG. 1. Concentration of choline esterase in different sections of the electric organs of the electric eel, *Electrophorus electricus* (Linnaeus), taken successively from the head to the caudal end. Length of the animal 120 cm. Abscissae: QCh.E. values. Ordinates: Distance of the section from the snout in centimeters.

FIG. 2. Concentration of choline esterase in successive slices of a piece of electric tissue cut with a freezing microtome. Abscissae: QCh.E. values. Ordinates: Number of the successive slices.

There are three superimposed organs on each side: the main organ, Hunter's organ, and the bundle of Sachs which forms the greater part of the posterior section. In the bundle of Sachs number of plates per centimeter and E.M.F. per centimeter increase towards the caudal end (Cox, Rosenblith, Cutler, Mathews, and Coates, 1940), making the conditions more complex. It may be that the pieces at a distance of 68 cm. from the snout belonged to the bundle of Sachs and that therefore the values were low, even lower than at the caudal end. When these determinations were made, no attention was paid to this point. In the organ of Hunter the concentration of the enzyme does not differ appreciably from that in the main organ. This again is in agreement with the number of plates per centimeter.

In spite of all restrictions pointed out the shape of the three curves: (I)

TABLE II

Concentration of choline esterase in successive slices cut with a freezing microtome. Piece I and II were taken from a section 60 cm. from the snout; same eel as in Table I. Piece III was taken from an eel of similar size; the section was near the head end of the organ.

Thickness of slices in μ	I		II		III	
	150-200		100		150-200	
	W	QCh.E.	W	QCh.E.	W	QCh.E.
1	6.3	57.0 60.0	2.3	70.5	2.8	125.0
2	11.8	50.0 51.0	5.0	56.3	2.4	88.0
3	8.8	62.0	6.6	70.5	—	—
4	12.1	49.5	2.7	82.0	3.1	132.0
5	9.4	67.5	2.2	76.0	3.9	125.0
6	9.8	46.2			4.5	108.0
7					5.3	90.0
8					5.5	90.0
9					5.7	87.0

TABLE III

Concentration of Choline Esterase in the Electric Organ of an *Electrophorus* of 68 Cm. Length

D	W	QCh.E.		D	W	QCh.E.		D	W	QCh.E.	
		s	a			s	a			s	a
17	17.5	612.0	630.0	25	12.4	638.0	658.0	39	15.3	530.0	530.0
		648.0				677.0				394.0	
	10.2	682.0	690.0		7.3	567.0	567.0		12.8	460.0	460.0
		697.0				520.0				510.0	
20	6.9	615.0	615.0	32	14.5	500.0	510.0	53	16.9	191.0	189.0
	14.0	620.0				610.0				610.0	
		11.8	720.0		700.0	16.3	630.0		632.0	8.0	161.0
	680.0		680.0				683.0				139.0
	11.7	740.0	745.0		12.9	680.0	683.0		20.4	150.0	152.0
		750.0				685.0				153.0	
10.1	745.0	718.0	15.2	690.0	690.0	59	150.0	152.0			
690.0	149.0										
11.1	735.0	738.0				11.4	149.0	149.0			
740.0											

D = Distance from snout in cm.

W = mg. tissue ground.

QCh.E. s = single determination, a = average.

The amount of tissue taken per vessel was about 0.5 mg.

enzyme concentration, (II) number of electric discs per centimeter, and (III) E.M.F. per centimeter seems to be essentially the same. This becomes even more obvious by the experiment carried out on the smaller specimen. The length of the electric organ in this animal was 52 cm. The enzyme concentration was determined at seven sections and more samples were taken from each section than in the first animal examined. The results are given in Table III. The S-like form of the curve is here quite obvious (Fig. 3).

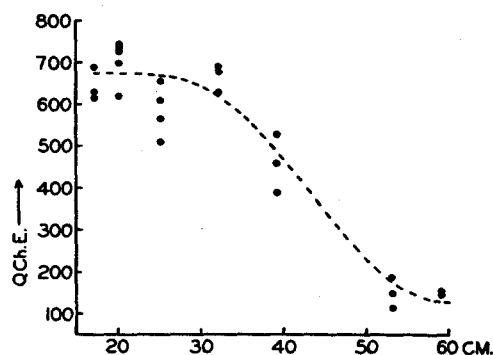


FIG. 3. The same as in Fig. 1, carried out on the specimen of 68 cm. length.

TABLE IV

Concentration of choline esterase in different sections of the electric organ of the *Electrophorus* of 68 cm. length at the 8th day following death. The symbols used are the same as those in Tables I and III. b.o.S. = bundle of Sachs.

<i>D</i>	<i>W</i>	QCh.E.	<i>D</i>	<i>W</i>	QCh.E.
22	17.5	608.0	50	11.3	410.0
29	12.8	818.0	(Main org.)		
36	15.6	690.0	50	8.7	220.0
43	17.9	550.0	(b.o.S.)		
			55	11.0	250.0

The E.M.F. per centimeter *versus* distance from the snout has not been determined accurately as in the larger animal. But the observations available indicate that the shape of the curve is the same (Coates, Cox, and Granath, 1937). The values of QCh.E. are around 6-700 near the head end and around 150 near the caudal end as compared with 120-140 and around 40 respectively. The determinations were made a few days following death. Although the animals were kept in the ice box at 1-2°C., it may be that the absolute values were a little lower than those found. The enzyme remains stable for many months (Nachmansohn and Lederer, 1939). But the tissue in view of its peculiar high water content may lose some water, and the real weights may be a little higher than those actually found. In Table IV the QCh.E. values are

given of samples taken at different sections 2 days later than those of Table III. The values are definitely a little higher. When these samples were cut out it appeared that the tissue did not retain its water as well as in the first few days following death. But if the absolute values may be a little too high even for the first days, they are comparable in any case for the smaller and larger specimen because the determinations were made during the same period following death.

In the section at a distance of 50 cm. from the snout the bundle of Sachs could be clearly distinguished from the main organ, and samples were taken separately in this case. The concentration in the main organ is nearly twice as high as in the bundle of Sachs: 410 and 220 respectively (Table IV).

II. Central Nervous System

It was always believed that the electricity of electric organs is not extraordinary as compared with that of ordinary nerves, and that it is only the arrangement of the plates in series by which these organs are distinguished and by which the great E.M.F. is attained (Du Bois-Reymond, 1877; Burdon Sanderson and Gotch 1889). It is therefore interesting to know whether the concentration of choline esterase in the nerves supplying the electric organ differs from that in ordinary nerves. In *Torpedo marmorata* the enzyme concentration of electric lobes and the nerves innervating the electric organ appears to be higher than in the rest of the brain and in motor nerves (Feldberg, Fessard, and Nachmansohn). But in determinations carried out on *Torpedo occidentalis* Storer no significant difference was found between the QCh.E. values in the electric lobe and its nerves and other parts of the central nervous system (Nachmansohn and Meyerhof, 1941). These experiments did not support the assumption that the nerves supplying the electric organ are distinguished from ordinary nerve by a special concentration of choline esterase.

In order to get more information about this question the enzyme concentration was determined in brain and spinal cord of *Electrophorus* and compared with that in a gold fish (*Carassius auratus*). The *Electrophorus* belongs to the series *Ostariophysii* like the *Cyprinidae* among which are classified the carps and the gold fishes. The specimen examined was the larger eel. Whereas in *Torpedo* there are special centers, the electric lobes, which innervate the electric organs, the *Electrophorus* has no such centers. The cell bodies of the nerves innervating the electric organs are located in the spinal cord around the central canal. These cells begin to appear in the spinal cord not far from the medulla oblongata; their number increases toward the middle of the spinal cord and then decreases again. The spinal cord was therefore examined at several distances from the medulla.

The values obtained are given in Table V. The QCh.E. values of the spinal cord of *Electrophorus* are rather low. They do not differ at various distances

from the medulla. In the spinal cord of the gold fish they are four times as high. In the central nervous system the values of the two species are similar. Only in the hypothalamus of the gold fish are they particularly high: 40.0 and 44.0 as compared with 16.8 in the *Electrophorus*.

III. Striated Muscle

Electric organs are considered as modified muscle end plates phylogenetically evolved by transformation of striated muscle. Since the time that Babuchin

TABLE V
Concentration of Choline Esterase in Brain and Spinal Cord of *Electrophorus* and *Carassius auratus*

Part of C.N.S.	W	QCh.E.	Part of C.N.S.	W	QCh.E.
<i>Electrophorus</i>					
Left cerebral hemisphere	50.5	7.2	Hypophysis	25	4.6
Right cerebral hemisphere	55.5	8.9	Medulla obl.	39.5	9.4
2 optic lobes	75.0	12.4	Spinal cord close to	24.0	5.3
Cerebellum	124.0	12.5	Spinal cord 30 cm. from	48.0	2.8
Area acustico—later	221.4	9.8	snout		
Hypothalamus	45.0	16.8	Spinal cord 60 cm. from	53.0	3.0
			snout		
			Spinal cord 75 cm. from	24.0	3.0
			snout		
<i>Carassius auratus</i>					
1 cerebral hemisphere	25.9	6.0	Hypothalamus	52.6	40.0
2 optic lobes	80.3	15.2			44.0
Cerebellum	67.6	10.7	Base of mid-brain	27.0	11.0
2 vagal lobes	90.8	15.8	Medulla obl.	83.8	16.9
		16.7	Spinal cord	42.0	12.5
					12.2

studied the ontogenetical development of *Torpedo* and described how the electric plates gradually develop from embryonic muscle fibers, there has been no doubt as to the genetic relations between the two tissues. Every possible transition has been observed between the phylogenetically lowest to the highest form, especially in weak electric organs which are not so highly differentiated as the strong organs, and in which the discs may retain their muscular characteristics even when the formation is perfect.

Quite different groups of striated muscles can be transformed into electric organs. In *Gymnotus* the deepest part of the ventral trunk muscles is transformed into the large electric organs except the "intermediate muscular layer" (Biedermann). It was thought possible that striated muscles near the electric

organ might be in a state intermediate between striated muscle and electric organ, and that in this case the concentration of choline esterase in these muscles might be higher. Therefore the enzyme activity was determined in a few samples of the dorsal trunk muscles and in the intermediate layer. The determinations were carried out on the smaller eel. The data obtained are given in Table VI. Only a few experiments were carried out but they clearly indicate that the QCh.E. values are not comparable with those of ordinary striated muscle but are much nearer to those of electric organs. It appears moreover that the enzyme concentration is higher the nearer the muscles are located to the electric organs: the relatively highest QCh.E. values were found in the "intermediate layer:" 210.0 and 141.0. In the dorsal muscles the

TABLE VI

Concentration of choline esterase in muscles of *Electrophorus*. D = distance from the snout. L = location. Inf. = inferior dorsal trunk muscles, l = left, r = right side; sup. = superior dorsal trunk muscles. I.m.l. = intermediate muscle layer.

D	L	W	QCh.E.	D	L	W	QCh.E.
32	Inf. l	29.8	90.5 90.0	39	Inf. r	29.0	103.0
	Inf. r	25.8	190.0		Sup. l	18.3	29.0
	Sup. l	19.9	55.0 57.0	46	Inf. r	28.8	39.0
	I.m.l.	12.8	210.0				
39	I.m.l.	9.4	141.0				

superior group has a lower concentration than the inferior group. As far as we know no histological studies have been made on these muscles. It would be interesting to know whether these muscles are in a process of transformation towards electric organs and, if so, how far this process is developed.

IV. Preparation of Enzyme Solutions from the Electric Organ

Electric organs are a suitable material for the preparation of active enzyme solutions, owing to the great amount of enzyme present and the low protein content. Very active solutions were obtained from the electric organ of *Torpedo marmorata* (Nachmansohn and Lederer, 1939) and recently from *Torpedo occidentalis* Storer.² It appeared interesting to compare the solutions which can be obtained from the electric organ of *Gymnotus* with those of *Torpedo*. The preparation was carried out in the same way as that with the elec-

² Nachmansohn, unpublished experiments.

tric organ of *Torpedo*: about 500 gm. of organ from the large specimen were minced with an automatic machine. The minced tissue was ground with silicate and centrifuged about 30 minutes. About 500 cc. clear supernatant fluid were obtained. 1 cc. of this preparation split 650 mg. ACh in 60 minutes. The protein content was 11.2 mg. per cc. 1 mg. protein split therefore 53 mg. ACh in 60 minutes. In the preparations obtained in the same way from electric organs of *Torpedo* 1 cc. of the solution split 400–1500 ACh in 60 minutes 1 mg. protein split 100–200 mg. ACh per hour. After the ground tissue had been centrifuged and the supernatant fluid removed 250 cc. of 10 per cent ammonium sulfate solution were added to the extracted tissue. The tissue was ground again and centrifuged. The solution obtained in this way is more active per protein unit: 1 cc. split 487 mg. ACh per hour and contained 3.71 mg. protein. 1 mg. protein split therefore 131 mg. ACh per hour. But solutions prepared in this way from electric organs of *Torpedo* were also more active per protein unit: 1 mg. protein split 2–300 mg. ACh in 60 minutes.

The electric organs of *Torpedo* appear therefore to be a more suitable material for the preparation of enzyme solutions than those of *Gymnotus*. This was to be expected from their higher enzyme concentration. It is possible and even probable that in the organ of the small specimen where the enzyme concentration is not only higher than in the large specimen but also higher than in *Torpedo*, the solution obtained would be more active than that from the organs of *Torpedo*. But the amount of material available is rather small.

DISCUSSION

These experiments furnish new evidence for the parallelism between number of plates per centimeter E.M.F. per centimeter, and concentration of choline esterase. Whereas until now this parallelism was apparent only when different species were compared, here it is shown that in the same organ great variations of enzyme concentration occur which are essentially the same as those of E.M.F. per centimeter and number of plates per centimeter.

The experiments support the view that a relation exists between ACh metabolism and the intensity of the discharge. If ACh is connected with the discharge it must appear and disappear in milliseconds. If speculation were to be excluded, the only known way for removing the active substance so rapidly is by the activity of the specific enzyme choline esterase. The greater the potential difference becomes, the greater must be the amount of active substance liberated, and the higher the concentration of the enzyme. Electric organs are highly specialized in their function. The discharge is here the final event. The fact that a specific enzyme is so highly concentrated in this organ—so poor in protein—is in itself support for the assumption that the substrate is connected with its function. If we also recall (1) that ACh can produce potential differences if injected into the organ, (2) that the potential difference is much

greater if the choline esterase is inactivated by eserization of the organ, and (3) that the appearance of ACh during the discharge can be demonstrated in the electric organ (Feldberg, Fessard and Nachmansohn, 1940), the theory of a close correlation between electrical changes and ACh metabolism appears justified. As potential differences occur at surfaces (Hodgkin and Huxley, 1939) the evidence for a concentration of choline esterase at surfaces (Boell and Nachmansohn, 1940), is in this connection particularly pertinent.

The voltage developed in a discharge between two points along the electric organ depends upon the E.M.F., the current, and the internal resistance according to the equation:

$$V = E - IR$$

where E is the E.M.F., I the current, and R the internal resistance. The special conditions of these relations in the electric organ have been recently discussed (Cox and Coates, 1938). Two assumptions can be made about the way in which ACh may act: (1) it can produce the E.M.F. directly by action on the surface, (2) it can decrease the resistance and this again by action on the surface, e.g. by increasing the permeability of the disc boundary. In either case the parallelism described here could be explained.

For the difference in enzyme concentration found between the large and small eel the following explanations appear possible. The maximal discharge varies considerably from one specimen to another even in animals of the same size. The actual discharge of the two specimens has not been recorded. It may be that the E.M.F. per centimeter was higher in the small specimen although it is not at all likely that it was four times as high. On the other hand the possibility is envisaged that ACh may act upon the resistance, and it may be that the drop in resistance per square centimeter of the disc boundaries varies with the size of the individual.

SUMMARY

1. If the concentration of choline esterase is determined at different sections from the head to the caudal end of the electric organ of *Electrophorus electricus* (Linnaeus) S-like curves are obtained. These curves are essentially the same as those which show the number of electric discs per centimeter and the E.M.F. per centimeter.
2. In the organ of Hunter the concentration of the enzyme does not differ from that in the adjacent parts in the main organ. This again coincides with the observations on the number of plates per centimeter in this organ.
3. The concentration of the enzyme was determined in different parts of the brain and the spinal cord and compared with that in a gold fish. The concentrations here are of the same order, but in the spinal cord of the eel the

concentration is even lower than in the gold fish. As the cell bodies of the nerves innervating the electric organ in the spinal cord, these results do not lend support to the assumption of a special concentration of the enzyme in these nerves.

4. In the muscles adjacent to the electric organ an enzyme concentration has been found which is of the order of that in the electric tissue itself and much higher than in ordinary striated muscles.

5. The suitability of the organ for the preparation of enzyme solutions has been investigated and compared with that of the organ of *Torpedo*.

It is a pleasure to express our thanks to Dr. R. G. Meader (Section of Neuroanatomy, Yale University School of Medicine) for assistance in the dissection of the central nervous system.

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