EARLY TENSION RELAXATION DURING CONTRACTION OF UNSTRIATED MUSCLE

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Rauh (1922) demonstrated that a frog skeletal muscle relaxes very slightly during the latter part of its latent period, just prior to the development of tension. Little attention was paid to it till Sandow (1944, 1945 *a*, *b*, 1946) using the piezo-electric technique further studied the phenomenon and developed a theory to explain it. Schœpfle and Gilson (1945) concluded that the early relaxation is an artifact produced in the propagation of a tension wave through a viscous elastic medium. This argument was not supported by Sandow (1947) and by Abbott and Ritchie (1951) who found that the early relaxation was still visible when the tension was recorded at the point of stimulation. Hill (1951) proposed that the early relaxation occurs in the parallel elastic structures. Sandow (1952) has counteracted this argument. He has shown that the latency relaxation can be dissociated from the excitatory process and that it is very labile. It changes markedly with previous activity of the muscle (Sandow, 1945 *a*; Sandow and Karczmar, 1950), with temperature and hydrogen-ion concentration (Sandow, 1947), under excess potassium treatment (Sandow and Kahn, 1949) and under the action of nitrate—Ringer's solution (Kahn and Sandow, 1950). According to Sandow, all this strongly suggests that a relatively inert structure like the sarcolemma or the series elastic connective tissue cannot be the locus of latency relaxation, but this phenomenon must be associated with some highly physiologically active material such as some part of the actual contractile system.

Unstriated muscle is known to relax prior to contraction (Singh and Singh, 1949 *a*). In the present research, an attempt has been made to study this phenomenon (henceforward designated as LR). In the present paper we are only concerned with the depth of LR. It will be interesting to compare this with the LR of striated muscle. The movements of unstriated muscle are so slow and the magnitude of LR comparatively so great, that there can be no question about its genuineness.

The LR in unstriated muscle was also compared with electrical and chemical inhibition, in order to elucidate its relationship with inhibition

in general. Further an attempt has been made to trace its relationship to the processes that may activate the contractile mechanism.

Methods

The movements of unstriated muscle are so slow, and the magnitude of LR comparatively so large, that no special apparatus was required, other than usually used for stimulation of the muscle. To produce LR, dog's stomach muscle from the cardiac end was stimulated with potassium or ammonium every 30 minutes. To stimulate with potassium, 40 p.c. of the sodium of the saline at pH 8 (Singh, 1940, 1942) was replaced with potassium, and to stimulate with ammonium, the whole of the sodium was so replaced. Frog's stomach muscle from the cardiac end was used for production of inhibition by adrenaline (1 in million).

Results

Unstriated muscle when stimulated electrically or chemically, relaxes a little prior to contraction. This has been obtained with *Mytilus* muscle, especially with excess potassium treatment, in frog's stomach muscle and dog's stomach muscle. But with the apparatus used, it is not always apparent. It is obtained most consistently if dog's stomach muscle, especially from the cardiac end, is stimulated with potassium or ammonium, the latter being preferred; the temperature of the saline should be 23–25° C.

The magnitude of the LR is variable. It may be just visible or may be quite deep, about 10 p.c. of the peak tension. The breadth or the duration of the LR usually increases with its depth.

The after-relaxation (*AR*).—Not only the muscle relaxes prior to contraction, but the contraction curve dips below the starting level before it returns to normal (Figs. 2, 11, 13). This is produced by all forms of stimulation in *Mytilus* muscle (Singh, 1938 *c*), frog's stomach muscle (Singh, 1939), dog's stomach muscle and intestine, the intestine of rabbit and hen, the human appendix and the guinea pig's uterus. The properties of AR will also be described; it was produced by stimulating dog's or frog's stomach muscle with alternating current, 10 volts for 10 seconds.

The relation between LR and peak tension.—There are two kinds of responses. In one kind, the magnitude of LR varies in the same direction as the peak tension (Fig. 9) and in the other, they vary oppositely. In the latter instance, as the preliminary relaxation increases, the subsequent tension disappears and pure inhibition is produced. Similarly the AR is also of two kinds.

It is clear that here we are dealing with two phenomena, which are mixed in these observations. One is inhibition and the other LR proper; similarly the relaxation occurring after the contraction has subsided, is a mixed phenomenon, one of the responses being inhibition, and the other, AR, corresponding to LR. The AR, corresponding to LR, suggests that the events inside the muscle, which are produced during contraction, are now repeated in the reverse order before the tissue returns to its original state. The inhibition occurring after the contraction has subsided, corresponds to the positive after potential in nerve.

Effect of initial length or tension.—The LR increases if the initial length of the muscle is increased up to a certain extent, and thereafter it decreases (Fig. 1). This corresponds to simialr results in striated muscle (Abbott and Ritchie, 1951). Inhibition produced by potassium in guinea pig's uterus (Singh, 1942) and adrenaline in frog's stomach muscle, and AR, also required an optimum length for their maximal production.

Unloaded dog's stomach muscle also shows LR and AR, so that these can be produced by active relaxation of unstriated muscle (Singh and Singh, 1949 *a*; 1952 *a*). In the present experiments, the LR and AR appear to be due to passive relaxation, as their properties with loaded and unloaded muscles do not correspond exactly.

Effect of temperature.—The temperature of the saline was increased from 15° C. to 40° C. in steps of 5°. The LR and AR in dog's stomach muscle and adrenaline inhibition and AR in frog's stomach muscle, have an optimum temperature of about 23–25° C. (Figs. 2, 3), which is the same as that found by Sandow (1947) for LR in frog's sartorius.

The above responses are absent at 40–41° C. If the muscle is kept at 41° C. for a few minutes and then returned to the optimal temperature of 25° C., the magnitude of these relaxations is not as great as it was at 25° C. before submission to higher temperature. This is especially so in dog's stomach muscle, the frog's stomach muscle being less affected. In dog's stomach muscle, there are individual variations, some requiring shorter, and other longer exposure, to high temperatures for inactivation, the muscle from the pyloric part being more susceptible than from other parts of the stomach; the irreversible inactivation begins between 37–38° C. Sandow (1947) found in frog's sartorius, that irreversible inactivation of LR begins at a critical temperature of about 37·5° C., and the rate of irreversible inactivation increases very rapidly within the range of next few degrees. Another critical temperature exists at about 41° C., for at or above this temperature, complete irreversible inactivation of LR occurs in a few minutes. It appears

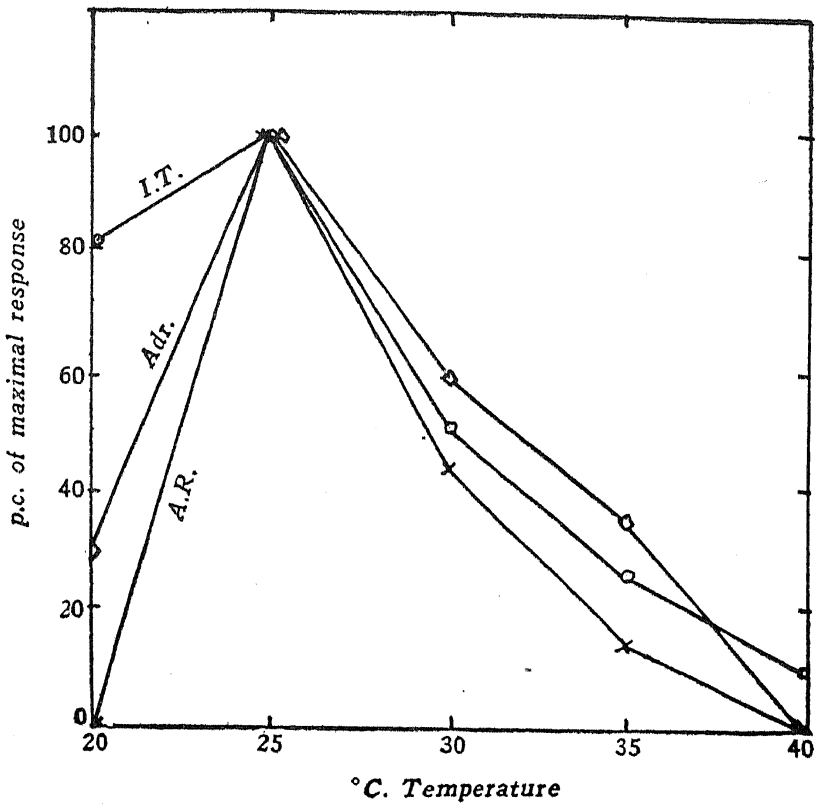


FIG. 3

that a temperature of about 24° C. is a critical one for muscle, as this is the optimum temperature for LR in frog's sartorius, for the response to alternating current in dog's retractor penis (Winton, 1927), dog's stomach muscle (Singh, 1940), and for other responses as mentioned above.

The optimum temperature for active relaxation of dog's stomach muscle was found to be 30° C. (Singh and Singh, 1949 *a*), of frog's stomach muscle, 25 to 30° C., of guinea pig's uterus, 25–30° C. (Singh and Singh, 1951 *c*, *d*, *e*). It is interesting to note, that active relaxation is impaired, if the muscles are exposed to high temperatures as described above.

Inhibition produced by ammonium in dog's stomach muscle increases up to 20° C. and then decreases to a minimum at about 25° C., and then again increases upto about 35–37° C., if inactivation does not set in or to about 30° C., if inactivation sets in. Tonus in frog's stomach muscle increases up to 20° C. then decreases to a minimum at about 25–30° C., and then increases again (Rao and Singh, 1940); the same may be found in dog's stomach muscle (Singh and Singh, 1952 *c*). Sandow (1947) found that the magnitude of the action potential of the frog's sartorius rises in value up to 20° C., and then falls to a minimum at about 24–25° C., then rises again to

a new maximum about 35° C., and finally at still higher temperatures, falls, until at 41° C., it is practically zero.

The above experiments suggest that the LR in striated and unstriated muscles are identical, and that they are both identical with inhibition, that has an optimum temperature of about 25° C.; the inactivation by higher temperatures also supports this view. In frog's stomach muscle, this is the only optimum temperature, found for inhibition.

Effect of activity.—Unstriated muscle is always in a state of activity, hence all that can be tested is the effect of change of activity. Besides, ammonium or potassium do not produce a twitch but a tonic contraction. Previous stimulation with potassium, ammonium, nitrate, iodide, thiocyanate, barium or other stimulants decrease the LR in dog's stomach muscle, AR in frog's and dog's stomach muscle and adrenaline inhibition in frog's stomach muscle. As ammonium and potassium produce a tonic contraction, the LR produced by these substances in dog's stomach muscle may decrease with repeated stimulation (Fig. 4). It may even disappear if the muscle is stimulated a second time, especially at higher temperatures, such as 30° C.

If the dog's stomach muscle is stimulated with alternating current about once a minute, the LR produced by ammonium decreases (Fig. 5). The same result is produced of the muscle is tetanised. The preliminary relaxation may increase, but this is due to inhibition, as the subsequent peak tension decreases.

Effect of iodoacetic acid.—Sodium iodoacetate (1 in 10,000) decreases the LR produced by ammonium in dog's stomach muscle, AR in dog's and frog's stomach muscle and adrenaline inhibition in frog's stomach muscle (Figs. 6, 7); the latter at first slightly increases. In these experiments, the muscle was not previously tetanised, as it constantly shows tonic activity, and as pointed above, each previous stimulation by ammonium is a tonic contraction. If the muscle is further stimulated in between the responses, the depressant effects of iodoacetic acid are still more marked.

Effect of sodium cyanide.—Sodium cyanide (1 in 10,000), abolishes the tension subsequent to LR, so that only inhibition remains (Fig. 8).

Effect of calcium ions.—In the absence of calcium, there is decrease of LR, produced by ammonium in dog's stomach muscle, of AR in frog's and dog's stomach muscle and adrenaline inhibition in frog's stomach muscle; excess of calcium at first increases and then decreases these relaxations.

Effect of hydrogen ions.—Increase in the hydrogen-ion concentration of the saline (experimental range, pH 8 to 6), diminishes LR in dog's stomach

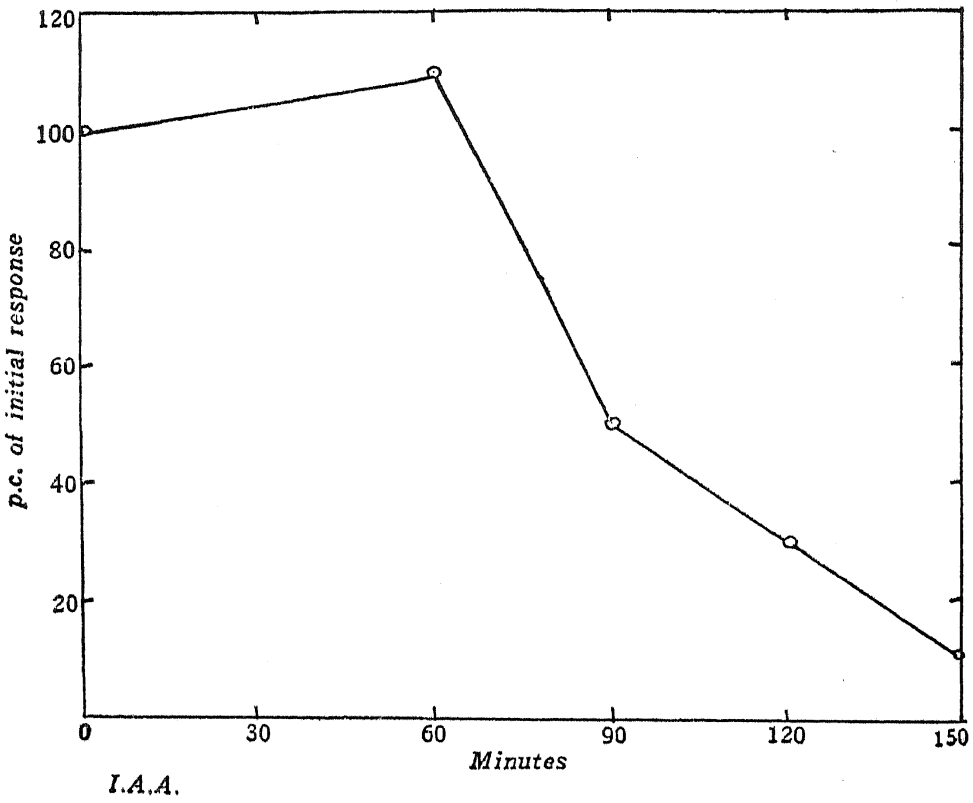

120
100
80
60
40
20
p.c. of initial response
0
30
60
90
120
150
Minutes
I.A.A.

FIG. 7

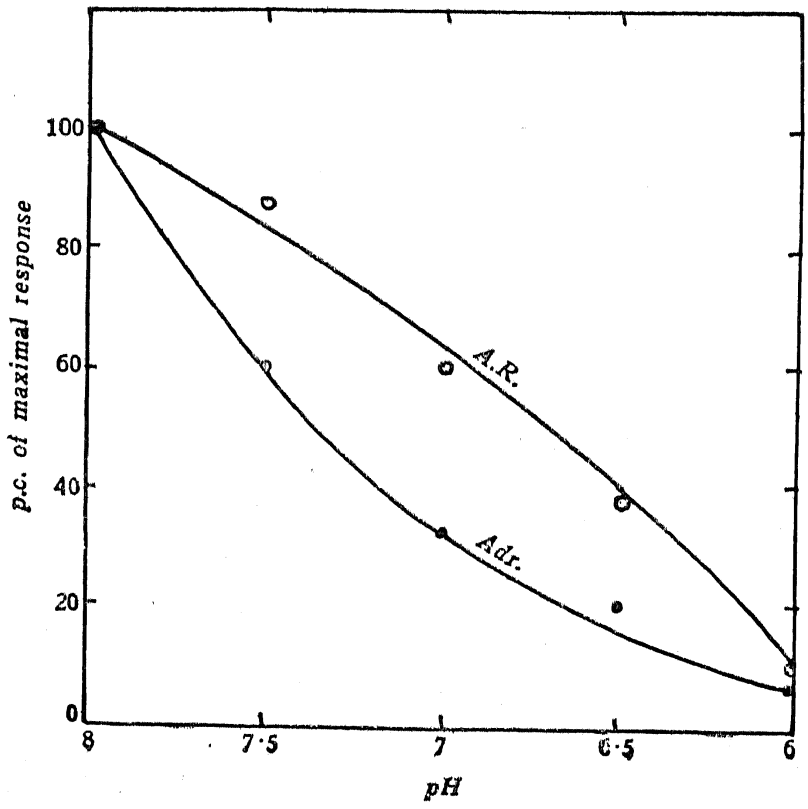

100
80
60
40
20
0
p.c. of maximal response
A.R.
Adr.
8
7·5
7
6·5
6
pH

FIG. 10

muscle, AR in frog's and dog's stomach muscle, and the inhibition produced by adrenaline in frog's stomach muscle (Figs. 9, 10). Pure inhibition may be increased by hydrogen ions (Singh, 1942). Active relaxation of dog's stomach muscle and frog's stomach muscle by adrenaline is decreased by hydrogen ions (Singh and Singh, 1949 *a*, 1051 *c*, *d*, *e*).

Effect of potassium.—If the potassium content of the mammalian saline (24 mg. % K) is doubled, the LR produced by ammonium in dog's stomach muscle is greatly increased; in fact, potassium is the most powerful substance in increasing the LR (Fig. 11). The effect of potassium diminishes with time, so that ultimately the effect may be opposite. If larger concentrations of potassium are used, the preliminary relaxation increases, but the peak tension diminishes and ultimately disappears, so that only pure inhibition remains, increasing potassium concentration thus dissociating LR and inhibition produced by ammonium. The decrease of LR by potassium may be ascribed to activity; the effect is enhanced by increase of temperature, such as up to 30° C.

Exactly similar effects of potassium are produced on the AR. In the dog's stomach muscle, increase in the concentration of potassium in the saline up to 24 mg. % K increases the peak tension as well as the AR. With further increase in the concentration of potassium, there is decrease of peak tension but increase of AR; ultimately the AR is decreased. Similar effects are produced in the frog's stomach muscle, the AR and peak tension both increasing with increase in the concentration of potassium in the saline up to 40 mg. % K; thereafter they are affected oppositely as in the dog's stomach muscle; ultimately the AR decreases.

Inhibition produced by adrenaline in frog's stomach muscle is affected similarly. If the concentration of potassium in the saline is increased from about 5 mg. % K to 40 mg., the adrenaline inhibition at first increases and then decreases (Fig. 12); or the concentration may be increased from 40 to 80 mg. Ultimately, the adrenaline inhibition decreases and may be abolished altogether.

Addition of many substances to the saline causes changes in tonus of unstriated muscle, but the changes in LR appear to be independent of these changes in tonus. Thus in Fig. 9, there is increase in tonus, but the LR diminishes; in Figs. 11, 13, increase in tonus is associated with increase in LR. In such experiments, the muscle must possess sufficient tone, so as to show relaxation.

Active relaxation of dog's and frog's stomach muscle is decreased by excess of potassium (Singh and Singh, 1949 *a*; 1951 *c*, *d*, *e*).

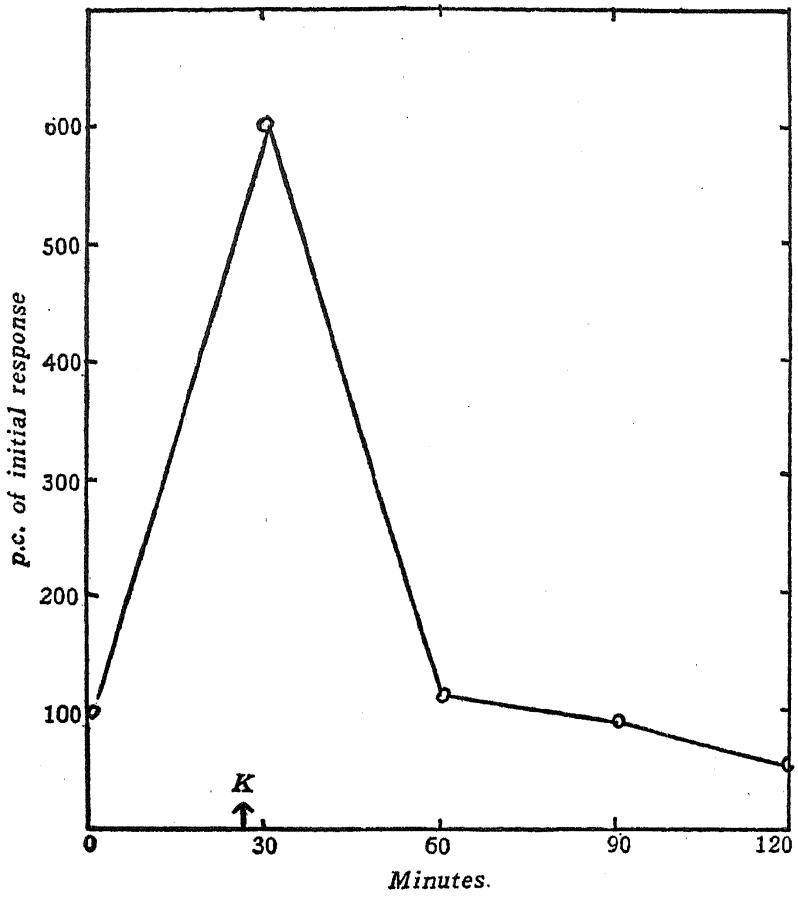


FIG. 12

Effect of nitrate.—Replacement of the chloride of the saline with nitrate increases LR produced by ammonium in dog's stomach muscle (Fig. 13), AR in frog's and dog's stomach muscle, and adrenaline inhibition in frog's stomach muscle (Fig. 14). The effect of nitrate decreases with time, so that ultimately it may be opposite; this latter effect may be ascribed to activity. Nitrate decreases active relaxation of frog's and dog's stomach muscle (Singh and Singh, 1949 *a*; 1951 *c*, *d*, *e*).

Relation between LR and inhibition.—If the concentration of ammonium in the saline is decreased, the preliminary relaxation in dog's stomach muscle increases, the peak tension decreases and ultimately vanishes till only inhibition remains (Fig. 15).

DISCUSSION

The results described hitherto disclose two interesting facts. (1) The LR in frog's sartorius and dog's stomach muscle are more or less similar, even though there is such a great difference between their magnitudes. (2) LR is identical with inhibition in unstriated muscle. There are at present two

theories concerning LR. Sandow believes that it is due to relaxation of muscle fibres. According to A. V. Hill, it is due to elongation of a parallel structure, perhaps the sarcolemma or some other hypothetical membrane. The facts are such, that the author is inclined to agree to both these views; at least in unstriated muscle, there can be no doubt, that the LR is due to relaxation of muscle fibres. In consideration of the second view, the existence of two parallel contractile elements in the same fibre have been proposed (Singh and Singh, 1951 *c*).

There is hardly any doubt that relaxation in unstriated muscle differs from that in striated muscle. In the latter, relaxation occurs on cessation of stimulation. This also occurs with certain kind of contractions in unstriated muscle. But this mechanism alone does not appear to be enough. In unstriated muscle, there are a special set of inhibitory nerves to produce relaxation. It is most likely that motor and inhibitory nerves activate different mechanisms, which may be respectively present in two kinds of fibres or in the same fibre. In striated muscle, it would appear that the mechanism corresponding to that supplied by inhibitory nerves in unstriated muscle, is very poorly developed, hence the small magnitude of LR.

There is another possible explanation. If the contraction is due to the liberation of some substance such as adenosinetriphosphate (ATP), then small concentrations might cause relaxation and larger concentrations, contraction. Thus the LR would be due to the time taken in building of the requisite concentration of ATP.

The above view is supported by the following observations. Small concentrations of potassium mercury iodide cause relaxation of tendon, and larger concentrations, contraction. Large concentrations may cause an initial relaxation prior to contraction (Pryor, 1950). These results are similar to those produced by ammonium, as described above, so that excitation by ammonium presumably liberates a substance which acts on the contractile mechanism in a way similar to potassium mercury iodide on tendon. It is well known that if strong stimuli cause contraction of unstriated muscle, weak stimuli may cause relaxation. If the excitability is diminished, then strong stimuli, which usually cause contraction, may cause relaxation. Thus in *Mytilus* muscle, small voltages of alternating current cause relaxation; if the excitability of the muscle is decreased by excess of ammonium, potassium, bromide, nitrate, iodide, thiocyanate, diminution of the calcium concentration of the saline, etc., then stronger stimuli cause relaxation. Similarly small concentrations of ammonium, potassium, calcium, nitrate, thiocyanate, adrenaline, veratrine, caffeine, acetylecholine, cause relaxation

whilst larger concentrations cause contraction. It is known that small concentrations of adrenaline may cause vasodilatation, whilst larger doses cause vasoconstriction. Similarly weak stimuli applied to nerves may produce dilator effects, and strong stimuli constrictor effects. There is antagonism between tone and twitch (Singh, 1938 *a*), so that increase in tonus decreases excitability. This explains a peculiar property of unstriated muscle, that a stimulus (*e.g.*, electrical or mechanical) which when applied to the relaxed muscle, causes a contraction, will when applied to the tonically contracted muscle often provokes a rapid relaxation. The same even holds true in some instances for the effects of stimuli applied to nerves supplying unstriated muscle (Evans, 1952). It is therefore quite possible, that vasodilator effects recorded on stimulation of the splanchnic nerves after administration of ergotamine (Dale, 1913), dibenamine (Nickerson and Goodman, 1947; Folkow *et al.*, 1948), adrenaline (Burn, 1932), may be due, not to the presence of vasodilator fibres, but to the diminished excitability of unstriated muscle of the blood vessels. Fatigue, as it diminishes excitability, may also convert a vasoconstrictor effect into a vasodilator one; thus whilst the first injection of pituitrin produces rise in blood pressure, a second dose soon after produces a fall of pressure.

If we postulate two sets of mechanisms, the above results can be explained by supposing that the threshold for the relaxing mechanism is lower than for the contracting mechanism. It is possible that the relaxing mechanism is well developed in unstriated muscle, and only vestigeal in striated muscle, hence the differences in some of the properties of the two kinds of muscles. Whatever the action of ATP during contraction, one thing is certain, that rigor in muscle is associated with the breakdown of ATP (Erdos, 1943; Bate Smith and Bendall, 1947); the function of ATP might be to keep the muscle in a relaxed state by combining with the contractile proteins. This is in agreement with the fact, that though unstriated muscle is always found in a contracted state, yet it contains about one-seventh of the high energy phosphates as in striated muscle (Csapo and Gergely, 1950). Engelhardt (1941) has demonstrated that artificially spun myosin fibres undergo an increase in extensibility especially in the act of splitting ATP.

It has been suggested that unstriated muscle contains two systems, one requiring energy for contraction and the other for relaxation, striated muscle containing the former system only (Singh and Singh, 1949 *b*; 1950 *a*, *b*; 1951 *a*, *b*, *c*; 1952 *a*, *b*; Singh, 1951). These presumably consist of two contractile proteins or combination of proteins, let us say X and Y respectively. It is further presumed that X relaxes on release of a substance such as ATP and Y is a complex of X and ATP–XATP, though it is possible that

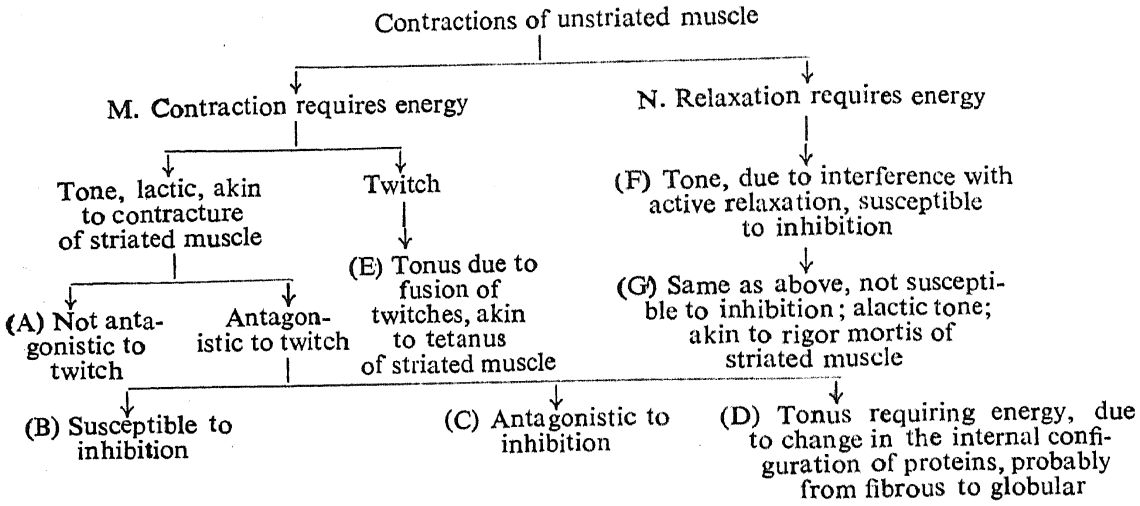
the protein part of Y may not be identical with X. Unstriated muscle would, therefore, contain less ATP than striated muscle, as actually shown by chemical estimation. XATP contracts on further release of ATP, if we assume that small concentrations of ATP cause relaxation and larger concentrations, contraction, as suggested by experiments described above. XATP may contract on release of a substance, other than ATP. In this connexion the findings of Bozler (1952) are relevant; he finds that in the relaxed condition the contractile elements of glycerinated psoas are present in an activated state, possibly brought about by chemical combination of ATP with the contractile proteins, and that calcium ions in very low concentrations cause rapid contraction of this activated system, even in the absence of free ATP. The findings of Buchthal, Deutch, Knappeis and Munch-Petersen (1949) are also relevant; they have demonstrated phosphorylation of myosin. Striated muscle would contain only traces of X, hence the minuteness of LR. X and XATP would be in parallel and would contract or relax together (Singh and Singh, 1951 *c*). Whilst shortening of XATP would require energy, the shortening of X might give up energy, and so be responsible for the Fenn effect. In this connexion, it may be mentioned, that during one kind of tonic contraction, the metabolism of unstriated muscle decreases, such as diminution of oxygen consumption (Rao and Singh, 1940) and diminished production of lactic acid (Bharadwaj and Singh, 1951), and as expected one kind of tonic contraction of unstriated muscle is not susceptible to asphyxia or may actually increase on asphyxiation. In rigor of striated muscle, XATP releases X, so that rigor in striated muscle is akin to a physiological contraction of unstriated muscle, provisionally termed as alactic tone (Singh, 1951). The twitch contractions in unstriated muscle are similar to those of striated muscle, possibly produced by XATP. This is supported by the fact, that though unstriated muscle contains about one-seventh of the high energy phosphates in striated muscle, the energy requirements for a single contraction appear to be of the same order of magnitude in both muscles (Csapo and Gergely, 1950), and the twitch contraction in unstriated muscle is accompanied by increase in oxygen consumption (Rao and Singh, 1940) and lactic acid (Bharadwaj and Singh, 1951); it follows therefore, that a greater part of the sustained tension of unstriated muscle could not be due to the same chemical changes. On the contrary, relaxation of X would require energy, hence active relaxation in unstriated muscle and not in striated muscle, and increased consumption of oxygen (Rao and Singh, 1940) and lactic acid production (Bharadwaj and Singh, 1951) of relaxing muscle. In unstriated muscle, therefore, both contraction as well as relaxation are energised.

Unstriated muscle shows two kinds of tone, one which is susceptible to asphyxia and the other which is resistant; these have been provisionally termed as lactic and alactic tones respectively (Singh and Singh, 1948; Singh, 1949), though the terminology is not strictly correct, because lactic tone may derive energy from sources other than glycolysis, as it may be maintained if the muscle is poisoned with iodoacetic and alactic tone is maintained without expenditure of energy, whether from glycolytic or other sources. The asphyxia-resistant tone is of two kinds, one susceptible to inhibition, or capable of being relaxed by glucose or oxygen; it is due to interference with active relaxation. This tone passes into the next one, which is not susceptible to inhibition and cannot be relaxed by glucose or oxygen. It corresponds to rigor of striated muscle and presumably due to contraction of X protein. The phasic contraction and lactic tone are presumably due to the contraction of XATP; lactic tone corresponds to contracture of striated muscle. Alactic tone is not antagonistic to twitch.

In these and previous experiments it has been found that lactic tone is of two kinds. One kind is antagonistic to twitch, and the other is not antagonistic. Thus many tonic contractions are antagonistic to twitch (Singh, 1938 *a*). The human appendix shows considerable tone which is not antagonistic to twitch (Khan and Singh, 1947). Similarly, in frog's stomach muscle, small concentrations of potassium increase tone which is not antagonistic to twitch, and larger concentrations produce tone which is antagonistic. Tone antagonistic to twitch is again of two kinds; one kind is susceptible to inhibition and the other is antagonistic. The former kind of tone is shown by guinea pig's uterus and intestines of rabbit and hen. Excess of potassium and other ions such as iodide, thiocyanate, barium, produce tone which is antagonistic to inhibition (Singh, 1942). The antagonism to twitch in the former tone appears to be due to increased accommodation (Singh, 1938 *b*) and in the latter tone is due to increase in the threshold for excitation, though accommodation is decreased (Singh, 1938 *a*); in the former, inhibition is readily produced, as it is identical with accommodation (Singh, 1945).

Various unstriated muscles differ from one another in two respects: (i) They contain various mixtures of lactic and alactic tones. (2) They exhibit varying capacities for lactic tone and twitch. Some produce powerful twitches and little lactic tone, and others show the opposite; skeletal muscle may be considered to be an extreme example of the former group. If we designate alactic tone as A, lactic tone as L, and twitch as T, then the formula for unstriated muscle would be $xA + yL + zT$; different kinds of unstriated muscle would differ from one another in having different values

for the constants x, y, z. Striated muscle would be a variety of unstriated muscle in which x is practically zero, and the value of y less, and that of x greater than in unstriated muscle. It is difficult to say whether unstriated muscle contains different proteins (or combinations of proteins) for twitch and lactic tone; if so then it will contain three contractile proteins and striated muscle two; in this connexion, it is interesting to note, that besides actomyosin discovered by Szent-Gyorgyi and Straub (1947), another protein, tropomyosin, has been found in striated muscle (Bailey, 1946). The responses of unstriated muscle may now be summarised. It will be seen that unstriated muscle produces sustained tension in seven different ways (A, B, C, D, E, F, G); group M, with the exception of D is susceptible to asphyxia and group N is resistant.



SUMMARY

1. Unstriated muscle relaxes a little prior to contraction, and the contraction curve dips below the starting level before it returns to normal; the former relaxation has been termed as LR and the latter, AR. Properties of LR, AR and adrenaline inhibition have been studied.

2. LR, AR and adrenaline inhibition require an optimum length for their production.

3. The optimum temperature for LR, AR and adrenaline inhibition is about 25° C.; higher temperature cause inactivation.

4. Previous activity decreases LR, AR and adrenaline inhibition.

5. Iodoacetic acid decreases LR, AR and adrenaline inhibition.

6. Sodium cyanide abolishes the peak tension, but increases inhibition.

7. LR, AR and adrenaline inhibition decrease in the absence of calcium ions; excess of calcium at first increases and then decreases these relaxations.

8. Increase in hydrogen-ion concentration from pH 8 to 6, decreases LR, AR and adrenaline inhibition.

9. Potassium at first increases and then decreases LR, AR and adrenaline inhibition.

10. Nitrate at first increases and then decreases LR, AR and adrenaline inhibition.

11. It is concluded that LR and AR are identical with inhibition and are produced by relaxation of muscle fibres.

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EXPLANATION OF FIGURES

FIG. 1. Dog's stomach muscle. Length 52 mm. On first addition of ammonium, LR is absent and peak tension very small. The initial length is then increased by 10 mm. Note that on subsequent addition of ammonium, LR increases in depth and breadth.

FIG. 2. Dog's stomach muscle. Effect of temperature on LR.

FIG. 3. Frog's stomach muscle. Effect of temperature on tension produced by alternating current (I.T.), on AR, and inhibition produced by adrenaline, 1 in million (adr).

FIG. 4. Dog's stomach muscle. Effect of activity on LR.

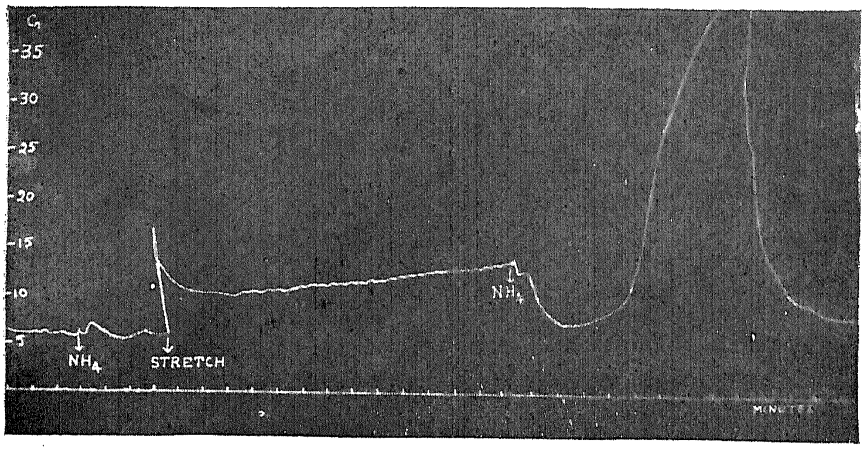

FIG. 1

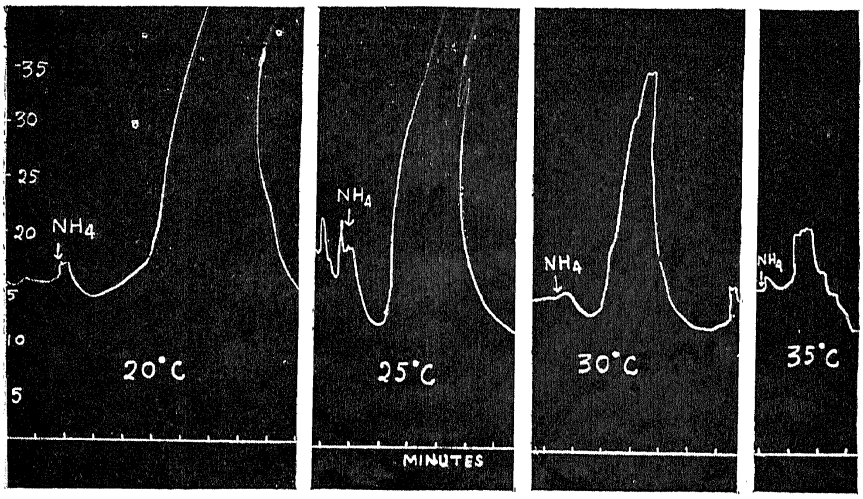

FIG. 2

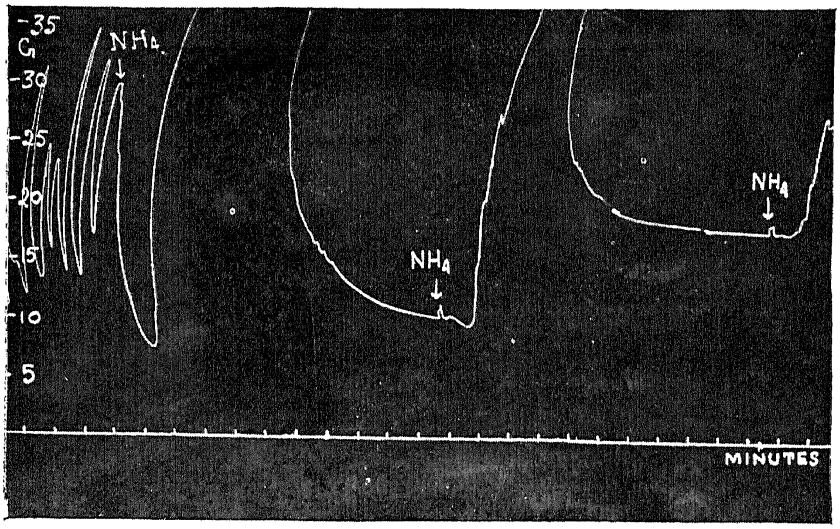

FIG. 4

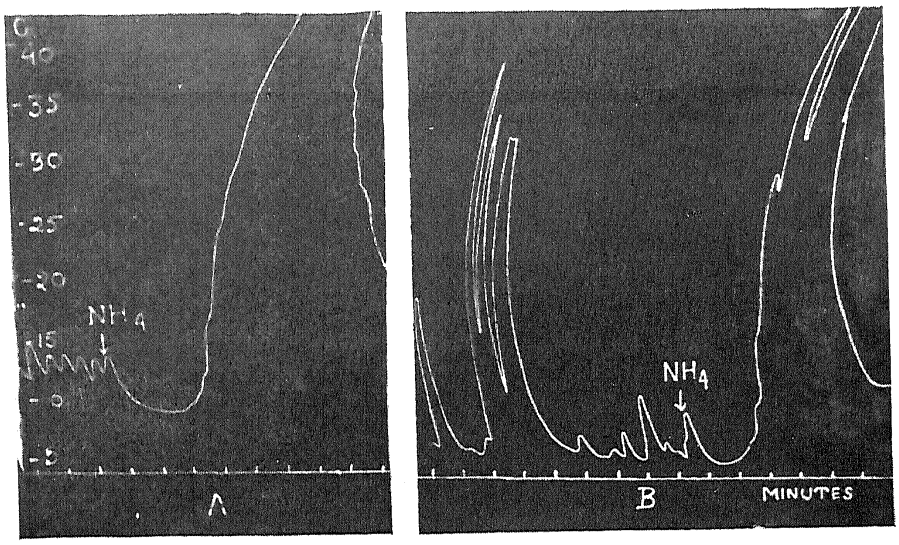

FIG. 5

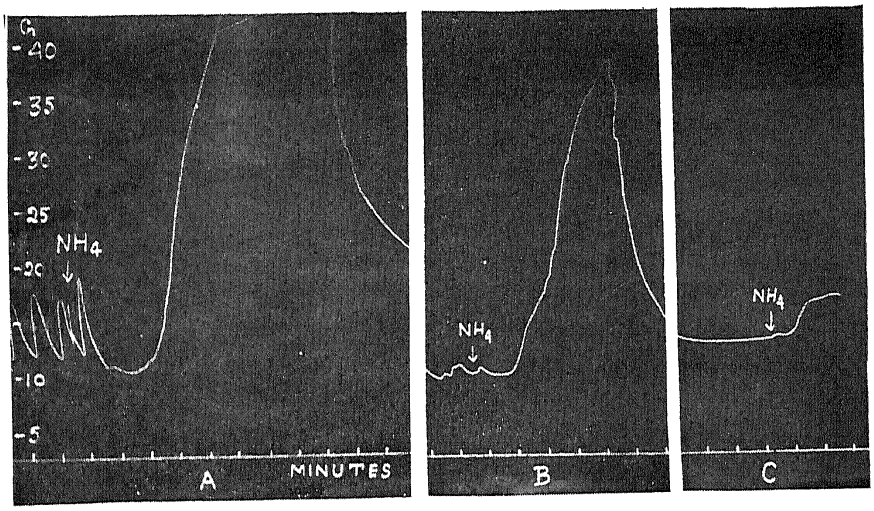

FIG. 6

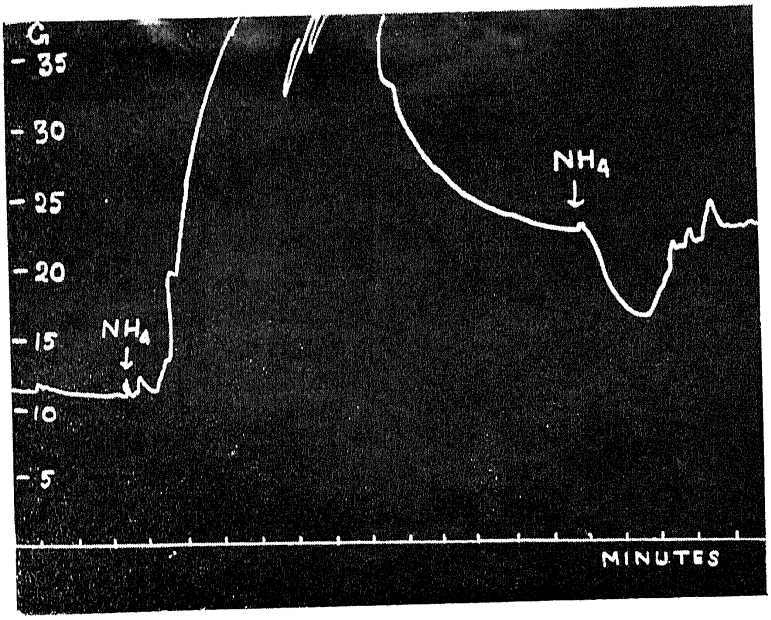

FIG. 8

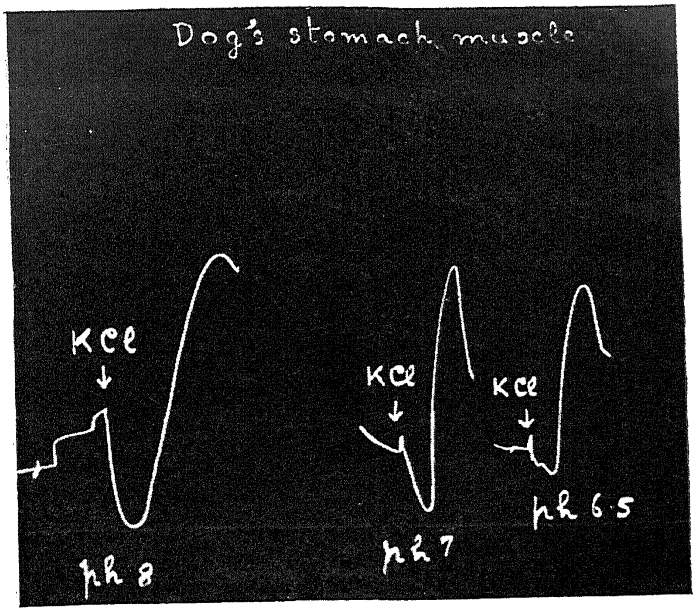
Dog's stomach muscle
KCl
KCl
KCl
hR 8
hR 7
hR 6·5

FIG. 9

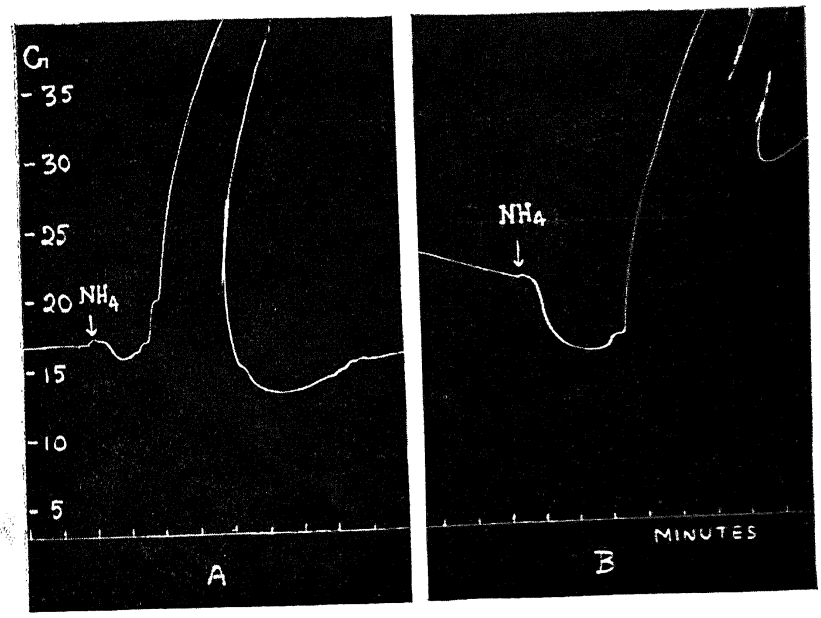
G
- 35
- 30
- 25
- 20
- 15
- 10
- 5
NH4
NH4
MINUTES
A
B

FIG. 11

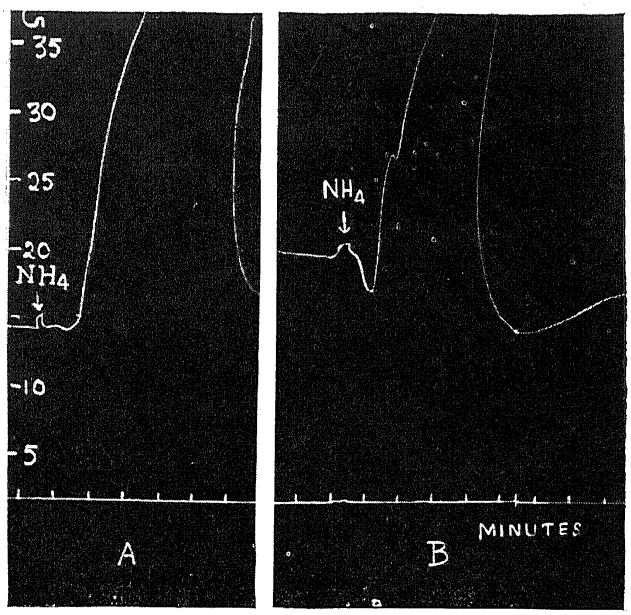

FIG. 13

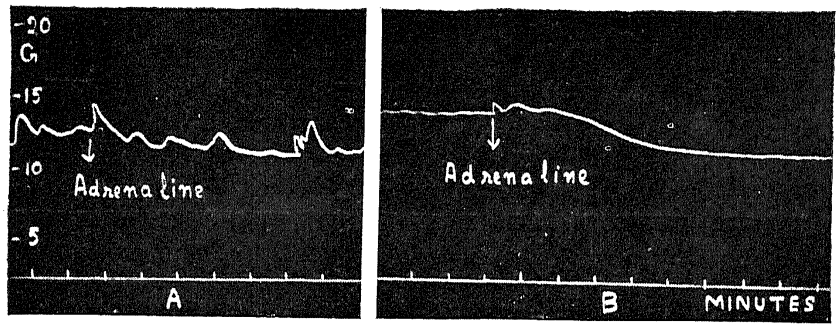

FIG. 14

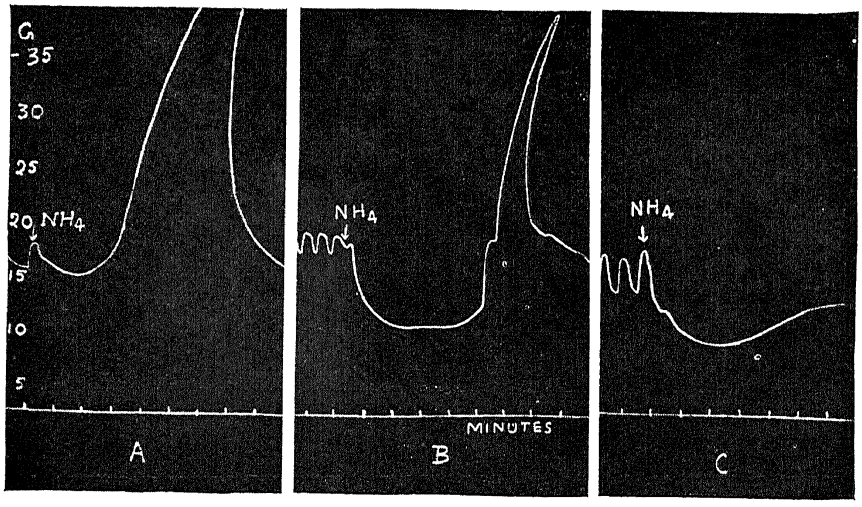

FIG. 15

FIG. 5. Dog's stomach muscle. Effect of activity on LR.

A. Normal.

B. Effects of stimulation with alternating current 10 volts for 10 seconds per minute for 15 minutes on LR.

FIG. 6. Dog's stomach muscle. Effect of sodium iodoacetate (1 in 10,000) on LR.

A. Normal.

B. After soaking in iodoacetic acid for 1 hour.

C. After further 20 minutes.

FIG. 7. Frog's stomach muscle. Effect of sodium iodoacetate (I.A.A.) on inhibition produced by adrenaline (1 in million).

FIG. 8. Dog's stomach muscle. Effect of sodium cyanide (1 in 10,000) on LR. 1st response is normal, 2nd response after the muscle had been in cyanide.

FIG. 9. Dog's stomach muscle. Effect of pH on LR. The drum is stopped for about half an hour in between the responses. pH 8 made with borate, pH 7 and 6·5 with phosphate.

FIG. 10. Frog's stomach muscle. Effect of pH on AR and inhibition produced by adrenaline (1 in million); ADR.

FIG. 11. Dog's stomach muscle. Effect of potassium on LR.

A. Constant LR response in saline.

B. Effect of excess of potassium on LR.

FIG. 12. Frog's stomach muscle. Effect of excess potassium (K) on inhibition produced by adrenaline (1 in million).

FIG. 13. Dog's stomach muscle. Eflect of nitrate saline on LR.

A. Constant response in saline.

B. LR in nitrate saline.

FIG. 14. Frog's stomach muscle. Effect of nitrate saline on inhibition produced by adrenaline (1 in million).

A. Constant response in saline.

B. In nitrate saline.

FIG. 15. Dog's stomach muscle. Effect of concentration of ammonium on LR.

A. All the sodium of the saline is replaced with ammonium.

B. 20 p.c. of the sodium is replaced with ammonium.

C. 5 p.c. of the sodium of the saline is replaced with ammonium.