

# COMPARATIVE PHYSIOLOGY OF UNSTRIATED CARDIAC, AND STRIATED MUSCLES

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UNSTRIATED, cardiac and striated muscles differ structurally and functionally in many ways, yet there is an essential similarity in their responses. The question arises whether the differences are quantitative or qualitative. Does any one of the muscles possess some mechanism, which is not possessed by the other two, or if any special quality significant of one variety is merely held in abeyance in the other two. Thus it is well known that the chief property of cardiac muscle is rhythmicity, but under appropriate conditions, both the striated as well as unstriated muscles can be made to beat spontaneously. Isolated unstriated muscle shows tone; this is also exhibited by striated as well as cardiac muscle under certain conditions. The object of this paper is to correlate some of the phenomena presented by three kinds of muscles, and to see whether light can be thrown on the phenomena presented by unstriated muscle by a study of the other two. The author has repeated some of his experiments on unstriated muscle also on other kinds of muscle under identical conditions, so that the results may be comparable, as also the behaviour of the tissues is likely to show differences in the various parts of the world.

## EXPERIMENTAL

The rectus abdominis of the frog was stimulated by Winton's method, as this method has been mainly employed previously in stimulation of unstriated muscle. The muscle was stimulated by alternating current, 2 volts for 10 seconds every 10 minutes. The voltage had to be increased to 8 volts as the muscle rapidly fatigued after a few tetanisations. The frog gastrocnemius was stimulated by single make and break maximal induction shocks every 5 or 10 minutes, the break shock following the make shock an interval of 15 seconds. In this way, the electrical stimulation was comparable to chemical, as the latter was resorted to every 5 or 10 minutes. The contractions were recorded with an isotonic lever slightly loaded or isometrically.

The experiments were performed at room temperature (32-37° C.). To compare the results of electrical, nervous or chemical stimulation, the

gastrocnemius of the opposite limbs were dissected out; one was then stimulated electrically or through the nerve, and the other with potassium or acetylcholine. Sometimes the same muscle was stimulated through the nerve or by acetylcholine every 5 minutes alternately, so that the effects of the two might be comparable on the same muscle under identical conditions.

## RESULTS

### *Two Excitabilities*

Unstriated muscle can be made inexcitable to electrical stimulation and hyperexcitable to potassium (Singh, 1938 a). In the heart muscle the spontaneous contractions can be abolished, while the response to potassium is retained or may even be increased (Burridge, 1911, 1921, 1923 a). These results have been confirmed, though much smaller concentrations of potassium (0.04 M KCl) were required to produce a powerful contraction. The heart muscle thus behaves like unstriated muscle in this respect.

In the striated muscle, I have not been able to find any significant difference between the responses to electrical stimulation and that to potassium, except in a few experiments. Burridge (1911) described the differential action of drugs on the response to electric current and potassium. I have tried the reagents which gave a differential action on *Mytilus* muscle, such as calcium, magnesium, the anions, chloride, bromide, nitrate, iodide, and the drugs adrenaline, acetylcholine, veratrine, strychnine, eserine, pilocarpine, curare (6 experiments each, but 8 in the case of adrenaline and curare). Curare used was an impure product (Merck).

Gelhorn and Northrup (1932) found in the frog striated muscle, that the response to potassium increased after indirect stimulation. In the present experiments (2 out of 8) it was found that curare (saturated solution in the Ringer) in the frog gastrocnemius muscle, increased the response to potassium, while diminished that to electrical stimulation. The response to acetylcholine as well as that to indirect stimulation was decreased (Fig. 1). These results are significant in view of the fact that heavy doses of curare increase the chronaxie (Lapique, 1906; Watt, 1924), and make the neurone more sensitive to potassium and insensitive otherwise (Brown and Feldberg, 1936). In the other 6 experiments, the response to potassium was also depressed.

Adrenaline, 1 in  $10^5$ , in 2 out of 8 experiments increased the response to potassium, and decreased that to electrical stimulation (Fig. 2). In the remaining 6 experiments, the response to electrical stimulation was either slightly increased or unaffected. Increase in the osmotic pressure of the saline by addition of sodium chloride or sucrose to twice normal, increased

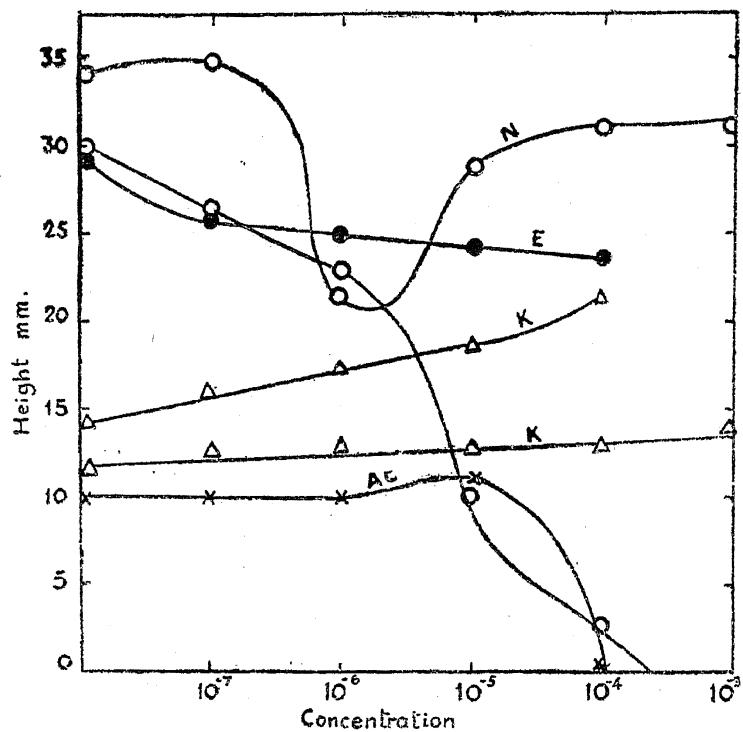


FIG. 1. Frog gastrocnemius. Effect of curare on the response to induction shocks (E), potassium (K), acetylcholine (A.C.) and nervous stimulation (N)

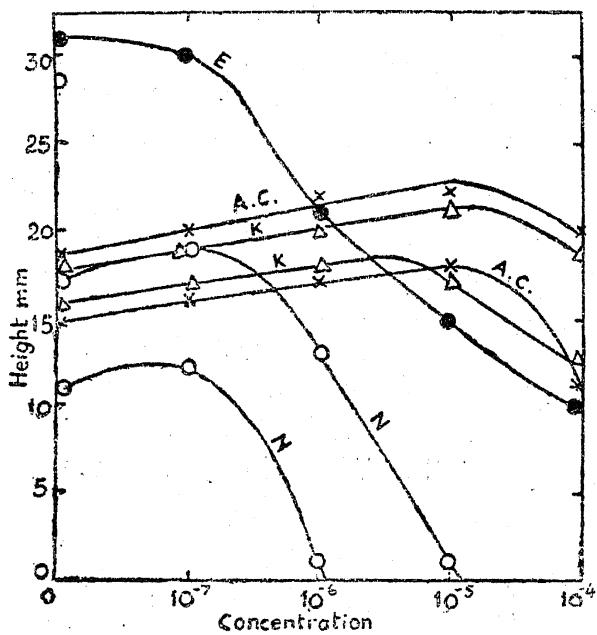
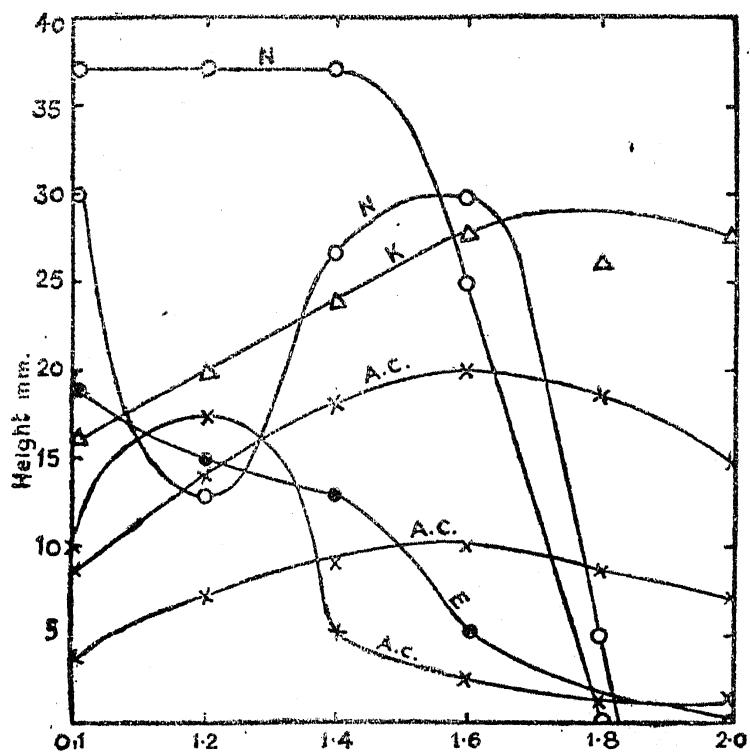


FIG. 2. Frog gastrocnemius. Effect of adrenaline

the response to potassium and decreased that to electrical stimulation in 2 out of 6 experiments (Fig. 3). In the remaining 4, the response to potassium was also depressed; in 2 experiments the response to electrical stimulation



Osmotic Pressure increased by adding NaCl; times normal  
F.G. 3. Frog gastrocnemius. Effect of osmotic pressure

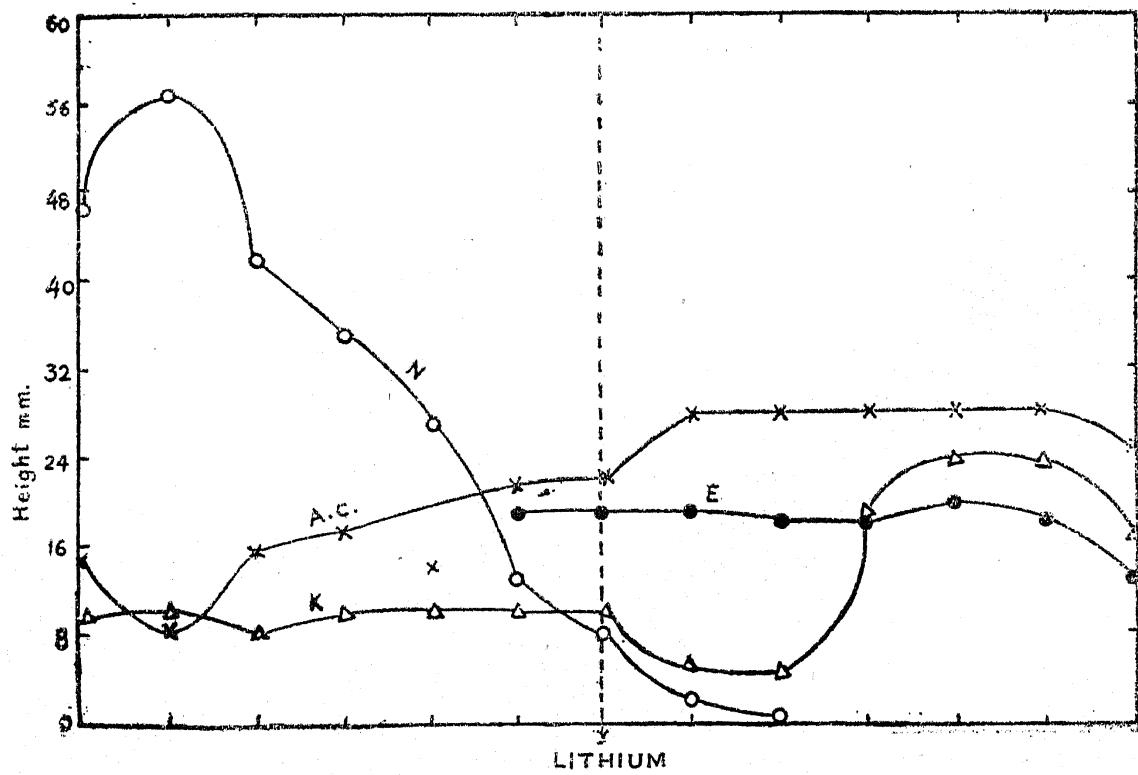


FIG. 4. Frog gastrocnemius. Effect of lithium

was also increased with increase of osmotic pressure to 1.4-1.6 times normal. If 60% of sodium chloride of the saline was replaced with lithium, the response to potassium was increased in three experiments, and that to electrical stimulation was not much affected (Fig. 4). In the other 3 experiments, the response to potassium decreased. Thus in the striated muscle, there is some evidence of the existence of two excitabilities.

#### RESPONSE TO NERVOUS STIMULATION AND ACETYLCHOLINE

Previously we have described antagonistic action of the vagus and acetylcholine on the frog heart (Singh, Sehra and Mrs. Singh, 1945). Similar results have been obtained on the frog gastrocnemius. Thus in the absence of calcium, the response to acetylcholine was increased and that to nervous stimulation decreased (Fig. 5), though in others the response to

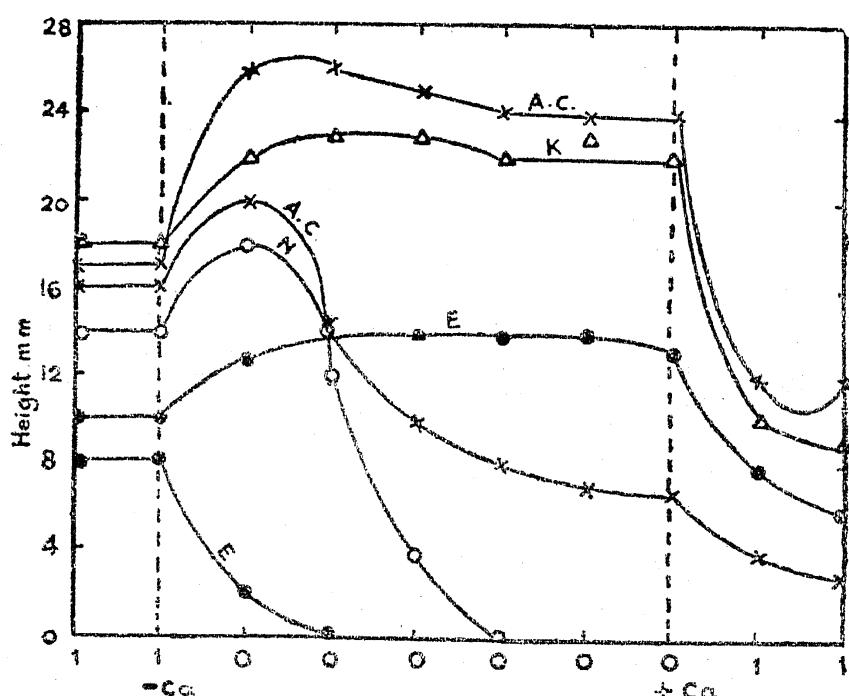


FIG. 5. Frog. gastrocnemius. Effect of calcium

acetylcholine was also depressed. Excess of calcium produced opposite results (Fig. 6), the optimum concentration for indirect stimulation being 0.002 M  $\text{CaCl}_2$ . Adrenaline 1 in  $10^5$  also depressed the response to nervous stimulation and increased that to acetylcholine (Fig. 2). Lithium had similar action (Fig. 4). Increase of osmotic pressure also produced similar results (Fig. 3), though in some experiments, the response to acetylcholine was enhanced.

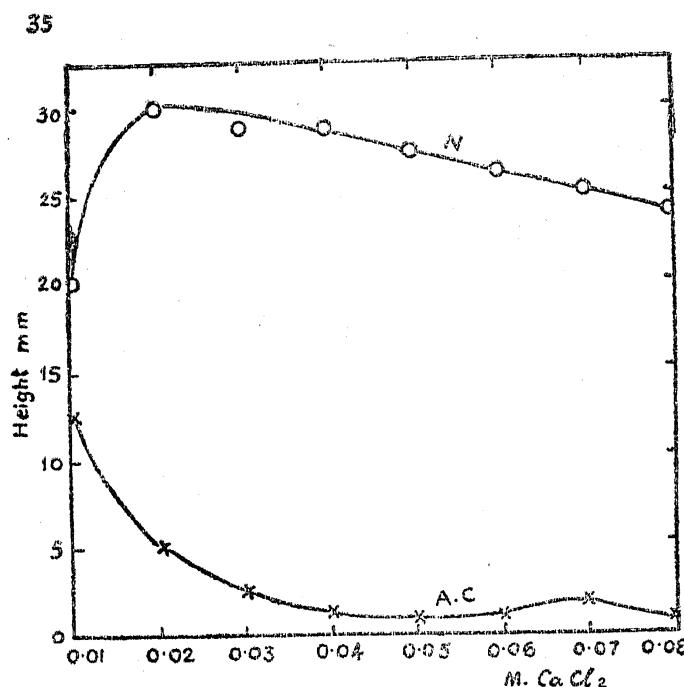


FIG. 6. Frog gastrocnemius. Effect of calcium

Then further it was sometimes noticed, that when the muscle was highly sensitive to nervous stimulation, it was relatively insensitive to acetylcholine, the concentration of the latter required to stimulate being 1 in 2,500. At other times, the muscle behaved in an opposite manner (Fig. 4), the muscle becoming inexcitable to nervous stimulation, and hypersensitive to acetylcholine.

The dog stomach preparations also sometimes behaved in a similar way. With repeated stimulation the response to vagus disappeared, while that to acetylcholine remained.

#### Effect of Temperature

While at Allahabad, I often wondered, how my gardener could work in the intense heat, that would have killed me. I found that the optimum temperature for the response of dog stomach preparations at Bombay to be  $25^{\circ}\text{C}$ . At Patna, where the temperature was  $115^{\circ}\text{F}$ . in the shade, the optimum temperature was  $30^{\circ}\text{C}$ . This difference is probably due to adaptation on the part of the animals to a higher temperature.

The frogs in India have to pass through extremes of seasonal variations of temperature. In Hyderabad, the frogs which were experimented upon had seen exceptionally hot summer and an exceptionally cold winter. The room temperature in our laboratory is often  $37^{\circ}\text{C}$ . The frog gastrocnemius

presented a most interesting phenomenon of adaptation. If the temperature of the saline was 30° C. at room temperature, raising of temperature to 35° C. at first depressed the response, which then increased, so that the isotonic response at 35° C. may be bigger than at 30° C. Adaptation was thus found to occur upto 35-37° C. In one muscle it occurred upto 40° C. At 42.5° C., the muscle practically becomes inexcitable.

Similarly hearts which had adapted to higher temperature, would at first stop beating when the temperature was lowered, and then resume again.

#### TONUS

Both unstriated and cardiac muscles exhibit tone. The frog striated muscle here, when immersed and aerated in Ringer solution, develops tone (*cf.* Ringer tonus; Winton, 1930). This tone is inhibited by adrenaline and by increase in osmotic pressure, as with frog stomach. Time extension curves are like those of unstriated muscle. It is possible that this is a contracture due to increase of temperature.

When tone develops in unstriated muscle its excitability diminishes. After a contraction is produced by alternating current, nervous stimulation, potassium and acetylcholine, this tone diminishes for a brief period. It happens with gastrocnemius also. The contracture produced by acetylcholine is diminished by twitch. After preliminary inhibition following the twitch, the contracture re-develops. The same thing was found in the heart with potassium contracture (Singh, Sehra and Mrs. Singh); from this we concluded the presence of two excitabilities in the heart muscle. The above experiments show that this conclusion was wrong, the inhibition was due to the fact that every excitatory process is accompanied by an inhibitory one. As regards the veratrine effect it also becomes less and less marked if the muscle is made to give repeated contractions, but re-appears after a suitable period of rest.

In unstriated muscle, tonic contraction is due to some structural change, probably increase in viscosity, or to active contraction; the twitch affects the contraction as above, but with this difference that in the former, tension does not re-develop, but does so with tonic contraction. It thus appears that tone or viscosity are due to similar causes as both are antagonised by twitch. Some ionic change, therefore acts upon plain muscle to produce either tone or increase in viscosity. Striated muscle is comparatively much less susceptible than unstriated muscle in undergoing changes in viscosity. One kind of tone in the unstriated muscle is therefore identical with contracture in the striated muscle. This tone requires oxygen.

Whatever causes contracture in striated or unstriated muscle, causes slowing of relaxation in both. The special property of unstriated muscle leads to structural changes, so that energy is not required for maintenance of the contraction.

Contracture is antagonised by twitch; it depresses excitability in striated, cardiac and unstriated muscle. Thus if potassium, acetylcholine cause a contracture, further responses by heavier concentrations of these substances are depressed. Thus acetylcholine is depressant to acetylcholine. This shows that the contracture is produced by another agency, these substances setting up a chain reaction. This substance is present inside the fibres, as a depressant contracture and slowing of the relaxation occurs in isotonic sucrose, and as it is diminished by decrease of osmotic pressure (Singh, 1944 a), though there is evidence that sodium chloride of the saline may also be concerned (Singh, 1938 b, 1943). The above view is supported by experiments of Langley (1913) on striated muscle, and those of Gokhale and Singh (1945) on unstriated muscle; they found that the contracture may persist, though the stimulating substance is withdrawn.

Contracture also occurs which is synergistic to twitch in striated and unstriated muscle. Thus in frog rectus abdominis acetylcholine contracture may be synergistic to contractions produced by alternating current. In frog gastrocnemius and frog stomach lithium may produce similar results. This suggests that the contractile mechanism ultimately for tonic contractions and twitch is the same. But the differential action of certain substances on the viscosity and the contractile mechanism suggests that at least the slow relaxation is sarcoplasmic and contraction, the property of myosin in the sarcostyles. This is a modification of the view put forward by Botazzi.

#### EXCITABILITY TO CHEMICAL AND ELECTRICAL STIMULATION

Skeletal muscle is more excitable to electrical stimulation than unstriated muscle, the heart muscle showing an intermediate value but the excitability to chemical stimulation varies. I have not noted much difference between the sensitivity of striated and unstriated muscles to potassium. Sometimes I have found the frog stomach to be much less excitable to acetylcholine than the rectus abdominis or the gastrocnemius.

The heart muscle is least excitable to potassium and acetylcholine. The reasons for this are probably as follows:—Every stimulus produces both excitatory and inhibitory effects (adaptation). In the heart muscle the inhibitory process is probably more labile than in the other two muscles. This is shown by the fact that it reacts by intermittent contractions rather

than a continuous contraction to a constant stimulus. Calcium may convert complete tetanus into intermittent contractions in cardiac muscle (Singh, Sehra and Mrs. Singh, 1945 *a, b*). This is quite a common effect of calcium in unstriated muscle (Singh, 1938 *c*; 1942).

The depressant action of drugs and ions varies in the three kinds of muscle, there being a gradation from unstriated to cardiac and striated muscles. Thus large doses of adrenaline (1 in 10<sup>5</sup>) are most depressant to frog stomach, less to frog heart and frog gastrocnemius. The anions bromide, iodide, nitrate and thiocyanate have similar actions. This is probably determined by the resistance of their membranes. The calcium concentration is greater in frog striated muscle than in unstriated muscle (Meigs and Ryan, 1912), though in other animals it is the opposite (Wilkins, 1934).

The resistance of the membranes is probably determined not by the concentration of calcium in the whole fibre, but that in the membrane itself and these may not run parallel. In this connection it is interesting to know that the electrical resistance of unstriated muscle is less than that of striated muscle (Singh and Mrs. Singh, 1944).

Acetylcholine and potassium are more depressant to the heart than unstriated or striated muscles. This anomaly is due to the fact that inhibition has to be distinguished from toxic action. In hearts, where acetylcholine has a stimulant action, large doses are required to produce depression. In such cases the question arises whether the depression due to these toxic doses is the same as the inhibition produced by small concentrations. As acetylcholine sometimes produces stimulation of frog heart in small doses and depression in large doses, is the action of acetylcholine purely stimulant? Vagus in these hearts have produced complete standstill. The question then arises whether the action of acetylcholine is antagonistic to that of the vagus or the concentration of acetylcholine secreted by the nerve is high, and is in more intimate contact with the muscle fibres.

#### ADAPTATION

The frog stomach and the gastrocnemius behave very differently when stimulated by alternating current. In the former adaptation is rapid and in the latter slow. Adaptation to acetylcholine also is similarly affected. If adaptation is due to calcium, then it shows that though the frog stomach contains less calcium than gastrocnemius, it is in a more labile form. Frog stomach is more resistant to the toxic action of potassium (Hoher, 1927) than the gastrocnemius; this also suggests more labile calcium in the former, as calcium is antagonistic to the action of potassium.

#### EFFECT OF DRUGS AND IONS

*Effect of calcium.*—The frog gastrocnemius resembles *Mytilus* muscle in that it contracts in the absence of calcium. In both, when calcium is excluded, there is hyperexcitability to potassium and acetylcholine, and this is followed by a depression in a few minutes. In the frog gastrocnemius, however, the excitability to electric current is raised, whilst that in the *Mytilus* muscle, is depressed. This is probably due to the fact that in frog gastrocnemius adaptation plays a major part (Singh, 1938 d). This is shown by the fact that the response to potassium and acetylcholine also increases. If contracture develops, then these responses are depressed.

The opposite kind of response was also noticed, that is the muscle became inexcitable to electrical and nervous stimulation, and hyperexcitable to potassium and acetylcholine. The response of the first kind could be changed into second by fatiguing the muscle by tetanising it with alternating current for 10 seconds every 10 minutes. When the steady state is reached, the muscle becomes inexcitable to electric current in the absence of calcium.

A fatigued striated muscle thus resembles unstriated muscle in that (i) it becomes inexcitable in the absence of calcium; (ii) its movements are sluggish; (iii) it may show contracture; (iv) it may be more sensitive to potassium; (v) threshold to electrical stimulation increases; and (vi) its sodium content may increase (Fenn and Cobb, 1934).

The frog heart resembles the stomach, in that its excitability diminishes in the absence of calcium. The heart muscle is thus nearer to unstriated muscle than to striated muscle in this and other properties.

After being deprived of calcium, the frog gastrocnemius, the guinea pig uterus, and the frog heart (Burridge, 1915) become more sensitive to it. This is due to adaptation.

*Action of Sodium Chloride.*—Replacement of part of the sodium chloride of the saline with sucrose (or glucose in the case of *Mytilus* muscle), decreases the response to electric current in frog stomach and gastrocnemius, *Mytilus* muscle and the spontaneous contractions in the frog heart, though the exactly opposite also happens. In *Mytilus* muscle, the response increases when it shows much tone and the increase is excitability is due to removal of excitatory action of sodium chloride which is antagonistic in the same way as is potassium chloride. In the frog heart and frog gastrocnemius it is due to removal of the inhibitory effect of sodium chloride. In *Mytilus* muscle, decrease in excitability to electric current occurs in sodium deficient solutions, when it does not show much tone; this is a common finding in the frog gastrocnemius, which does not show tone.

The response to potassium decreases in the *Mytilus* muscle and increases in the frog stomach in sodium deficient solutions for the above reasons. In the guinea pig uterus and *Mytilus* muscle, tone decreases. In the frog gastrocnemius also the response at first increases.

When 80% of the sodium chloride is replaced, the frog gastrocnemius may become hyperexcitable to potassium and less excitable to electric current or the two excitable may be identically affected.

Partial replacement of sodium chloride of the saline increases the inhibitory action of adrenaline and ammonium in frog stomach, the inhibitory action of adrenaline in guinea pig uterus, and that of acetylcholine in frog heart, if the contractions decrease in height. If the contractions increase in height, then the opposite happens.

When sodium chloride is completely excluded, then the frog stomach, frog heart, frog gastrocnemius and guinea pig uterus enter into contracture, and adrenaline loses its inhibitory action on the guinea pig uterus and the frog stomach and acetylcholine on the frog heart. Their excitatory action is also lost (Singh, 1945). Thus these drugs bring about their action probably through a chain reaction, by sensitising the muscle to other ions. The contracture in sodium chloride deficient solution shows that in all the three kinds of muscle, contraction is produced by a difference in concentration of ions on two sides of the muscle membrane.

In the electrolyte-free medium, the frog gastrocnemius becomes absolutely inexcitable, though Chao (1937) has described that toad muscle remains irritable for 6 hours in the pure sucrose solution. Some frog hearts may become hyper-irritable, in that the magnitude of contractions of ventricles and auricles, which beat independently, is increased; in others, there is complete inexcitability. Frog stomach also behaves similarly. The magnitude of the spontaneous contractions may be greatly increased, though in others they are completely suppressed. In some of the latter, a trace of potassium chloride (1 in  $10^5$ ) may restore them.

*Effect of lithium chloride.*—In frog stomach, guinea pig uterus, *Mytilus* muscle and frog gastrocnemius, some of the effects are those of sodium deficiency. Frog stomach contracts and becomes hyperexcitable to alternating current and potassium, owing to the fact that its inhibitory action is less than that of sodium. Similarly in the guinea pig uterus and *Mytilus* muscle, tone decreases, as its excitatory action is less than that of sodium. *Mytilus* muscle becomes hyperexcitable to potassium. In frog gastrocnemius, replacement of 60% of the sodium chloride of the saline renders the

muscle hyper-irritable to potassium and acetylcholine, less excitable to electric current and inexcitable to nervous stimulation.

The response of the frog gastrocnemius to potassium decreases if contracture develops, and that to electric current may increase. In *Mytilus* muscle the response to acetylcholine decreases or increases. The increase is due to the increased excitability to stimulations from without, and the decrease to removal of potentiating effect of sodium.

The varied responses mentioned above are due to the fact that the action of sodium chloride may be inhibitory or excitatory and that contracture diminishes the excitability.

*Effect of ammonium.*—Ammonium is depressant to the frog stomach, but increases the excitability of the gastrocnemius and the heart in small concentration (0.002 M  $\text{NH}_4\text{Cl}$ ). Larger concentrations are depressant. In *Mytilus* muscle the excitability to alternating current is increased.

*Effect of potassium.*—0.02 M KCl stimulates frog stomach and gastrocnemius, but depresses the heart, though I have come across frog hearts in which the action was excitatory. The resistance of the frog stomach as well as the gastrocnemius to excess of potassium varies. All the three muscles exhibit adaptation to normal concentrations of potassium (potassium paradox). In guinea pig uterus, all concentrations of potassium may be inhibitory.

*Effect of hydrogen-ion concentration.*—The action of hydrogen ions may be excitatory or inhibitory in striated muscle and unstriated muscle. In all the three kinds of muscle, alkali increases the excitability. *Mytilus* muscle and guinea pig uterus show adaptation to hydrogen ions. In *Mytilus* muscle, sudden increase of hydrogen ions to pH 4.4 increases the excitability to potassium or cause contraction; slow increase has an opposite effect.

*Effect of adrenaline.*—In the *Mytilus* muscle, frog stomach and gastrocnemius small concentrations (1 in  $10^7$ ) increase the response to electric current, and the spontaneous contractions in the frog heart. In *Mytilus* muscle which are inexcitable to potassium and show little tone, larger contractions have a similar action, so also in the frog gastrocnemius which has no tone. In other *Mytilus* muscles and in frog gastrocnemius, adrenaline (1 in  $10^5$ ) decreases the response to electrical and nervous stimulation, and increase that to potassium and acetylcholine. Adrenaline has also a depressant action on frog heart and frog stomach. Thus like most substances adrenaline may have a depressant or excitatory action.

*Effect of acetylcholine.*—Acetylcholine may also have an excitatory or inhibitory action on the frog stomach, heart and gastrocnemius.

*Effect of initial length.*—Increase in the length of the fibres increases the excitability in all kinds of muscle, though the opposite has also been found in *Mytilus* muscle and frog heart. I have come across frog hearts which do not obey the Starling's law. This is probably due to stimulation of the intracardiac vagus, as the action of acetylcholine and that of vagus also increases with the initial lengths in these hearts; hearts which obey Starling's law behave oppositely.

*Effect of osmotic pressure.*—Increase of osmotic pressure diminishes tone. In the frog stomach and heart, increase of osmotic pressure to 1.4 times normal may increase or decrease the excitability; actual contraction may be caused. In the frog gastrocnemius, the response to potassium and acetylcholine increases. In *Mytilus* muscle it decreases; the response to electric current may increase or decrease.

The effect of osmotic pressure depends upon the fact that it increases the concentration of ions within the muscle fibres and thus may increase their excitatory or inhibitory action, and antagonises the excitatory and inhibitory action of the ions outside. This is shown by the fact that in the frog stomach, increase in osmotic pressure increases the response to potassium, but if the potassium contracture is induced, then increase of osmotic pressure diminishes the contracture. In the first instance the inhibitory effect of sodium was antagonised, but when the contracture develops this is done by the potassium itself, so that increases in osmotic pressure now cause relaxation.

The effect of increase in osmotic pressure shows that the action of sodium chloride on the frog gastrocnemius is inhibitory; that of calcium lack shows that it is excitatory, so it probably contains two antagonistic factors (Singh, 1942).

When tonicity of the saline is increased by adding sodium chloride, the response to electric current at first decreases and then increases in *Mytilus* muscle, frog stomach heart (spontaneous contractions) and the gastrocnemius. Burrdige (1922) has shown that the depression and increase in excitability are determined by independent factors, which is in agreement with my views that depression is due to the action of ions without, and the increase to increase in concentration of ions within the fibres the depressant action of sodium chloride being akin to that of potassium.

#### EXCITATION AND INHIBITION

Both in unstriated and cardiac muscles excitation and inhibition may be affected identically. Thus calcium antagonises the stimulant as well as the depressant action of pilocarpine (Burridge, 1923 b), and those of acetylcholine

(Burridge, 1935) on the frog heart. This shows that they are dependent upon some common property of the muscles (Singh, 1945), inhibition being a result of excitation. In such instances, increase in permeability will increase excitation, as well as inhibition. If the inhibitory agent is very labile, then the causative excitatory action may be masked, and only inhibition produced. This probably accounts for the inhibitory action of acetylcholine on the heart muscle. If it is possible to antagonise the excitatory process, then all excitatory substances should produce inhibition. If it is possible to antagonise the inhibitory process, then all inhibitory substances should produce excitation. This dual action is latent in all excitatory or inhibitory substances, and by suitable alterations in the environment either action should be produced.

#### THE MOTOR END PLATE

A most interesting result is that substances which produce curarisation in the frog nerve muscle preparation abolish the response of *Mytilus* muscle to electrical stimulation. These are lack of calcium, curare, excess of strychnine, veratrine, etc. Ammonium also produces similar results (Ing and Wright, 1931; Singh, 1938 a). This would suggest that either the motor end plate is similar to *Mytilus* muscle in the constitution of its excitability or that the muscle can only be excited through its nerves. The latter is most unlikely, as curarisation is not known in plain muscle.

It therefore appears that unstriated muscle can be directly excited by nerves, but not striated muscle. For the transmission of the impulse, a structure like that of plain muscle must first be excited which will then conduct the excitation to the striated muscle. This explains why motor end plates are not necessary for the excitation of unstriated muscle.

The above conclusion would be strange, because excitation will have to pass from a more excitable to a less excitable tissue through a least excitable one. But then unstriated muscle is known to be very sensitive to chemical stimulation, so that a chemical transmission from nerve to the motor end plate would be very proper. From the motor end plate to the muscle, the transmission would be electrical, so that the whole transmission from nerve to muscle would be electrochemical in striated muscle, and chemical in unstriated and cardiac muscle.

Nerve endings in unstriated muscle may end within the cell or without. This provides a twofold method of nervous action, that is, excitation from within and that from without (Singh, 1944 b).

## SUMMARY

1. Unstriated, cardiac and striated muscles show differential action of substances on the excitability to electrical stimulation and potassium.
2. The response to nervous stimulation and acetylcholine may be similarly or oppositely affected.
3. Muscle shows adaptation to temperature.
4. Tonus may be shown by three kinds of muscle; one kind of tone in unstriated muscle is similar to the contracture of striated muscle.
5. In all the three kinds of muscle, twitch is antagonistic to contracture; a synergistic contracture also occurs.
6. In some instances, there is a gradation in the properties of unstriated, cardiac and striated muscles.
7. Adaptation to electric current is more rapid in unstriated than in striated muscle.
8. Many drugs and ions act similarly on the three kinds of muscle.
9. Many agencies affect excitation and inhibition similarly.
10. The properties of *Mytilus* muscle and the motor end plate of striated muscle are in many respects similar.

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