Observations on the Electromotive Phenomena of Non-medullated* Nerve." By Miss S. C. M. Sowton. Communicated by Dr. Waller, F.R.S. Received March 8,—Read March 29, 1900.

[Plate 4.]

Kühne and Steiner in their work on the olfactory nerve of the pike,† published in 1880, showed that the laws of electromotive action in medullated nerve, as formulated by Du-Bois Reymond, held good in the case of non-medullated fibres. Having demonstrated the resting current in a suitably prepared olfactory nerve, they proceeded to compare the value of this current with that obtained from medullated nerves of the same fish as well as from the sciatic nerve of the frog. The result showed a much higher E.M.F. for non-medullated than for medullated nerves, their diameter being about equal; a result confirmed by Biedermann and others working on the non-medullated nerves of Anodonta.

Kühne and Steiner found that the resting current diminished rapidly, but a new transverse section restored it to, and in some cases even augmented, its original E.M.F.

On stimulation with induction currents, a negative variation of high value was obtained. The response was unfailing while the nerve was fresh, provided that the stimulating electrodes were not applied too near the peripheral end of the nerve where its character becomes modified.

While working at Leipzig during the early part of 1899, Professor Hering was good enough to suggest that I should use the nerve which had given such good results in the hands of Kühne and Steiner for a further study of electromotive phenomena in non-medullated nerve, and especialty with reference to the occurrence in such fibres of the "positive after-variation" which his own researches‡ and those of Head§ had made familiar in the case of medullated nerve. Hering had himself occasionally observed this effect in 1885, while using the olfactory nerve for experiments on electrotonus. The positive after-effect occurred most frequently on mechanical stimulation of the nerve by cutting, more rarely it followed when induction currents were used.

In the present experiments, the pike used ranged from $1\frac{1}{2}$ to $2\frac{1}{2}$ kilos.

* "Non-medullated" is used in its ordinary sense as applied to grey nerve, and without prejudice to the conclusions of Gad and Heymans that such nerves may be slightly myelinated, conclusions which Ambronn and Held have confirmed by means of their "optical method." 'Archiv für Anat. und Physiol.,' 1896, p. 210.

† K. und S. 'Untersuchungen des Physiol. Instituts der Universität Heidelberg,' Bd. 3, p. 149.

‡ 'W. S. B.,' vol. 89, 3 Abth., p. 137.

§ 'Pflüger's Arch.,' vol. 40, p. 207.

in weight. As described by Kühne and Steiner the E.M.F. of the resting current of the olfactory nerve was found to be very high, and a few experiments, made by the "opposition method" of those authors, gave results similar to theirs; that is to say, the resting current of the non-medullated nerve overpowered that of a medullated nerve of approximately similar thickness, whether taken from the fish itself or from a frog.

The galvanometer used was a sensitive and quickly reacting instrument by Siemens and Halske, of Berlin, a modified form of the D'Arsonval pattern. It was used with a telescope in the usual way.

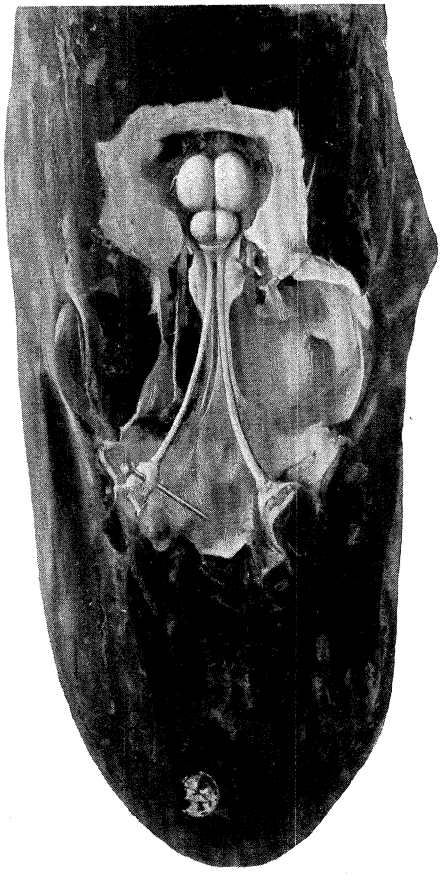
Method.—To prepare the olfactory nerves: the head of the pike was cut off, the lower jaw removed, and the head fixed to a small board. The bones of the upper surface of the skull, from the brain down to the nostrils, were removed with bone forceps, care being taken that only bone was cut away, the cartilage below being left uninjured. The cartilage thus exposed forms a thin capsule over the lobes of the brain, becoming thicker towards the olfactory lobes, and forming, where these are prolonged into the olfactory nerves, a substantial sheath which encloses the nerves entirely, and through the semitransparent walls of which the nerves are just visible. To expose the nerves a fine sharp scalpel was used, with which the upper surface of the cartilaginous sheath was sliced away, great care being taken not to cut too deeply and so injure the nerves themselves. Having removed in this way their upper covering, the two grey nerves are found lying side by side in their canal: they run parallel for the greater part of their length, then fork, right and left, to enter either nostril. Before attempting to remove the nerves, it must be carefully ascertained that they are freely exposed in their entire length, with no overhanging shreds of cartilage to catch and injure them. The way being clear, the end-organ of each nerve is separated from its nostril and serves as a handle by which the nerve is lifted from its canal; a clean scissor cut then severs its central end from the olfactory lobe, and the nerve is ready for experiment* (see Plate).

The central end of the nerve was led off from transverse and longitudinal sections by brush electrodes; their distance apart was usually 5 mm. The stimulating electrodes were of platinum wire, with Hering's† extra loop to cut off unipolar effects. The induction coil was supplied by a single Daniell cell, the distance between primary and secondary coils varying from 6 to 0 c.m.

A good olfactory nerve, freshly prepared, gave in response to single stimuli, electrical or mechanical, a negative variation that was perfectly legible on the galvanometer scale, but it must be noted that

* If, as sometimes happened, the two nerves were united near their central end they were used together as one nerve.

† Described by Pereles and Sachs, 'Pflüger's Arch.,' vol. 52, p. 529.



OLFACTORY NERVES OF PIKE PREPARED FOR EXPERIMENT.

only while the nerve was quite fresh could such responses be obtained by *single* stimuli. The momentary mechanical stimulus consisted in a clean cut through the nerve with fine sharp scissors, the blades of which had been moistened with normal saline; the nerve was supported, so that there should be no pull upon the led-off portion.

In the tables of experiments given below, a few cases will be noticed in which there is a back swing + beyond the position of rest. This is partly instrumental swing, but partly also due to a slight positive after-effect. The galvanometer used, although highly damped, was not perfectly dead-beat, and the small after-effects could not be accurately estimated. All that can be said is that there is a slight tendency towards positive after-effects on good nerves when quite fresh; later the back swing tends to fall short of the position of rest.

With tetanising induction currents the positive after-effect was only once observed with any certainty.

Olfactory Nerve of Pike.—Nerve current compensated. The nerve current is +, the negative variation −, on the scale throughout the experiments.

Exp. 1.—March 8, 1899. Pike, weighing 5½ lbs. Nerve I. Stimulation by single break induction shocks.

Coil distance.	Position of rest.	Negative variation.	Back swing.	Value of neg. var.	Back swing + or −*.	
0 cm.	71	69·5	71·7	−1·5	+0·7	..
,,	63	61·5	63·2	−1·5	+0·2	..
,,	54	52·7	54·4	−1·5	+0·4	..
0 cm.	47	45·6	46·7	−1·4	..	−0·3
,,	41	39·7	40·7	−1·4	..	−0·3
,,	45	43·7	44·5	−1·3	..	−0·5
Nerve moistened. Stimulation by single make induction shocks.						
0 cm.	49	48	49·6	−1	+0·6	..
,,	47	45·9	46·2	−1·1	..	−0·8
Same nerve. Ten stimuli make and break alternately at half-second intervals.						
0 cm.	38·5	27·7	36·8	−10·8	..	−1·7
,,	49	38·6	47	−10·4	..	−2

* In this column the + sign signifies a back swing beyond the position of rest, the − sign signifies that the back swing fell short of that position.

Exp. 2.—Nerve 2. Stimulation by single break induction shocks.

Coil distance.	Position of rest.	Negative variation.	Back swing.	Value of neg. var.	Back swing + or −.	
5 cm.	52·5	50·7	52·5	−1·8	..	..
,,	49	47·2	48·8	−1·8	..	−0·2
0 cm.	45	43·4	44·9	−1·9	..	−0·1
Stimulation by ten shocks, alternate make and break, at half-second intervals.						
0 cm.	41	26·2	41·5	−14·8	+0·5	..
,,	47·5	38·4	47·4	− 9·1	..	−0·1

Exp. 3.—February 21, 1899. Pike, 4¼ lbs. Nerve II. Momentary mechanical stimulation by cutting.

Position of rest.	Negative variation.	Back swing.	Value of neg. var.	Back swing + or −.	
88·5	86·8	87	−1·7	..	−1·5
86·6	85·2	very slow return	−1·4	..	..

Exp. 4.—March 6. Pike, 4 lbs. Nerve II. Stimulation by cutting.

48	44·5	50	−3·5	+2	..
40	36·2	41	−3·8	+1	..

Exp. 5.—March 8. Pike, 5½ lbs. Nerve II. Stimulation by cutting.

48	46	49	−2	+1	..

Through the kind co-operation of Dr. Siegfried Garten, Assistant in the Leipzig Laboratory, I was enabled to make observations with the capillary electrometer on the response of the olfactory nerve to single stimuli. The photographic records of three such observations are given below. The curves as reproduced are rather less than half their original size; they read from left to right. The negative variation appears as an upward movement of the mercury meniscus.

Fig. 1.

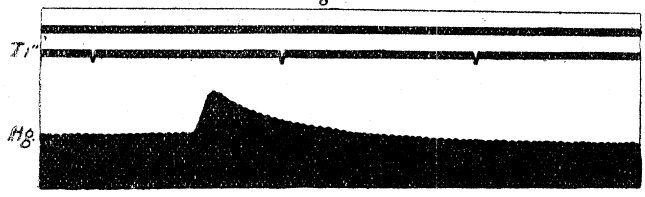


Fig. 2.

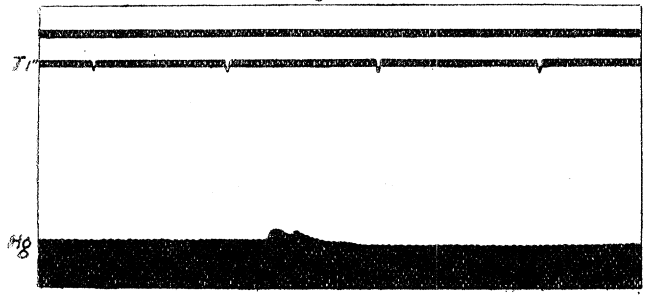


Fig. 3.

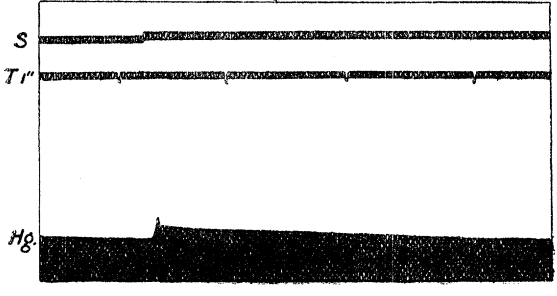


FIG. 1.—March 23, 1899. Pike of $2\frac{7}{10}$ lbs. weight. Olfactory nerve I quite fresh. Momentary mechanical stimulation by scissor-cut. Following upon the negative variation there is a very slight and slowly developed positive after-effect.

FIG. 2.—March 20.—Pike of $5\frac{1}{2}$ lbs. The two olfactory nerves are used together, quite fresh. Mechanical stimulation by cutting. The negative variation is seen as two responses incompletely fused, obviously owing to the fact that the stroke of the scissors affected the two nerves successively.

FIG. 3.—March 18. Olfactory Nerve I. Stimulation by single break induction shock coil O.C.M. The signal S shows the moment of stimulation. In all three curves the time is marked in seconds.

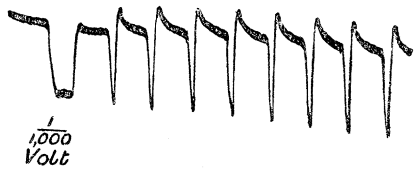
In a further series of observations the nerve was stimulated at regular intervals by brief tetanising currents, the galvanometric deflections being sometimes photographically recorded (Waller's method*).

* Croonian Lecture, 'Phil. Trans.,' B, 1897.

These experiments brought out very evidently what I am disposed to regard as a principal difference between medullated and non-medullated nerve. Whereas in medullated nerve successive effects diminish very slightly or not at all, or actually increase ("staircase effect"), non-medullated nerve always exhibits a comparatively rapid decrease of successive effects.

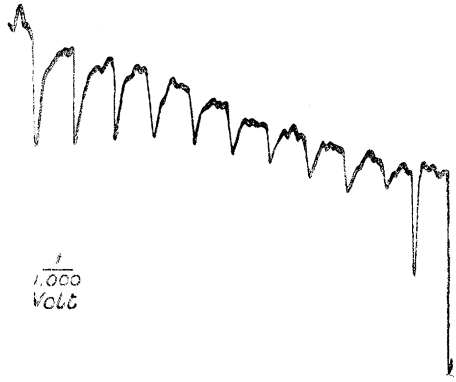
Figs. 4 and 5 illustrate this point.

FIG. 4.



Medullated nerve (frog). Stimulation at 1-minute intervals.

FIG. 5.



Non-medullated nerve (pike). Stimulation at 1-minute intervals.

The galvanometer used in these experiments was a Thomson, of Muirhead's pattern, and was dead-beat. It was used with or without photographic apparatus, the spot of light being in the last case reflected on to a large transparent screen in the half-darkened room.

The highly damped Thomson reacted too slowly for such fleeting effects as the response of the nerve to single stimuli to be made visible, but being dead-beat was most suitable for the study of positive after-effect.

With a normal olfactory nerve in its fresh state the positive after-effect was never observed with this instrument, but a most striking development of the phenomenon followed on subjecting the nerve to a stream of carbon dioxide. The nerve was enclosed in a small moist

chamber with inlet and outlet tubes, and was led off in the usual way. The stimulation by platinum wires was given at one minute intervals. After a few normal responses—the character of which was a large negative deflection often with incomplete return to the position of rest—carbon dioxide was driven into the nerve chamber; its immediate effect was a marked diminution of the negative variation and the appearance of a positive after-variation, which increased in size for several minutes, attaining often as much as three times the size of the negative variation. At this point of highest development of the positive after-effect, the back swing was very rapid, and began before the close of stimulation. The positive after-effect then began to pass off, and a few minutes later the deflection was once more purely negative. Larger doses of carbon dioxide produced anæsthesia of the nerve, but with returning excitability the positive after-effect appeared as above described.

At the period when the distinct positive after-effect had passed off a curious phase was sometimes noticeable immediately after stimulation, viz., a quick to-and-fro movement, suggesting the struggle of two opposing processes before the slow return of the spot of light towards its position of rest. For instance, in the last line of figures in Experiment 6 the spot stands at 19·5; on stimulation it moves − to 9·5, then after the stimulus + to 11, − to 10, and slowly back to 18.

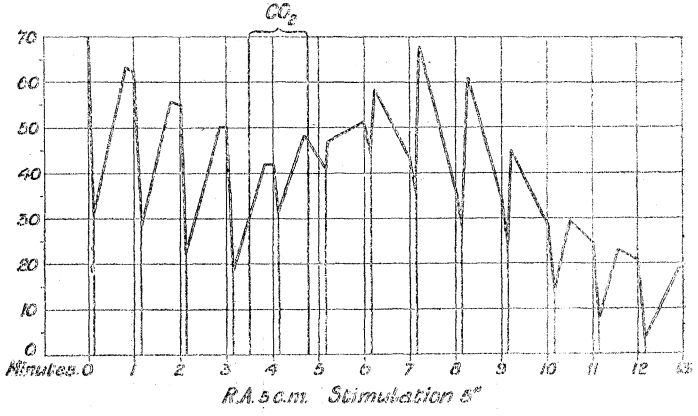
April 13, 1899. Olfactory Nerve I. Stimulation by Tetanising Currents. Nerve Current off Scale Spot, brought back by Magnet.

Stim.	Coil.	Zero.	Neg. var.	Back swing.	Value of neg. var.	Back swing.	
						+ or	Incomplete.
5″	5 cm.	70	33	63	−37	—	Less 7
At 1 min.	,,	62	29	56	−33	—	,, 6
intervals.	,,	55	23	50	−32	—	,, 5
	,,	50	18·5	42	−31·5	—	,, 8
		CO_2 1½ mins.					
	,,	42	31	48·5	−11	+6·5	
	,,	42·5	40·5	47·5	− 2	+ 5	
Exp. 6..	,,	51	45	59	− 6	+ 8	
	,,	43*	36	67·5	− 7	+24·5	
	,,	37*	28	61	− 9	+24	
	,,	34	24	45	−10	+11	
	,,	29	14	29·5	−15	+ 0·5	
	,,	25	8	23	−17	—	,, 2
	,,	21	4	19	−17	—	,, 3

* The + after effect began before the end of stimulation.

April 13, 1899. Olfactory Nerve I—*continued.*

Stim.	Coil.	Zero.	Neg. var.	Back swing.	Value of neg. var.	Back swing.	
						+ or	Incomplete.
			Spot readjusted.				
	5 cm.	51	*30·5*†	47	−20·5	—	Less 4
	,,	46	*26·5*,† *25·5*†	43	−21	—	,, 3·5
	,,	43	24·5, 25, *23*†	40	−20	—	,, 3
	,,	40	22, 22·5, 21	37	−19	—	,, 3
	,,	37	20, 19, 18	35	−19	—	,, 2
	,,	35	19, 19·5, 16	33	−19	—	,, 2
	,,	33	16·5, 17, 14·5	30·5, 31	−18·5	—	,, 2
	,,	31	15, 15·5, 13	—	−16	—	
			CO_2 2 mins.				
	,,	23*	24	35	− 4	+ 7	
	,,	31	30	31·5	− 1	+ 0·5	
	,,	39	—	—	—	—	
	,,	48	44·5	50·5	− 3·5	+ 2·5	
	,,	34*	31	51	− 3	+17	
	,,	31	26	45	− 5	+14	
	,,	29	23	34·5	− 6	+15·5	
	,,	26	19	27	− 7	+ 1	
	,,	24	16, *20·5*†	25	− 8	+ 1	
	,,	23·5	13, 16, 15·5	23	−10·5	—	,, 0·5
	,,	22	11·5, *14*†	20·5	−10·5	—	,, 1·5
	,,	19·5	9·5, 11, 10	18	−10	—	,, 1·5



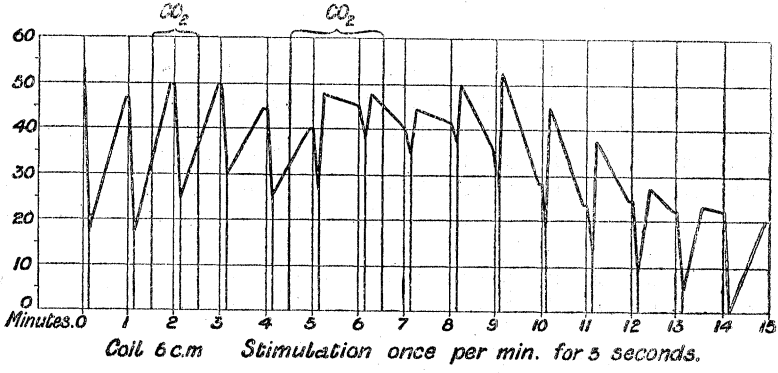
Curve of first part of Experiment 6.

* The + after-effect began before the end of stimulation.

† A pause of a second or so took place here.

April 14, 1899. Olfactory Nerve.

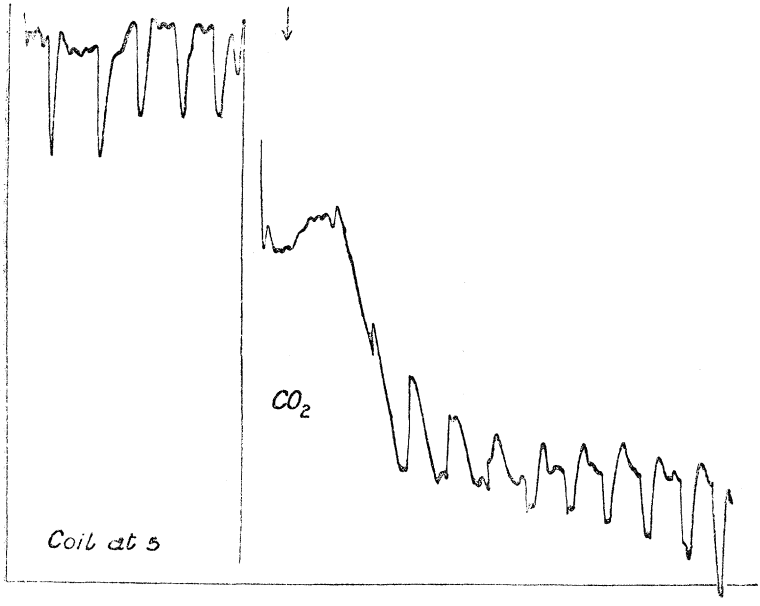
Stim.	Coil.	Zero.	Neg. var.	Back swing.	Value of neg. var.	Back swing.	
						+ or	Incomplete.
5″	6 cm.	53	18·5	47	−34·5	—	Less 6
	,,	47	17	—	−30		
			CO_2 1 min. (slow stream).				
	,,	50	25	50	−25	—	
	,,	50	30	44	−20	—	,, 6
	,,	44	25·5	—	−18·5	—	
			CO_2 2 mins.				
Exp. 7..	,,	40·5	28	47·5	−12·5	+ 7	
	,,	45	38·5	48	− 6·5	+ 3	
	,,	41	35·5	44	− 5·5	+ 3	
	,,	41·5	37	50	− 4·5	+ 8·5	
	,,	35	27·5	52	− 7·5	+17	
	,,	28	19·5	45·5	− 8·5	+17·5	
	,,	24·5	14	37·5	−10·5	+13	
	,,	24	8·5	27	−15·5	+ 3	
	,,	22	5	23	−17	+ 1	
	,,	22·5	1	20·5	−21·5	—	,, 2
			Spot adjusted.				
	,,	50	23	46·5	−27	—	,, 3·5
	,,	46·5	22·5	—	−24	—	
			CO_2 2 mins.				
	,,	50	44	60	− 6	+10	
	,,	47·5	45	48	− 2·5	+ 0·5	
	,,	46	43·5	52·5	− 2·5	+ 6·5	
	,,	48	40	58	− 8	+10	
	,,	36	30	55	− 6	+19	
	,,	35	28·5	59·5	− 6·5	+24·5	



Curve of first part of Experiment 7.

Fig. 6 is a photographic record of a similar experiment.

Fig. 6.



Effect of CO_2 on the negative variation of non-medullated nerve. Stimulation at 1-minute intervals.

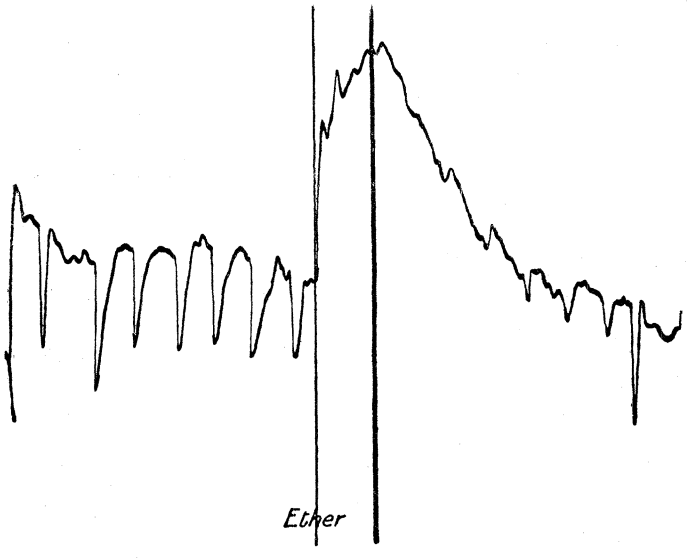
Another condition in which the olfactory nerve gave positive after-effects was after being kept for some time in normal saline. Isolated grey nerve appears to be far less resistant than white nerve, but the olfactory sometimes retained its excitability for as long as four hours after excision, and the electrical response of such a kept nerve was usually a negative effect followed by a large positive after-effect. In frog nerve there is also a development of positive after-effect in stale nerve; but whereas such effects are in this case markedly reduced if not abolished by a new transverse section, in the case of the olfactory nerve the positive after-variation persists after fresh section.

A few experiments were made to test the effect of ether and chloroform vapour on the negative variation of non-medullated nerve. The galvanometric effect was promptly abolished by brief administration of ether or chloroform vapour. Recovery after anæsthesia occurred to some extent—more markedly in the case of ether than in that of chloroform.

I wish to take this opportunity of thanking Professor Hering for the means of study which I enjoyed at Leipzig, and for his kindness in sparing me much of his own valuable time.

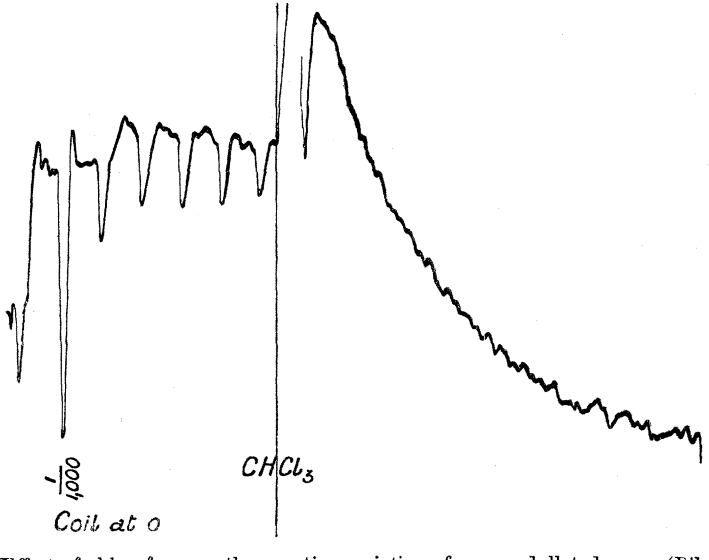
I would also thank Dr. Waller for kind help and suggestions.

FIG. 7.



Effect of ether on negative variation of non-medullated nerve (Pike).

FIG. 8.



Effect of chloroform on the negative variation of non-medullated nerve (Pike).

OLFACTORY NERVES OF PIKE PREPARED FOR EXPERIMENT.