SOME CONTRIBUTIONS TO THE PHYSIOLOGY OF UNSTRIATED MUSCLE. By LUCIAN A. E. DE ZILWA, B.Sc. (Lond.). (Twenty-one Figures in Text.)

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PERHAPS it hardly requires to be pointed out that in order to ascertain the behaviour of unstriated muscle, it is of advantage to employ a tissue in which the muscle-fibres are arranged in a single layer, as parallel fibres, and in which no nerve-cells are present. In mammals such tissue is represented, so far as we know, only by the sphincter pupillæ, studied by Grünhagen and Samkowy[1], and the retractor penis, which was the subject of special investigation by Sertoli[2]. Since the publication of Sertoli's paper the innervation of the retractor has been specially studied by Langley and Anderson; but, apart from a few observations by Schultz, the behaviour of the isolated muscle under variations of temperature, its reaction to stimulation, and similar points, have received no further attention.

Prof. Starling therefore suggested to me the desirability of repeating Sertoli's experiments, as well as continuing some which he had begun on the same subject with Dr W. M. Bayliss. My best thanks are due to Prof. Starling for his kind assistance and advice at all stages of the work.

THE MUSCLE AND ITS STRUCTURE.

An account of the anatomical arrangement of the retractor penis of the dog will be found in a paper by Langley and Anderson[3]. As these authors first pointed out, the muscle has a double innervation, inhibitory and motor. The inhibitory fibres run in the nervi erigentes. The motor fibres are derived from the sympathetic. They arise from the 12th thoracic to the 3rd lumbar nerve, run down to the sacral

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[1] *Pflüger's Archiv*, IX. S. 399. 1874; X. S. 165. 1875.

[2] *Rendiconti del R. Ist. Lomb.*, Ser. II., XV. f. 16. *Arch. ital. de Biol.*, III. p. 78.

[3] This *Journal*, XIX. p. 88. 1895.

ganglia, and thence by the grey rami communicantes to the sacral nerves. Most of these fibres travel along the pudic nerve to the dorsal nerve of the penis; others are distributed by the genito-anal branch of the pudic nerve. A tracing showing the antagonistic effect of these nerves is given in Starling's *Physiology*, 1900, p. 153.

The absence of nerve-cells from this muscle is supported by Fletcher's[1] results on the mode of termination of the nerves in the muscle of the hedgehog and rat. In the latter animal a superficial anastomosing plexus is formed on the muscle. From this plexus offsets pass inwards to form a dense intercellular network. After section of the pudic nerve the plexus and network were found unaltered both in the rat and in the hedgehog. In the hedgehog excision of the 1st pelvic ganglion, and section of the pudic nerve on one side, caused disappearance of nervous elements on that side. The conclusions suggested are (1) that there are no local trophic centres in the end-apparatus; (2) that possibly a plexus common to both sets of fibres is preserved from degeneration after section of the one set through its continuity with the other. The sensory ganglion-cells described by Schultz[2] in smooth muscular tissue were probably connective tissue cells.

I have studied the histology of the tissue in teased preparations and sections. With the exception of a few voluntary fibres at its perineal end, the whole muscle is made up of parallel plain muscle-fibres, which in a state of contraction are about ·3 mm. long and have a maximum diameter of ·008 mm. Each fibre has a single nucleus and is closely adherent to adjacent fibres.

VITALITY AND SPONTANEOUS CONTRACTIONS.

Sertoli found the excitability of the muscle persisting five, six, or even seven days after excision. He found also that the excitability lasted longer when the muscle was preserved in blood-serum at a temperature of 5° to 8°. At first I placed the muscle with defibrinated blood in an ice-chest; but later the whole penis was cut away with the scrotum, so that only the posterior cut end of the muscle was exposed to the atmospheric micro-organisms. The penis was then put into the ice-chest or left in snow. The spontaneous contractions were studied by Sertoli in the living animal, curarised and non-curarised (without

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[1] This *Journal*, XXII. *Proc. Phys. Soc.*, p. xxxvi. 1897.

[2] *Arch. f. Phys.* 1895. S. 542.

an anæsthetic ?), and in the excised muscle. They lasted for hours at a time, and were still perceptible after three or four days; in one case, though then very feeble, even on the fifth day. Muscle more than a day old was used by me only on a few occasions; in such I never saw spontaneous contractions on the third day after death, and only once on the second. But I have several times seen them in muscle 24 hours old. Even in the fresh preparation they have been quite absent. In this case a series of spontaneous contractions may often be started by a weak stimulation or by changing the environment of the muscle, *e.g.* by warming and cooling it.

The spontaneous contractions are sometimes quite small and frequent, eight or ten a minute. At other times they are powerful and infrequent, lasting two minutes or more, and the ascending part of the curve is marked with little steps or waves, especially near the apex. The relaxation is marked by an unbroken line (Figs. 1 A and 1 B).

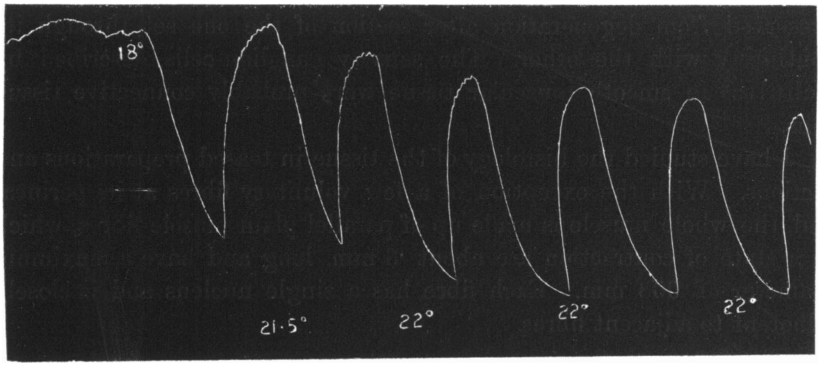

Fig. 1 A. Fresh muscle in normal salt solution. Spontaneous contractions. In this and other tracings, unless otherwise stated, the drum was revolving at the rate of 7 mm. a minute.

As I shall show later on, propagation of excitation along the muscle is feebly marked or absent; hence it seems that any muscle-fibre or group of fibres can have no information of the excitatory condition of adjacent fibres other than by changes of tension. A similarity of environment for all fibres will tend to produce approximately similar rhythms in all, but the features of the curve given by the whole muscle will be determined fortuitously by the clashing or concurrence of the rhythms of different parts of the muscle. In this way may be explained the great diversity of curves which are obtained from the spontaneously contracting muscle.

Sertoli draws a great distinction between the curve of a spontaneous contraction, in which "the period of shortening is almost equal to that of lengthening," and that obtained after electrical stimulation in which "the former is much shorter than the latter." But the difference is probably due, as is pointed out by Winkler, to the very strong currents used by him damaging the muscle. The curves in Fig. 13, for instance, in response to weak interrupted currents, do not differ materially from those of the spontaneous movements.

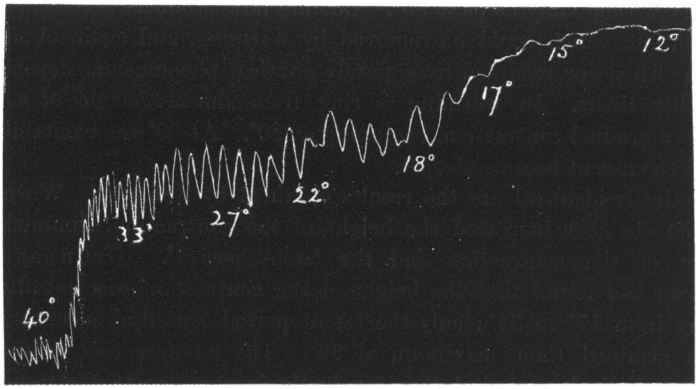

Fig. 1 B. Fresh muscle in defibrinated blood. Effect of temperature on spontaneous contractions.

CHANGES OF TEMPERATURE, AND THEIR INFLUENCE ON THE LENGTH, EXCITABILITY, AND SPONTANEOUS CONTRACTIONS OF THE MUSCLE.

Historical. The influence of temperature-variations on plain muscle has been studied by several investigators. Samkowy confirmed the observations of Schur that the pupils of different animals responded differently. The pupil of the frog dilates on warming, that of the rabbit contracts at first, but dilates later. The sphincter pupillæ relaxed by warmth, contracts on cooling to 28° or 29°; on further cooling it again relaxes. The fully dilated pupil of a dead cat narrows at moderate temperatures, but dilates at 37° or 0°. Plain muscle of warm-blooded animals kept at 37° relaxes. He used Grünhagen's thermotonometer, and, besides the sphincter pupillæ, muscle from the bladder of the frog, rabbit, and cat, and the rectococcygeus of the rabbit[1]. The loads employed in the above experiments were ·08 to ·2 grm. for weak, and 1 to 7·7 grms. for strong muscles.

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[1] *Pflüger's Arch.*, IX. S. 400. 1874.

Morgen[1] at first suspended his muscle-ring from the frog's stomach in salt solution, but later he made use of Grünhagen's thermotonometer. On warming from 17° there followed a relaxation beginning at 25° and reaching a maximum between 45° and 50°. On being stimulated between 25° and 40°, the muscle contracted with greater speed and strength, and relaxed more quickly. The electrical excitability gradually diminished after 40°, and was sometimes still found to be present at 45° on testing with a fairly strong current. If the warming had not exceeded 50° cooling again caused contraction. At 57° a contraction (which he calls heat rigor) set in, increasing gradually without any steps to 85°. Cooling now produced a certain amount of relaxation, which could be removed by warming, and again obtained by cooling. This was regarded as a purely physical phenomenon dependent on the elastic tissue. In warming a ring from the œsophagus of a dog he obtained a gradual contraction, beginning at 20°. At 50° the excitability was lost and the ascent became steeper.

Practically identical are the results obtained by Schultz. Warming in the moist chamber increased the height of the contraction, diminished the duration of the contraction and the latent period[2]. (Grünhagen and Samkowy had found that the height of the contraction was not altered on warming from 17° to 32°; only the latent period was diminished.) These changes attained their maximum at 39°. The latent period continued to decrease a little longer, and then gradually increased. If the muscle was cooled before it had reached 45° these phenomena could be repeated. As the temperature approached 50°, after each stimulation the relaxation became more and more imperfect. The muscle was relaxed between 40° and 45°. At 60° a slight contraction took place, which gradually increased on warming. The effect of cold on the duration, height, and latent period of the contraction was exactly opposite to that of heat[3]. His observations on very low temperatures will be mentioned later.

Bottazzi and Grünbaum found that for the toad's œsophagus the optimum temperature was 28°. On warming, the spontaneous contractions increased in frequency but diminished in amplitude[4]. At 39° the tonus was diminished. On cooling, the tonic contraction was increased; and at 13° the spontaneous contractions began to grow smaller. On further cooling they ceased altogether. On warming from 0° a relaxation begins at 5°. The spontaneous contractions reappear at 13°, and are now more energetic than before.

Vernon[5] studied the behaviour of smooth muscle taken from the œsophagus, stomach, intestines, bladder and aorta of various animals. He states

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[1] *Unters. aus. d. physiol. Inst. zu Halle*, H. 2. S. 161. 1890.

[2] *Arch. f. Phys.* 1897. S. 13.

[3] *Ibid.*, p. 17.

[4] This *Journal*, xxiv. p. 63. 1899.

[5] *Ibid.*, xxiv. p. 239.

that the temperature at which excitability disappears is about the same for plain as for striped muscle. Then follows a relaxation for over 10°, which he thinks might be due to the disappearance of tonus. Between 47–48° and 62° a marked heat-contraction sets in, lasting till 90°. Sertoli and Bottazzi's observations will be mentioned below.

Method. The following muscle chamber was designed by Professor Starling. Two glass cylinders 2·5 cm. and 7 cm. respectively in diameter are fitted up concentrically by means of rubber corks. Through the lower cork comes a metal tube which winds spirally about the inner cylinder and goes out through the upper cork. A stirrer *a* and thermometer *c* are in the space between the cylinders, which is filled with a saturated solution of salt. Ice, or a mixture of pounded ice and salt, is put into the vessel *k*, while *h* holds water warmed by a circular burner *n* (Fig. 2). Stop-cocks *l*, *m*, on the tubes leading from these vessels to a T-piece, enable one to circulate hot or cold water in the glass jacket, and to regulate the rate of flow. Through

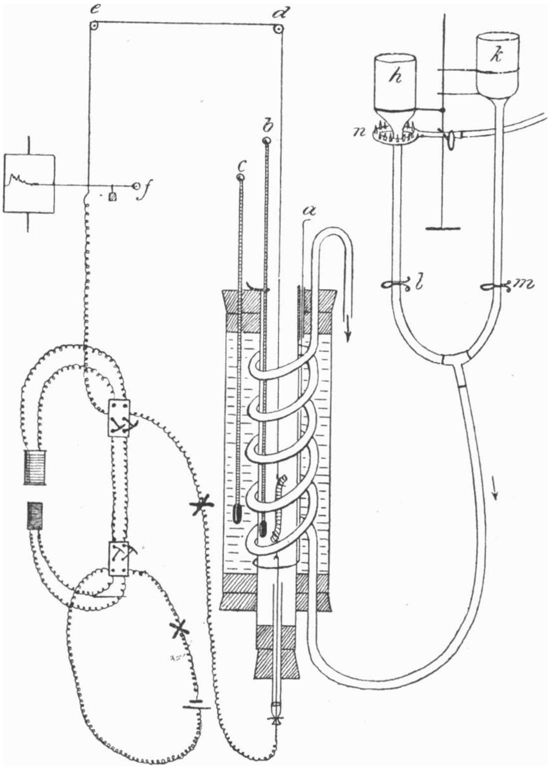

Fig. 2. Diagram of apparatus.

a cork fitting into the lower end of the inner cylinder passes a glass tube transmitting to the exterior the stem of a small iron hook. This stem is fixed below by means of a ligature about a piece of rubber tubing at the lower end of the glass tube. A piece of very fine copper wire or gold wire connects the hook to the end of the muscle, which would be brought into contact with two metals if it were put directly on the hook. The other end is also tied with fine wire which runs (insulated) over the pulleys *d* and *e* to the lever *f*, and thence to a battery or induction coil. In most of the experiments, however, the chamber was so placed that the end of a lever was directly above it. A thermometer *b* is introduced into the inner cylinder, and supported on the edge by means of a cork ring or a piece of wire. When the muscle is not in a fluid medium a strip of wet filter-paper adherent to the wall of chamber preserves the muscle from drying. The temperature is maintained fairly constant if the chamber is wrapped in a sheet of cotton wool. The load varied from 1 to 7 grm.

In the earlier experiments the electrical excitability was not tested, but later by the arrangement shown in Fig. 2, either an induced or a constant current could be sent through the muscle. The source of the current was an accumulator of E.M.F. two volts.

Changes between 15° *and* 60°. At 10° or 15°, in a moist chamber or a medium of blood, the muscle is in a state of tonic contraction and free from movement. On warming slowly a gradual relaxation takes place till 38° is reached, when spontaneous contractions set in. On further warming at about 40° they cease, and the relaxation is complete. These typical results are seen in Fig. 3. At 48° a marked contraction occurs which persists till 52°, then giving place to a slow relaxation. The top of this curve is sometimes broken even after 49° by small and frequent spontaneous contractions. At 58 to 60° the relaxation is complete (Fig. 4). Some variations however occur. The muscle might not

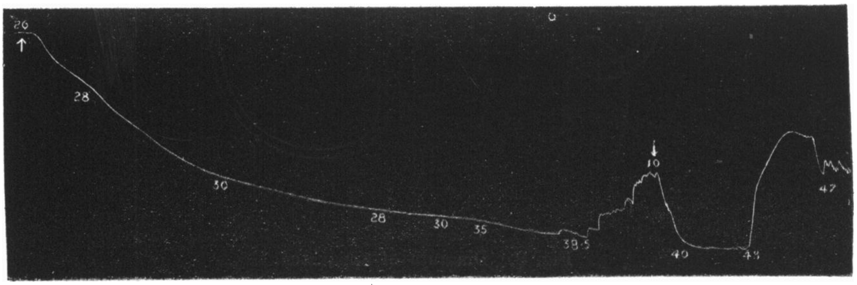

Fig. 3. Fresh muscle warmed in blood.

be in a state of great tonus at 15°. On warming from 10° a relaxation may occur at 14°, and slight spontaneous contractions be seen at 15·5°.

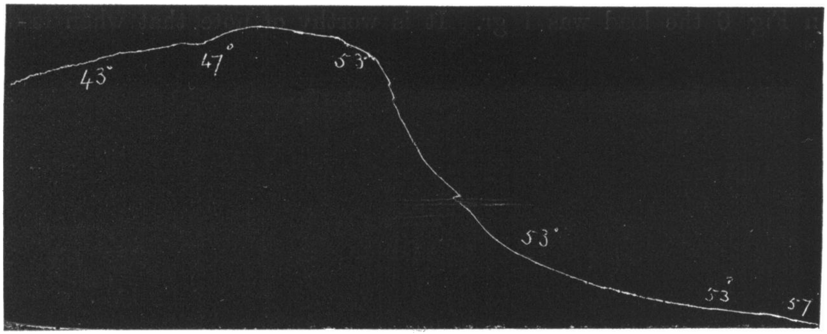

Fig. 4. Fresh muscle warmed in normal salt solution.

Occasionally on raising the temperature from 10°, a slow contraction (usually at 16°) precedes the relaxation. This is especially likely to occur if the change of temperature has been sudden. The relaxation at each stage on warming in these cases is apt to be followed by a contraction.

In cooling from 40° the above typical events appear in the reverse order. The spontaneous contractions which at this temperature are feeble, irregular, and frequent, gradually gain in amplitude and regularity and become less frequent. Below 20° their frequency and height diminish, and at 15° they cease. A well-marked tonic contraction appears immediately on cooling, and increases gradually to 10° (Fig. 1 B).

Sertoli did not heat his muscle above 37°. His observations were made on its changes in length, and are quite in accord with the facts stated above.

Changes between – 3° *and* 20°. On cooling below 10° the tonic contraction remains unaltered till 2° is reached, when a relaxation begins

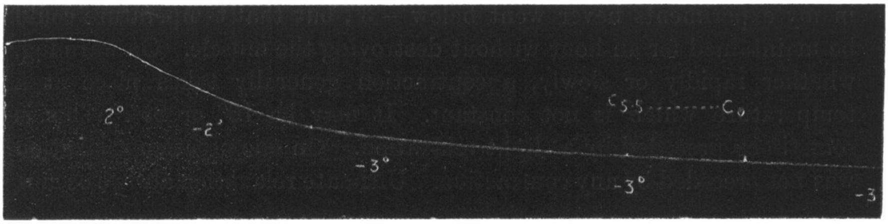

Fig. 5. Fresh muscle. Moist chamber. Relaxation on cooling to – 8°. Load 5 grms.

(Fig. 5) which appears to be more rapid if the temperature does not fall below zero. This relaxation seems to depend on the load. In Fig. 5 the load was 5 grm. When the load is small no relaxation occurs. Thus in Fig. 6 the load was 1 gr. It is worthy of note that when it did occur the contraction at 48° was ill-marked or absent; and when it did not the latter was good (Fig. 6). Sertoli states that the muscle is always relaxed between 2° and 5°. His load, which is described as moderate, was probably not very small. In this connection might be mentioned the observations of Schultz[1]. Between −8° and −10° a strong contraction occurred, which gave way to relaxation on warming, but now the muscle was found to be quite inexcitable. If this contraction had not taken place the excitability was unimpaired. The cooling in my experiments never went below −3°, but that temperature could be maintained for an hour without destroying the muscle. On warming, whether rapidly or slowly, a contraction generally takes place at a temperature which is not constant. It may be 16° or 25°. This is sometimes preceded by a slight relaxation. On one occasion relaxation was not preceded by any contraction. Ultimate relaxation always occurs.

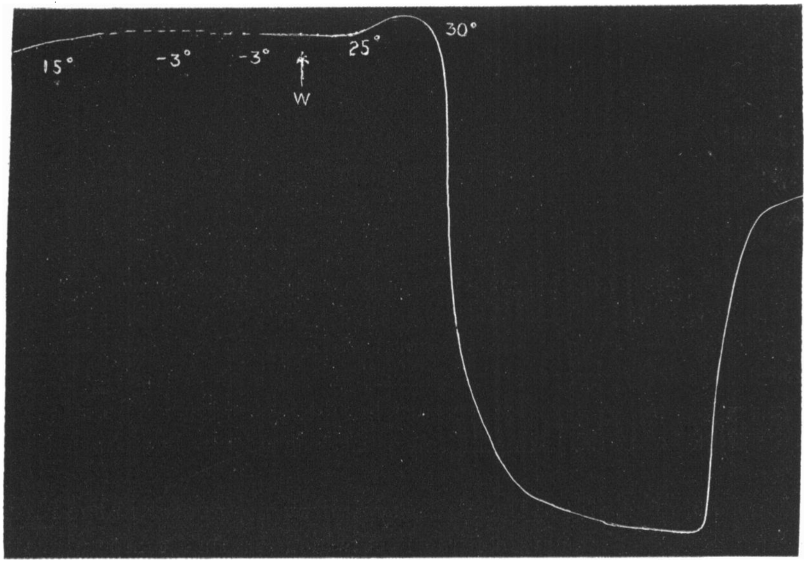

Fig. 6. Fresh muscle. Moist chamber. No relaxation on cooling to −3°. Load 1 grm.

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[1] *Archiv f. Phys.* 1897. S. 19.

Changes between 60° *and* 80°. Fig. 7 represents what usually happens. Contractions occur at 65°, 68°, 73° and 75°. In another case they were at 64°, 68°, 71° and 77°. In other cases no contraction occurs before 69°. If the warming is rapid there are naturally no steps on the curve. The variations in the figures are doubtless due to the varying thickness of the muscle and the variations in the time required to heat it. Taking the average of 19 cases, the first rise occurred at 65·58°.

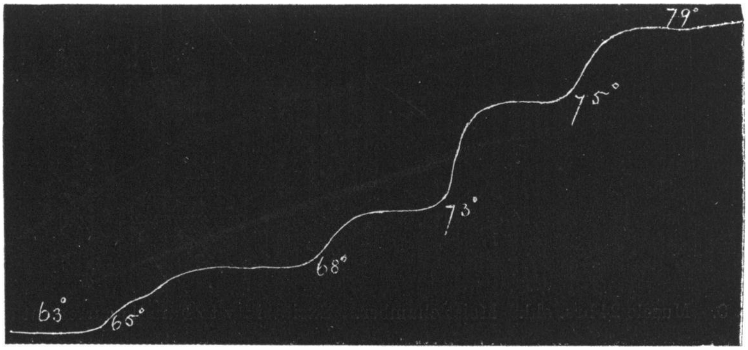

Fig. 7. Fresh muscle warmed in salt solution. Coagulation-temperatures.

Excitability. This is exceedingly variable, tested by means of an interrupted current. In one case a contraction occurred at 4° C. without any following relaxation. In others the muscle was inexcitable at 15° or at 10°. Speaking generally one may say that the excitability is absent below 10°, and present above it. In those cases where no response is obtained by stimulation, warming does not produce an immediate capability to respond, though it changes the length of the muscle. A thermic stimulus may be effective at a time when an electrical one is not.

Turning to the higher temperatures, Fig. 8 shows that a response was obtained when the temperature of the chamber was 57°. It is possible, however, that the temperature of the muscle itself may have been a little lower. In testing the excitability it was necessary to avoid placing the muscle in a fluid medium, owing to the short-circuiting produced except in the case of strong interrupted currents.

The main interest of these results is in their bearing on the question of heat rigor in voluntary muscle. In the retractor penis there is no evidence of a true rigor mortis occurring. The contraction which occurs in most muscles at about 47° C. and is apparently due to a direct excitatory effect of the temperature, either on the nervous or muscular elements of the muscle, passes off entirely at about 54° C. and gives place to complete relaxation. In this case the death of the muscle is marked by relaxation, not by contraction, and the muscle is often found to retain some trace of irritability as it is beginning to relax at a temperature of 52°—54° C. When complete relaxation has occurred the muscle is dead, and its response to excitation or changes of temperature cannot be restored by cooling. The further permanent contraction which comes on at about 65° C., *i.e.* long after the muscle has been dead, can only be due to the coagulation of proteids. The force and extent of this coagulation-contraction show that there is no mechanical difficulty in assuming proteid coagulation to be also responsible for the rigor mortis of voluntary muscle. (Cp. von Fürth and Brodie.)

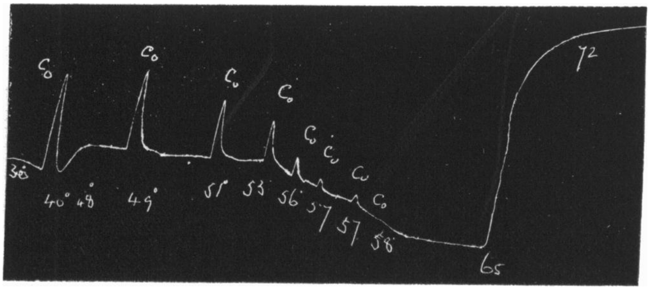

Fig. 8. Muscle 24 hrs. old. Moist chamber. Excitability to Faradic current at 57°.

A similar absence of heat rigor was observed by Bottazzi[1] in the œsophagus of the chick, though in the toad's œsophagus heat rigor (probably comparable to the coagulation rigor of the retractor at 68°) was observed at 47° C.

THE EFFECTS OF DIRECT EXCITATION OF THE MUSCLE.

Induced currents. Sertoli was unable to obtain any response of the muscle to single shocks, and the curve figured by him was obtained by stimulation with a faradic current. I have found no difficulty in eliciting a contraction in response either to a make or a break induction shock, although a considerable intensity of current is

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[1] "Sullo sviluppo embrionale della funzione motoria negli organi a cellule muscolari." Firenze, Carnesecchi. 1897.

required. In Fig. 9 are shown the curves of contraction obtained with single make-shocks. The "staircase" phenomenon is well-marked. The response to each stimulus, especially the later ones, shows a number of waves, which begin to appear at a higher and higher level on the ascending limb of the curve. While the height of the contraction increases gradually, the relaxation begins earlier and proceeds more rapidly up to a certain point, though the whole contraction is increased in duration. The temperature in this case was about 38°.

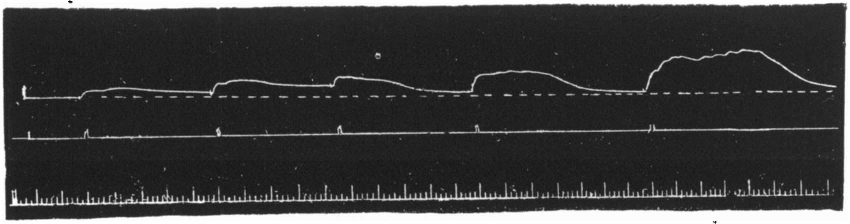
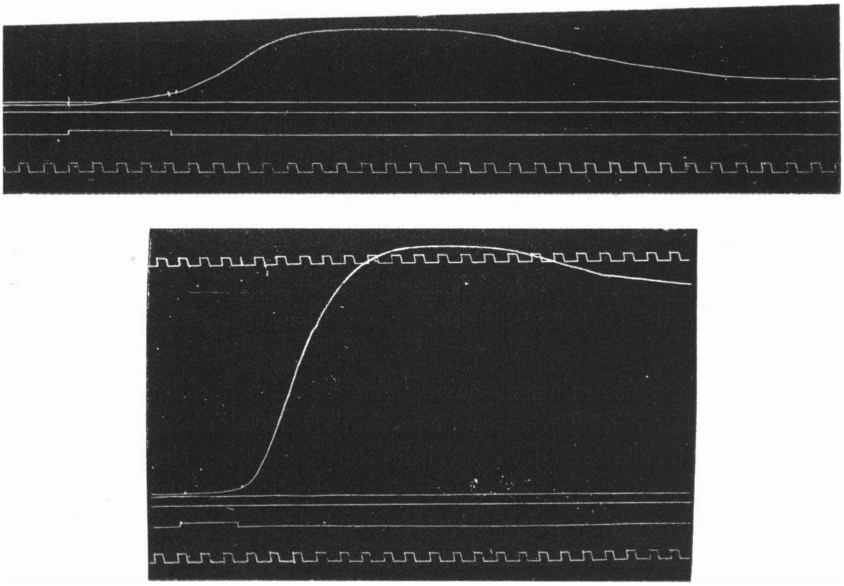


Fig. 9. Fresh muscle. Moist chamber. Staircase-phenomenon on stimulation with make induction shocks. Time-marking in seconds.

The make and break stimuli are usually equally efficient. Occasionally the second is found to be better. The character of the curve varies greatly with the temperature. At 40° the curve attains its height rapidly and then declines gradually to the base line in fifteen seconds. The apex is generally round. When cooled to 25° the duration of the contraction is increased, so that even stimulation at twenty-second intervals causes summation, while at 40° the contraction was over in fifteen seconds. The curve rises more slowly to a less height, and declines more gradually. Figs. 10 A and 10 B, taken with a quickly revolving drum, give the latent period. A strong make-shock was followed by a break. The influence of the interval between them on the amount of summation is well seen. The latent period is on the average ·4 seconds for make, and ·2 seconds for break, but diminishes somewhat with successive stimuli. Thus in Fig. 10 A, for make it was ·4 seconds, for break ·2; in Fig. 10 B, ·3 for make, for break ·15.

Repeated shocks. A summation of stimuli is produced, which will be discussed under another heading, if the intervals are sufficiently small. The ascent of the curve is broken by steps or not, according as the intervals are great or small. On one occasion slight relaxation was obtained on stimulating with the faradic current at 16°. Winkler sometimes saw relaxation follow faradisation, as also the opening or closing of a constant current.



Figs. 10 A and 10 B. Latent periods. Time-marking = ½ secs. Load 5 grms. Temp. 29°.

Voltaic currents. Sertoli employed a "feeble" current from six small Daniell cells and a stronger one from 20 elements. In the first case he obtained arrest of spontaneous movements, and relaxation. In the latter, on closure, after a latent period of two or three seconds, a slow contraction occurred, which persisted during the passage of the current. At break, after a lapse of ten or twelve seconds a relaxation followed. If the muscle was inexcitable to strong induced shocks, only relaxation occurred during the passage of the constant current, "through diminution of elasticity;" the original length being regained on the opening of the circuit.

In addition to my work under this head Professor Starling and Dr Bayliss have allowed me to use results of their preliminary experiments. The source of the current unless otherwise stated was an accumulator of E.M.F. 2 volts. The twin tracings were taken with a double myograph. The muscle in a moist chamber was clamped or pinned in the middle, and the ends were connected with levers writing in the same vertical line. The current was led to the ends of the muscle through Sanderson's electrodes.

The reaction of the muscle to make and break of the constant current is intimately dependent on the condition of the muscle. When the muscle is warm and thoroughly relaxed, it responds with a contraction both to the make and break, the former being generally more pronounced. In a state of well-marked tonus the passage of a constant current may cause only relaxation, which comes on at make and often gradually diminishes while the current is passing. In this case break of the current generally leads to a temporary increased tone, so that we get a break contraction. When the muscle is in a state of partial tonus, this latter contraction may be more marked than the inhibition during the passage of the current, so that it appears as if the break of the current were the only effective stimulus. Very similar behaviour was observed by Biedermann in the case of the adductor of anodon.

On several occasions it was observed that if an induction shock elicited only a feeble response, a much better one was obtained after the passage of a voltaic current. This seems to show that the latter has a beneficial effect on muscle.

Polar phenomena. On leading a voltaic current through a curarised sartorius the contraction at closure begins at the cathode, and spreads thence. Similarly the break-contraction spreads from the anode. Although Sertoli states that the same phenomena are visible in the retractor penis,

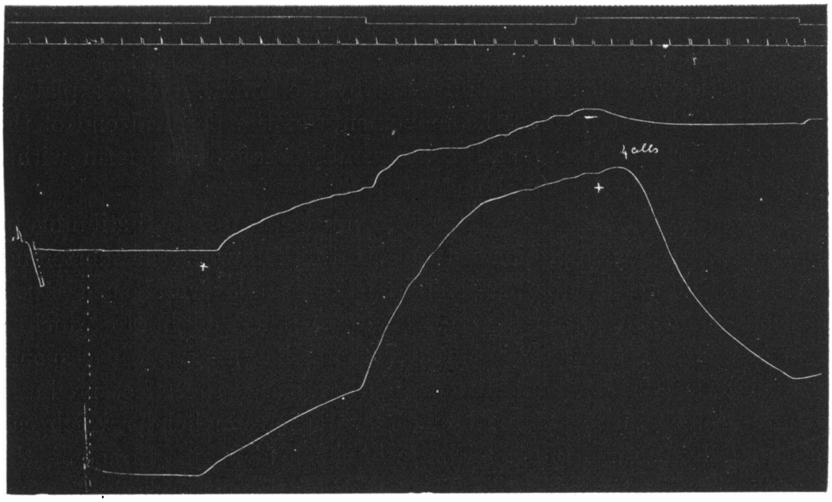


Fig. 11. Simultaneous tracings of both ends (upper curve penal). Muscle fully relaxed before first closing of the voltaic current. Sanderson's electrodes at ends of muscle. Contraction and inhibition. Time-marking = 6 secs.

records taken with the double myograph show that both halves contract or relax simultaneously. Each muscle-fibre is, therefore, a functional unit, and during the passage of a current must possess both anodic and kathodic parts. There is in this muscle no such physiological fusion of the individual fibres as is assumed by Engelmann in the case of the ureter. This is illustrated by Figs. 11 and 12. The greater amount of contraction or relaxation manifested by the lower curve is explained by the fact that it records the movements of the perineal end of the muscle which is thicker and consequently changes its form within wider limits than the penal end.

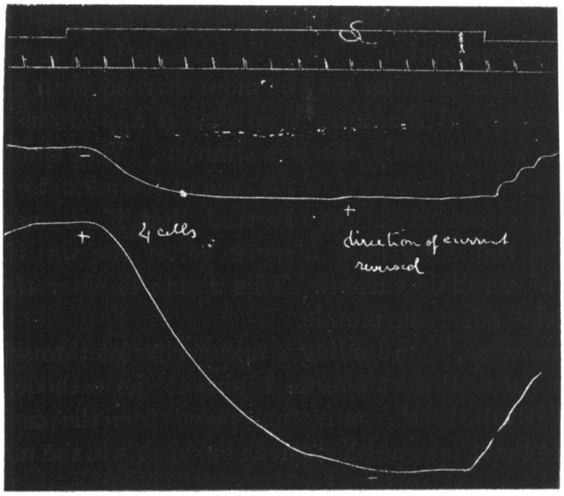


Fig. 12. Muscle in a state of tonic contraction before closure of current. Inhibition. Direction of current reversed during its passage.

Summation and tetanus. In striped muscle, if a second stimulus be applied before the completion of the relaxation following the shortening, the second curve is superposed on the first; and several such superpositions may be effected (Helmholtz). The height to which a tetanised muscle contracts is greater than that attained in response to a single stimulus. That in most of these cases the effect produced is purely mechanical is proved by the variations in height which can be caused by 'after-loading.' The later the load begins to act on the muscle, the greater becomes the height of the contraction. It has been shown by v. Frey[1] that a muscle can be made to contract by a

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[1] *Beitr. zur Physiologie, Carl Ludwig gewidmet.*

single stimulus to the same height as when tetanised, by preventing the load from acting till the tetanic degree of shortening has been almost reached. It is the extreme quickness of the excitatory process which causes the height of the contraction to be so much influenced by mechanical inertia. The mechanical response fails of its maximum effect for want of time. But this superposition of contractions is not to be regarded in every case as a summation of effects. In those muscles which show a tendency to contracture v. Frey's experiment does not succeed. The height attained on faradisation cannot be imitated by after-loading. Clearly we have here to deal with summation of a fundamentally different kind, in which there is a real addition of process. This summation of process in striped muscle is also illustrated by Kaiser's[1] observation that the second equilibrium-length of a muscle is less when two stimuli are sent together.

These two kinds of summation have not been sufficiently distinguished in voluntary muscle from the frequent merging of the one into the other, and the rapidity of the phenomena making them difficult of study. In smooth muscle, on the other hand, where the movements are sluggish, mechanical inertia has practically no influence on the height of the contraction. After-loading is not found to magnify the mechanical response to a single stimulus. The summation produced by repeated stimuli is consequently only of one kind—a summation of process and not of effects. This summation takes place when the second stimulus is applied at any stage of the contraction following the first stimulus, so long as the muscle has not completely regained its original length; a fact which proves the duration of the process of internal changes to be coterminous with that of contraction, the word 'contraction' being used to designate both the shortening and the relaxation.

From the alterations produced by changes of temperature in the form of mechanical response, we are justified in stating that warmth hastens the processes of internal change, while cold has the opposite effect. Further, the change attains a greater intensity more rapidly, and declines more quickly in the former case. Hence we should expect that stimuli which produced no summation at 40° when applied at certain intervals, would at the same intervals cause a summation if the temperature were lowered. And indeed we find that this does take place. Thus in Fig. 13 A, stimulation at intervals of fifteen seconds caused no

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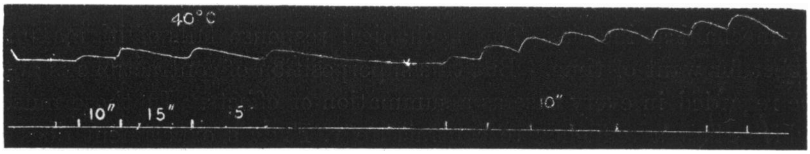
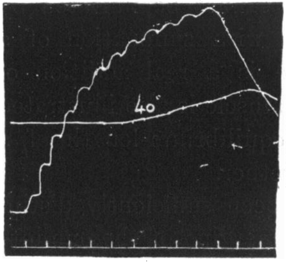
[1] *Schäfer's Text-Book*, II. 375.

summation. In Fig. 14 a summation is produced even at intervals of twenty seconds. In Fig. 13 B the stimulation was at intervals of five seconds.





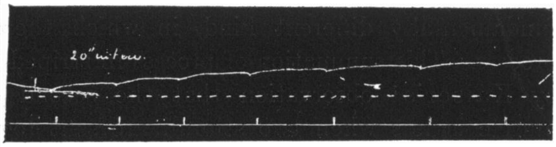


Fig. 13 A. Temp. 40°. Summation with 10 sec. intervals, but not with 15 sec. intervals. Muscle stimulated with double make induction shocks.

Fig. 13 B. Temp. 40°. Stimulation at 5 sec. intervals.

Fig. 14. Temp. 25°. Summation with intervals of 20 secs.

If more than one stimulus be applied in rapid succession, the height of the stimulus, as a rule, varies directly with the number of stimuli. (Fig. 15.)

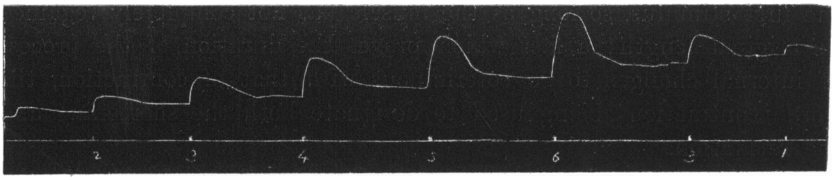


Fig. 15. Summation of process. Direct variation of the height of contraction with number of stimuli. Drum moving at rate of 5 cm. a minute.

On excitation with a series of subminimal stimuli at the rate of two per second, the contraction took place in steps, the first occurring after the eleventh stimulus. Having reached a maximum, the relaxation set in even while the stimulation was continued. (Fig. 16.) Apparently a contraction occurs as soon as the effects of a certain number of stimuli have been summed up. The slowness of the changes in the muscle seems to prevent sufficient repair for the maximum contraction to be maintained.

Pawlow[1] had observed summation in the adductor of anodon on stimulating the connective nerves at intervals of two seconds, and Fick[2] on stimulating the muscle, and Engelmann[3] in the case of the ureter; but no clear distinction had been drawn between the two kinds of summation.

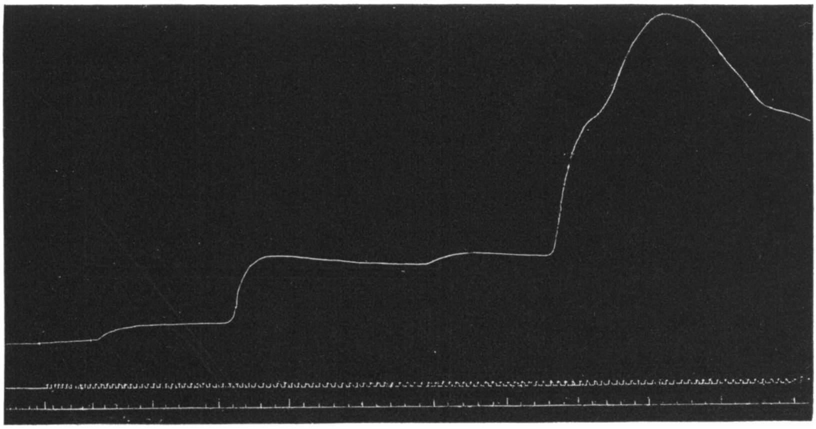


Fig. 16. Effect of subminimal stimuli 2 per sec. Time-marking = seconds.

Propagation of the excitatory process. It is very doubtful whether a wave of excitation or of contraction spreads from fibre to fibre, as happens in the case of the ureter according to Engelmann, and in the medusæ according to Romanes. It appears very much more probable that the retractor penis behaves like the retractor of *Sipunculus* (studied by v. Uexküll[4]), and that the cement-substance between the fibres is in the nature of a non-conducting material.

The muscle being in the double-myograph as in the experiments on polar phenomena, one end (penal or perineal) was stimulated by means of a faradic or galvanic current. Fig. 17 is a tracing obtained by stimulating the penal end with an interrupted current. It is seen that the other half of the muscle contracts almost simultaneously. The same result follows if a voltaic current is used. A pair of electrodes were placed on the penal half of the muscle, one at the end and the other a short distance from it. A voltaic current was then led through

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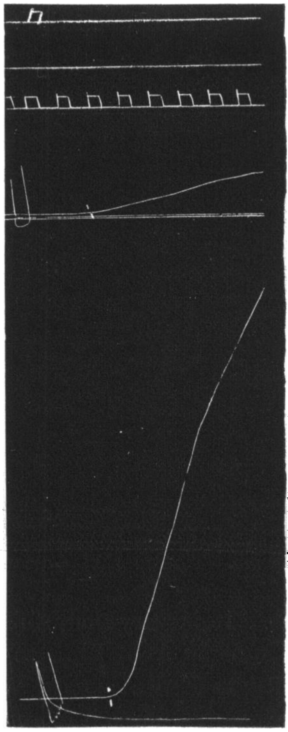
[1] *Pflüger's Arch.*, xxxvii., S. 15. 1885.

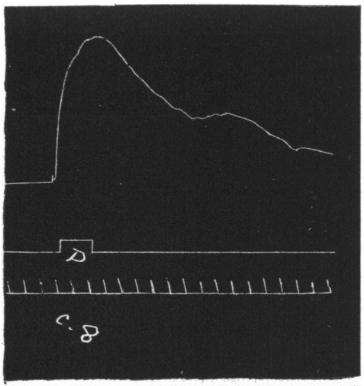
[2] *Beitr. zur vgl. Physiol. d. irrit. Subst.*, S. 49. Braunschweig, 1863.

[3] *Pflüger's Arch.*, iii., S. 281.

[4] *Zeitsch. f. Biol.* xxxiii. S. 1. 1896.

the muscle towards the penal end. After a latent period of one second both the levers rise together.





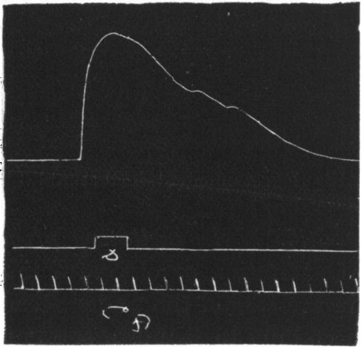


Fig. 17. Length of muscle 1½ in. Upper curve perineal. Penal end stimulated with Coil 7. Time-marking = 6 secs.

Fig. 18. Pudic nerve stimulated with Coil 8, after 80 mgms. of atropine had been injected. Time-marking = 6 secs.

Fig. 19. Pudic nerve stimulated after injection of 10 c.c. of 2 p.c. curare.

In a muscle whose movements are so slow, doubtless associated with correspondingly sluggish internal changes, it is highly improbable that there should exist such a rapid rate of propagation. Everything points to the conduction of the stimuli through a much more rapid channel—the nervous elements present in the muscle.

In a longitudinal strip of the toad's œsophagus Bottazzi[1] observed that the excitatory process was propagated at 17 to 28 mm. per second. This is remarkable in view of the otherwise close correspondence between the activity (automatic and induced) of the œsophageal strip

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[1] "Contributi alla fisiologia del tessuto di cellule muscolari." Firenze, Carnesecchi. 1897.

and that of the retractor penis, though it has an analogy in the rapid propagation of the myogenic contractions (5—10 cm. per sec.) observed by Bayliss and Starling in the small intestines of mammals.

INFLUENCE OF DRUGS.

Normal Salt Solution (made with tap-water) produces a tonic contraction, relaxation from which does not follow warming. This deleterious effect is seen only if the muscle has been in the fluid for a considerable time (1 or 2 hours). Warming produces a contraction at 38°, which is unaltered by cooling.

Morgen found that 2·5 p.c. to 5 p.c. solutions of NaCl caused a moderate contraction. The effect was slow, but when produced it was permanent.

Atropine and Muscarine. A full literature on this subject is given by Pickering[1], and the results obtained by different persons are seen to be of the most discordant nature. In the present experiments, by mixing a 1 p.c. solution of atropine with defibrinated blood, ·1 p.c. and ·2 p.c. solutions were prepared. The drug was applied by pouring it into the chamber. Muscarine was applied by dropping a ·1 p.c. solution directly on the muscle. Nicotine was applied in the same way, a 2 p.c. solution of the tartrate being used.

Very conflicting results were obtained with atropine. In most cases the effect of adding atropine to the defibrinated blood was to diminish the tonus of the muscle, and in some cases to abolish the spontaneous rhythmic contractions; whereas muscarine caused in every instance some increase of tone which could be again abolished by treatment with atropine. Similar results were obtained by Bottazzi in the toad's œsophagus.

Atropine injected into the circulation has no effect whatever on the nerve-endings. Fig. 18 shows the response of the muscle to faradic stimulation of the pudic nerve after 80 mgms. of atropine had been injected in successive doses varying from 5 to 20 mgs. Schultz's results on frog's muscle, as also those just described, must be due to a direct action on the muscle.

Curare, similarly, has no paralytic action on the nerve-ending in smooth muscle. Tracing 19 was obtained by faradic stimulation of pudic nerve after 10 c.c. of a 2 p.c. solution of curare had been injected in successive doses of 2 c.c.

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[1] This *Journal*, XIV., p. 448. 1893.

Nicotine caused an abolition of tonus, as does atropine. On cooling from 37° to 14° only a very slight tone was produced, with a tendency to relaxation. The excitability to single induction shocks was preserved.

GENERAL REMARKS.

The first question which arises is whether the tone and the rhythmic contractions are nervous or muscular in origin. Ranvier, Morgen, and Pawlow believed in a nervous causation. Morgen[1] stated that on removing the mucosa from his muscle-ring the spontaneous contractions were either absent or very feeble. This he ascribed to the damaging of the nervous structures. Ranvier[2], on the other hand, had found that removal of the mucosa did not prevent the appearance of spontaneous contractions in a stomach-ring, though it might retard them for fifteen minutes, or half-an-hour. Pawlow[3] asserted that removal of the posterior ganglion of anodon made the spontaneous contractions cease. Schultz believes in a local reflex. Engelmann however considered the movements to be muscular in origin; and Sertoli came to the same conclusion from the persistence of rhythmic power when all nervous structures must have died. In this connection one may record the remarkable vitality of the pudic nerve. Fig. 20 is a tracing obtained by stimulation of the nerve two hours after death.

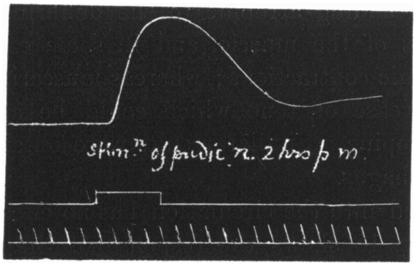

Fig. 20. Pudic nerve stimulated 2 hrs. after death.

From the number of the paths along which motor fibres may reach the muscle it is difficult to exclude nervous influences by causing degeneration through section. In several dogs the dorsal nerves of the penis were cut, but after a week or ten days the muscle behaved in

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[1] *Unters. aus d. physiol. Inst. zu Halle,* H. 2, S. 146. 1890.

[2] *Leçons d'anat. gén. Sur le système musculaire,* p. 420.

[3] *Pflüger's Arch.* XXXVII. S. 11. 1885.

every respect like one from an ordinary animal. In one dog both the nervi dorsales penis and the genito-anal branches were divided twenty-four days before the experiment, but the tracing was perfectly normal. There were no spontaneous contractions, but it relaxed on warming, and contracted on cooling, and showed a marked contraction at 49°.

From the evidence already given of the absence of nerve-cells in the retractor penis, we may assume that as in the heart, the contractions are not due to nervous causes, but have their origin in the muscle-substance itself.

One of the most striking properties of smooth muscle is its power of tonic contraction. Of the many hypotheses which have been put forward as explanations the following may be mentioned. Grützner had put forward the view that striped muscles were supported in tetanus and similar conditions by the red fibres, and Fano suggested a similar hypothesis of two kinds of elements to explain the oscillations of tonus which he observed in the auricles of *Emys Europæa.* Bottazzi[1] advocates the theory that only the quick contractions are due to the anisotropic substance, and that the slower undulations, which appear sometimes in curves of several orders, are caused by contractions of the sarcoplasm. He also invokes sarcoplasm to explain various phenomena such as the staircase and summation.

In the tracings of spontaneous contractions of the retractor penis it will be seen that the ascending limb of each contraction goes up in steps, while the relaxation is as a rule uninterpreted (Fig. 1). The absence of any steps on the line of relaxation is against the application of Bottazzi's suggestion to the present case. The relation between the small contractions and the large is so close as almost to exclude the possibility of their arising from different causes.

There is another possible explanation. Fig. 21 shows that each half of the muscle is capable of contracting spontaneously with an independent rhythm. This makes it probable that in the tracings often seen at warm temperatures, where a succession of fine waves in a horizontal line and a period of rest succeed each other, each wave is due to the contraction of a separate fibre or set of fibres. Now suppose the temperature were lowered. The duration of each contraction would be prolonged; and, if the rate at which the different sets of fibres followed each other remained unaltered, there would be produced a summation of contractions. In fact, we should

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[1] This *Journal,* xxi. p. 1. 1897.

have a curve typical of the large spontaneous contractions at 22° (Fig. 1 A). One can imagine the internal changes to be so prolonged by further cooling as to yield tonus by summation. Similarly the tonic contraction might be supposed to give way on warming, through the hastening of each process and the consequent analysis of the summation.

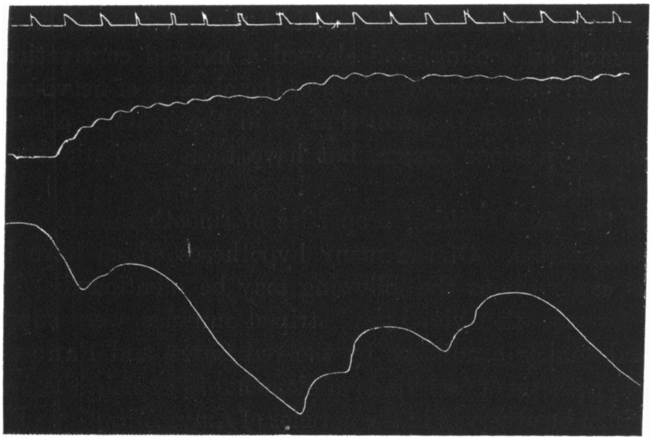

Fig. 21. Spontaneous contraction with independent rhythm of each half. Time-marking = 6 secs.

SUMMARY OF RESULTS.

1. The retractor penis muscle consists of a ribbon of parallel functionally isolated contractile fibres, with a tendency to automatic rhythmic activity. Hence the whole muscle above a certain temperature generally exhibits rhythmic contractions of very variable character and rhythm. The functional isolation of the constituent fibres determines the absence of any polar phenomena on stimulation by passage of a constant current, and also apparently the propagation of contraction from one muscle-fibre to another.

2. The tonus of a resting muscle or the diastolic length of a rhythmically contracting muscle are increased or diminished respectively by a fall of temperature, while a rise of temperature up to 40° C. causes an increase in the diastolic length or complete relaxation of the muscle. On warming the muscle still further, a contraction generally occurs at about 47° C. and is followed by a relaxation at 52° C., while the muscle is still excitable. A few degrees higher the relaxation of the

muscle becomes complete, and its excitability is permanently destroyed. The muscle is dead. The muscle therefore undergoes no rigor mortis, but on heating the dead relaxed muscle to 70° C., a powerful contraction occurs, evidently due to coagulation of the muscle-proteids.

3. The motor nerve-endings of the muscle cannot be paralysed by any dose which can be administered of atropine or curare. They also retain their power of propagating the excitatory condition from the nerve to the muscle for at least two hours after the complete death of the animal.

4. We see no reason to ascribe the large (tonic) and small variations in length of the muscle to the action of specifically different parts of each muscle-fibre (Bottazzi's sarcoplasm theory), but believe that the tonic state of the muscle is dependent on the greater or less fusion of the rhythmic contractions of the individual fibres.