Histology of muscles—*Vide* pages 52–65.

Composition of skeletal muscles

Water—75%.
Solid—25%

I. **Proteins**—20%. **Actin** and **myosin** form about half the total muscle protein. Myosin, actin and their complex **actomyosin, tropomyosin A** (*purified*) and **B** (*native* or *Bailey's tropomyosin* or *metin*), **troponin, α-actinin, β-actinin** and *M-band filament* (nature of the latter protein is not known) have been isolated. Proteolytic enzymes break myosin into *light meromyosin* (straight helical body portion) and *heavy meromyosin* (head portion). This heavy meromyosin can again be divided into *heavy meromyosin subfragment II* (neck portion) and *heavy meromyosin subfragment I* (proper head portion) that contains the ATP-*ase* activity of the myosin. Actin may be of **G-actin** or **F-actin** form. Actin also contains **tropomyosin** and **troponin.** *Actomyosin is a complex of three myosin and one actin.* Tropomyosin B (native) contains tropomyosin A and troponin. Tropomyosin and α-actinin are found at the Z-disc. **Myogen** is a protein of albumin nature and can be differentiated as **myosin A** and **B.** Enzymatic property is attributed to myosin A fraction. **Myoalbumin** is another protein found in sarcoplasm. **Myoglobin** is a conjugated protein and also named as *muscle haemoglobin.* Though it is functionally similar, still it differs from blood haemoglobin by molecular weight, isoelectric pH and absorption bands. The iron content is same in both cases. Several other proteins over and above the names already mentioned, are obtained in muscles in small amounts which are **component-C, delta protein, metamyosin, contractin, X-protein** and **Y-protein.** Little is known regarding their nature, properties and functions.

II. **Fats**—0·2% including cholesterol, lecithin and neutral fat.

III. **Carbohydrates**—1·0%. (*a*) Glycogen—0·5–1·0%. (*b*) Hexose phosphate—0·05%.

IV. **Inorganic salts**.–1·0–1·5%. Contains potassium phosphate mainly, (K about 0·3%) and also traces of Ca (0·007%), Na (0·06%), Mg (0·02%). Fe, Cl (0·04%) and sulphate. Phosphates remain in various forms (P—0·2%). The ratio between Na : K is 1 : 5.

V. **Extractives**—A. NON-NITROGENOUS:

1. **Lactic acid**—0·02% in fresh resting muscle.
2. **Inositol** (muscle sugar, hexahydroxycyclohexane)—0·25%.

B. NITROGENOUS: 1. Adenosine triphosphate (**ATP**)—0·25%. Adenosine diphosphate (**ADP**). Adenylic acid—also called Adenosine monophosphate (**AMP**)—0·15%.

2. **Creatine phosphate** ($CrPO_4$)—phosphocreatine or phosphagen —0·5%. (Creatine 0·35%).

[These phosphoric acid compounds—(1) and (2) act as coenzymes by working alternately as donors and acceptors of phosphoric acid. They form an essential part in the processes of phosphorylation involved in the chemical reactions underlying muscular contraction.]

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3. **Xanthine, Hypoxanthine** and **Inosinic acid**—derived from adenylic acid of the tissues and the nucleoprotein of the nuclei.
4. **Carnosine**—0·3%. It is a dipeptide (β-alanyl histidine). In some animals its methyl derivative is found and is called **anserine.**

VI. **Pigments** (Porphyrin derivatives)—

1. **Myoglobin** (Myohaemoglobin or Myochrome)—It is an iron-containing chromoprotein found in red muscles and is already discussed under 'protein'.
2. **Cytochrome** (Myohaematin)—It is an iron-porphyrin pigment, found in three forms—a, b, c.
3. Flavines and others.

VII. **Enzymes** and **Coenzymes:** 1. Enzymes and coenzymes of the glycolytic cycle.
2. Those that break down and re-synthesise ATP and phosphagen.
3. Enzymes of the citric acid cycle, that finally oxidise pyruvic acid into CO_2 and H_2O.
4. Other enzymes like deaminase, etc.

Composition of Plain and Cardiac muscles. Their composition differs from that of the skeletal muscle in the following respects. Both contain (1) less proteins, (2) less ATP, phosphagen and other phosphates, (3) less carnosine, (4) less glycogen. But both contain more (*a*) Na (Na : K = 1 : 2) and (*b*) nucleoprotein. Cardiac muscle contains more *phospholipids* and cholesterol than either plain muscle or skeletal muscle.

PROPERTIES OF SKELETAL MUSCLES

Skeletal muscle shows the following properties: (I) **excitability** and **contractility,** (II) **refractory period,** (III) **tonicity,** (IV) **conductivity,** (V) **extensibility** and **elasticity.**

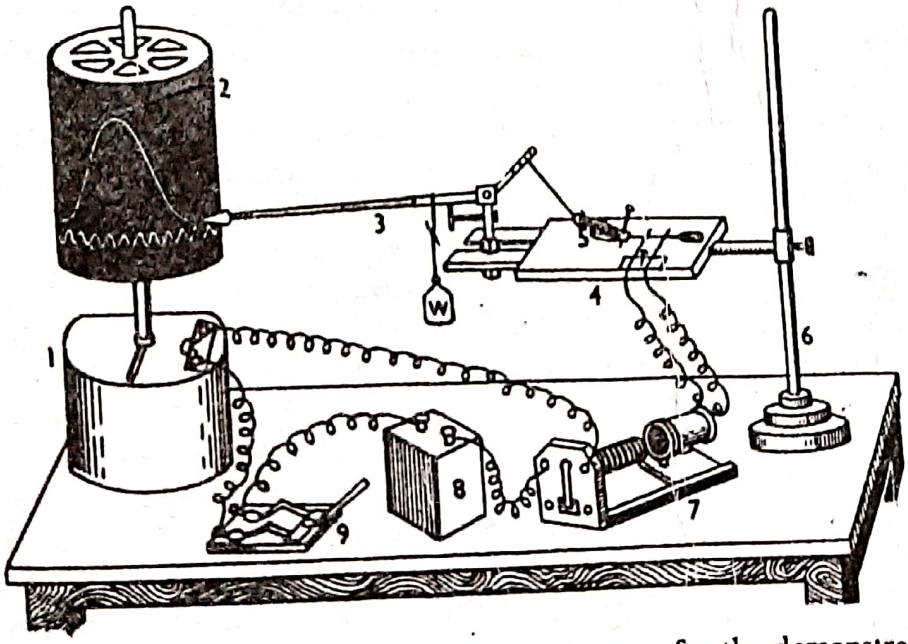

FIG. 115. Diagram shows the experimental set-up for the demonstration of simple muscle curve.
1—Motor. 2—Drum showing the curve. 3—Writing lever. 4—Myograph board. 5—Muscle and nerve with stimulating electrode. 6—Myograph stand. 7—Induction coil. 8—Battery. 9—Mercury key.

I. **Excitability and Contractility.** With an adequate stimulus, muscles are excitable. The stimulus may be *mechanical, thermal, chemical* or

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[illegible] the facilities of accurate adjustment, electrical stimulus is used in laboratory experiments.

When excited, the muscle contracts. This is immediately followed by relaxation. A single induction shock will produce a single contraction (twitch). The record of this on a moving drum (FIG. 115) will produce a curve, called the *simple muscle curve* (FIG. 116). But if the stimulus be strong, it may cause stronger contraction.

The **simple muscle curve** (FIG. 116), as obtained with a frog's gastrocnemius, has a total duration of about 0·1 second. It consists of three parts: (1) **Latent period** (0·01 second). It is the interval between the application of stimulus and the beginning of contraction. Latent period is due to time taken (*i*) for propagation of impulse from the point of stimulation to the neuromuscular junction and thence to the sarcolemma and (*ii*) for initiation of contraction. (2) **Period of contraction** (0·04 second), from beginning of the contraction up to the maximum contraction. (3) **Period of relaxation** (0·05 second), from the summit up to the original level.

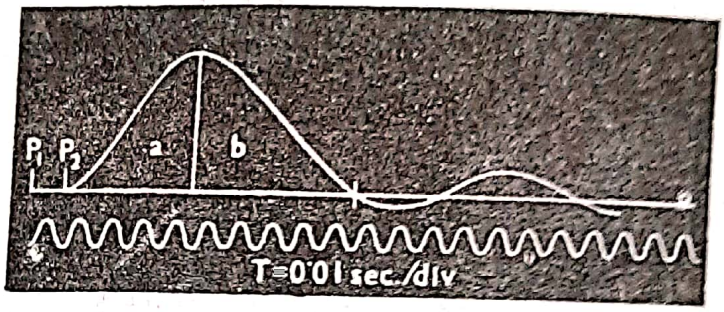

FIG. 116. Simple muscle curve (diagrammatic).
P_1—Point of stimulation. P_2—Beginning of contraction. P_1–P_2—Latent period.
a—Contraction phase. b—Relaxation phase.

The following factors affect **excitability** and **contractility** and therefore alter, in various ways, the nature of the simple muscle curve:

1. **Strength and duration of stimuli.** For stimulation to occur, two factors are necessary—a minimum strength and an adequate duration of the stimulus. Chronaxie, which includes both these factors, is the measure of excitability of a tissue (*vide* Chronaxie—pages 222–23).

2. **Effects of two successive stimuli** (FIG. 117). If the second stimulus is applied after sufficient intervals both first and second stimuli will cause contraction and two simple muscle curves will be recorded (FIG. 117, STAGE *a*). The second curve will be slightly higher than the first one due to the beneficial effect of contraction. If the second stimulus is applied in the relaxation period of the first, more or less two separate curves will be produced and the second curve will be higher (FIG. 117, STAGE *b*). If the second stimulus is applied within the contraction period of the first one the second curve will be superimposed on the first one with a higher height of contraction (FIG. 117, STAGE *c*). These are known as **summation of effects** (contraction). If the second stimulus is applied within the latent period but after refractory period of the first, then their effects are added together giving a simple muscle curve of larger height than either of them produced separately (FIG. 117, STAGE *d*). This effect is known as **summation of stimuli.** By using maximal or submaximal stimuli, these summated effects can be obtained. This is true for both

single muscle fibre or a whole muscle bulk. In case of submaximal stimuli, the summated effects are due to activation of more nerves and

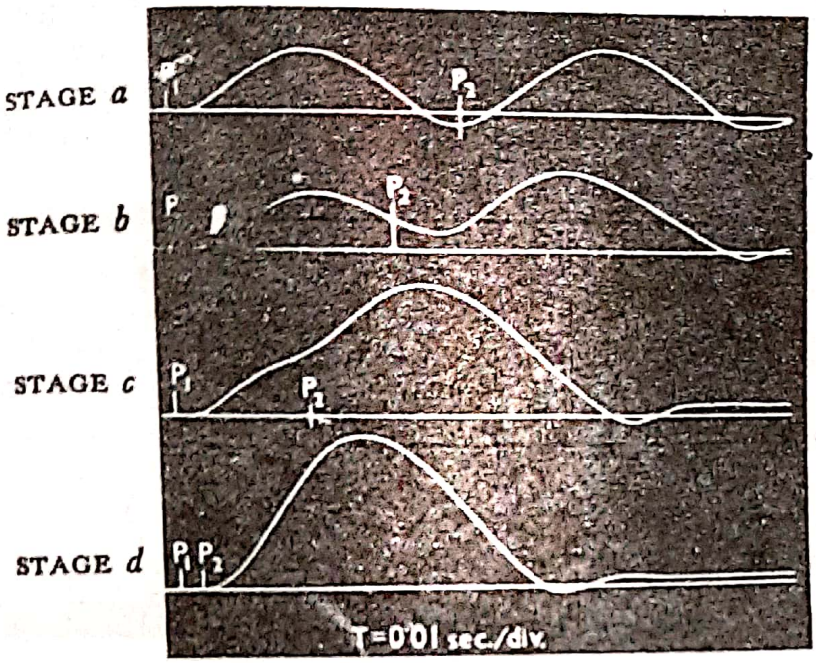

FIG. 117. Effects of two successive stimuli (diagrammatic).
P_1 & P_2—Points of stimulation.

STAGE *a*—The second stimulus is applied after sufficient intervals.
STAGE *b*—The second stimulus is applied in the relaxation period of the first.
STAGE *c*—The second stimulus is applied before the contraction of the first one is over.
STAGE *d*—The second stimulus is applied within the latent period of the first one.

muscle fibres, but in case of maximal stimuli, the greater response cannot be due to an increase in numbers of responding nerves and muscle fibres, but due to a difference in contractile mechanisms. It is claimed that these effects are due to beginning of second twitch before the active state for the first twitch is complete. That is the duration of the active state of the first response makes possible the augmentation of the second response. Thus this effect goes against the law of *all-or-none*.

3. **Effects of repetition of stimuli.** Following phenomena are observed:

(*a*) **Staircase phenomena.** When a freshly excised muscle is stimulated with a single induction shock of sufficient strength then a contraction of certain amplitude is recorded. If second stimulus of same strength is applied at an interval of about 1 second to the muscle after completion of the effect of first stimulus, then an increased amplitude of contraction is recorded. With a series of such stimuli (5 to 6 stimuli) but under the condition that each contraction is allowed to be completed before the next stimulus is applied, then a gradual increase in amplitude of contraction is obtained. This stair-like rise is called the **staircase (treppe) phenomenon.** Increased H^+ ion concentration and an increase of temperature within the muscle create a favourable condition for more work (**beneficial effect**). Hence, the contraction becomes stronger.

(*b*) **Clonus.** When repeated stimuli are applied, the type of response will vary according to frequency. When the frequency is such that each

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successive stimulus falls within the period of relaxation of the previous curve, the record will show a series of wavy oscillations. This is called **clonus** or **incomplete tetanus** (FIG. 118, B–E).

(*c*) **Tetanus.** When the frequency is more, so that the stimuli fall within the latent period of the previous curve, the record traces a clear steady line, which rises at first abruptly and then gradually, till maximum contraction takes place. This is called **tetanus** (FIG. 118, F). Here the

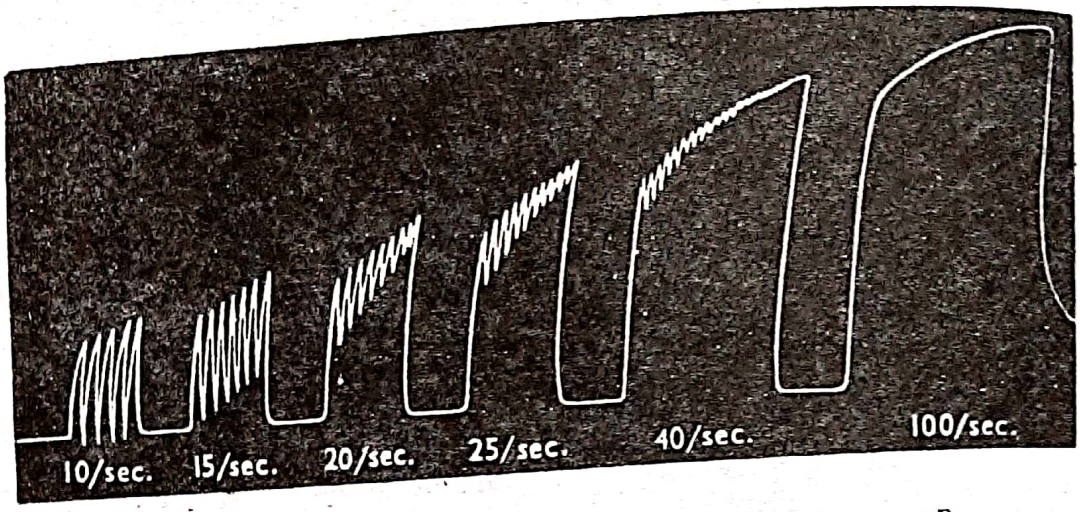

FIG. 118. Genesis of tetanus (diagrammatic).

fusion is complete and the muscle, instead of vibrating, exerts a steady pull. Due to summation, the height of tetanic contraction is usually higher than that of a single twitch. Frequency of stimulation, required for the induction of tetanus, varies with the nature of the muscle. In external eye muscle it is about 350/sec., in gastrocnemius muscle it is about 100/sec.

Clonus may be described as summation of successive contraction, whereas tetanus is summation of successive stimuli. The mechanical movement in response to voluntary stimuli is neither a twitch nor a tetanus (Lippold, 1957). During voluntary movement, the skeletal muscles are stimulated at low frequency, which is less than fusion frequency, and also asynchronously, so that the infrequent contraction of a large number of fibres give the appearance of a smooth response.

(*d*) **Fatigue.** When repeatedly stimulated, the muscle has lost its irritability, becomes gradually less excitable and ultimately ceases to respond. This phenomenon is called *fatigue* (FIGS. 119, 120 & 122). Muscular fatigue can be defined as the inability of the muscle to do further work. In the fatigue curve, all the periods are lengthened. The relaxation period is so much prolonged that the curve fails to reach the base line before the next stimulus arrives, thus leaving a **contraction remainder** (FIG. 119). The **causes of fatigue** might be due to (*i*) exhaustion of sources of energy of the muscle, (*ii*) accumulation of the end products of chemical reactions, such as lactic acid, carbon dioxide, ketone bodies and (*iii*) decrease of local synthesis of acetylcholine-like substances during prolonged exercise (Torda & Wolff, 1945). Oxygen is required for the removal of these substances and so for recovery. Fatigued muscle left in nitrogen does not recover. In studying fatigue in muscle *with circulation* and *without circulation*, the muscle gets

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fatigue more earlier in case of the latter and does not recover on rest (Fig. 120, 1). But in case of muscle with circulation, fatigue comes later and the muscle recovers on rest (Fig. 120, 2). This shows that oxygen, which is supplied through blood circulation, is required for recovery of

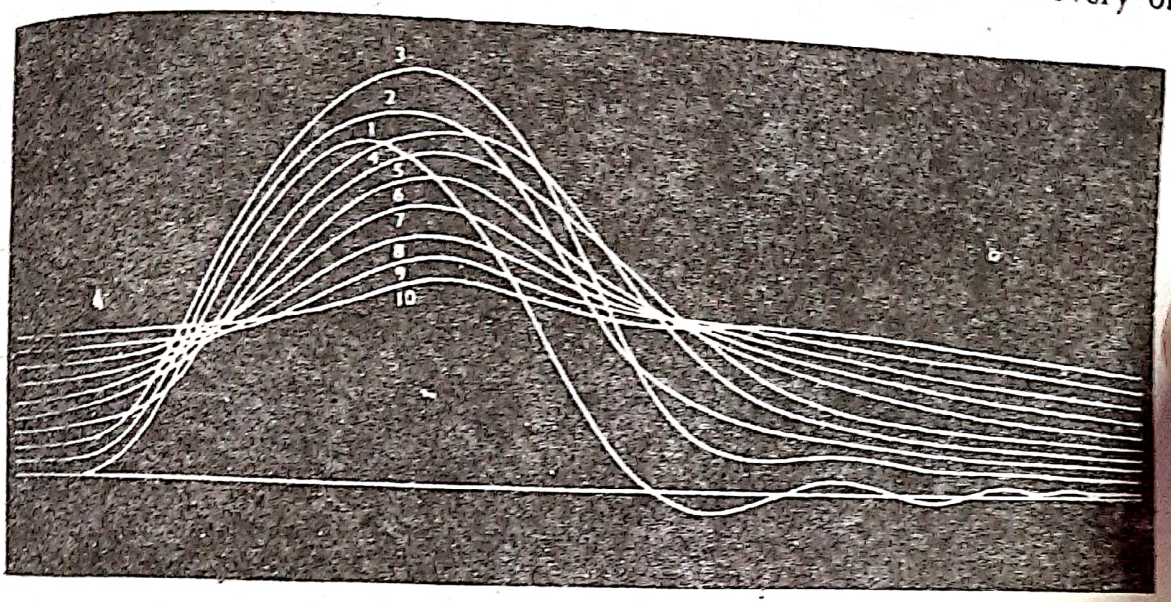

Fig. 119. Fatigue curve of a muscle in rapid moving drum (diagrammatic). The diagram indicates successive stages of the curve (beginning from 1). 2 and 3 are higher than 1 due to the beneficial effect of contraction. 10 shows the maximum development of contracture.

fatigue. The **seat of fatigue** lies in the muscle when it is directly stimulated. But when it is stimulated through the motor nerve, the seat of fatigue is in the neuromuscular junction. In physiological exercise, the *seat of fatigue* is neither in the muscle nor in the neuromuscular junction but at the synapses in the central nervous system (**central fatigue**). On comparison, it is seen that fatigue after voluntary work first appears in the synapses, then in the neuromuscular junctions and lastly in the muscle

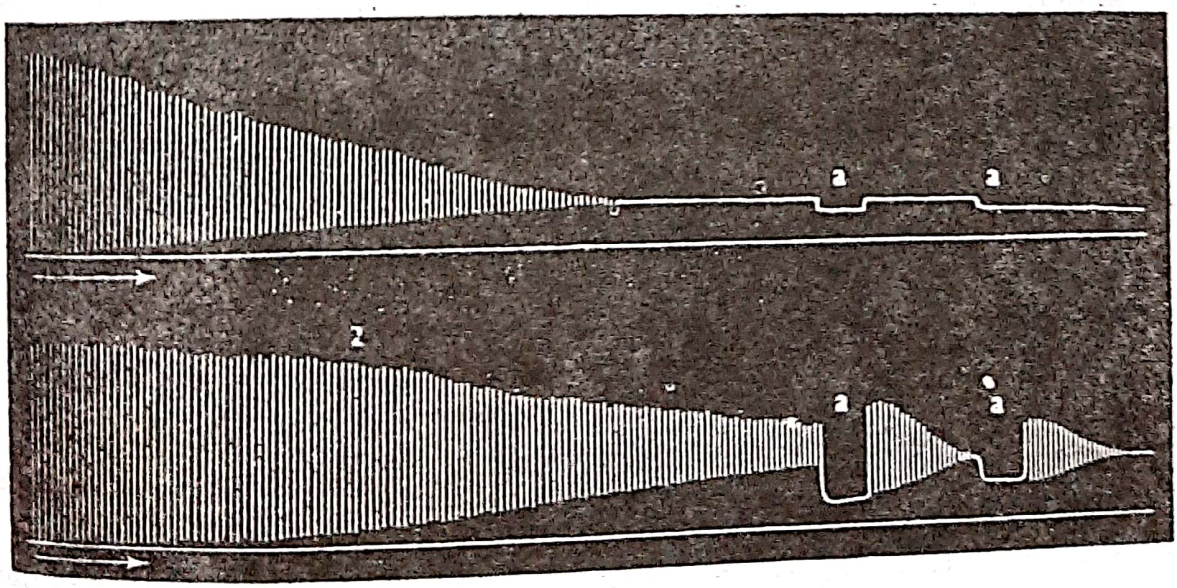

Fig. 120. Muscle fatigue in slow moving drum (diagrammatic). Diagram shows the effect of circulation on muscular fatigue. 1—without circulation. 2—with circulation. 'a' shows the effect of rest on recovery from fatigue. 2-a shows recovery from fatigue, whereas 1-a does not.

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Rigor mortis

Rigor mortis is a state of rigidity that develops in the muscles after death. Isolated muscles also develop rigor mortis. While in this condition the muscle (1) *loses its excitability*, (2) *shortens in length*, (3) *increases in thickness*, (4) *becomes viscous and loses translucency*, (5) *becomes distinctly acid* (pH 5·8), (6) *gradually becomes stiff*, (7) *glycogen disappears*, and (8) *the muscles give off carbonic acid*. Severe muscular exercise immediately before death hastens the onset of rigor mortis. This is found in soldiers killed in action and also in hunted animals. The time of onset is not the same in all muscles. On the average, rigor mortis starts in the second hour and is completed in three hours after death. The muscles of the body are involved in the following order—lower jaw, face, neck, thorax, abdomen, upper extremities and lastly the lower extremities. Rigor mortis disappears 24 to 36 hours after death due to autolysis. The disappearance also follows the same order. Caffeine, arsenate, chloroform vapour, increased temperature and acidity hasten rigor mortis. Rigor mortis is a state of permanent irreversible contraction and is associated with deficiency of ATP causing establishment of permanent link between actin and myosin. This deficiency of ATP fails to bring about dissociation of actomyosin to actin and myosin. It is postulated that during activity creatine phosphate level is associated with the ATP level of the muscle. The creatine phosphate is the high-energy resource of the muscle and its level is again dependent upon the ATP. $CrPO_4 + ADP \rightleftharpoons$ creatine + ATP. When ATP falls to 85% and creatine phosphate to 30% of its initial value, the symptoms of rigor mortis begin to appear when the ATP level falls to 15% of its value.

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CHARACTERISTICS OF SKELETAL, SMOOTH AND CARDIAC MUSCLES

Characteristics	Skeletal	Smooth	Cardiac
Histology			
1. Size and shape	Cylindrical; 1–40 mm long, 10 to 100 μ in diameter.	Elongated, fusiform, length 0·2 mm (aver.), width—6 μ (central portion).	Short cylindrical, rectangular in longitudinal section, polyhedral in transverse section.
2. Striations	Transverse, longitudinal.	Longitudinal (special preparation).	Both longitudinal and transverse.
3. Sarcolemma	Present and complete.	Present and complete.	Present and complete.
4. Nucleus	Multiple, just under the sarcolemma.	Single, at the centre with distinct nucleoli.	Single and central.
5. Sarcotubular system	Present, T-systems are at junctions of A–I band (in mammals). Terminal cisternae is prominent.	Present, but not so characterised.	Present, but without terminal cisternae. T-system is more prominent and present at Z-line (in mammals).
6. Branch	Nil.	Nil.	Multiple branches. In all directions—three-dimensional network without cytoplasmic continuity (false syncytial appearance).
7. Cell-to-cell conduction	Nil.	Through nexus.	Through specialised areas of intercalated disc.
Properties			
1. Rhythmicity	Nil.	Present.	Present and characteristic.
2. Conductivity	Very fast.	Slower.	Slower, different in different parts.
All-or-none law	True for single fibre.	True for single fibre.	True for the whole heart, because of functional syncytium.
3. Contractility	Simple muscle curve with characteristic features.	Slow and worm-like. All periods of the curve longer.	Characteristic muscle curve. Contraction, longer than relaxation.
4. Refractory period	Short—within latent period.	Longer than smooth.	Longest, whole contraction period is absolute refractory.
(a) Tetanus	Possible.	Not so.	Impossible.
(b) Fatigue	Possible.	Possible, difficult to demonstrate.	None. Long refractory period ensures recovery.
5. Tonicity	Tone depends on nerves.	Independent of nerve.	Independent of nerve.

CHARACTERISTICS OF SKELETAL, SMOOTH AND CARDIAC MUSCLES (*Contd.*)

Characteristics	Skeletal	Smooth	Cardiac
Composition			
1. Protein	Maximum.	Less.	Less.
2. Glycogen	Less.	More.	More.
3. ATP and Phosphagen	Present.	Present.	Present.
4. Carnosine	Maximum.	Less.	Less.
5. Fats	Mostly neutral fats.	Mostly neutral fats.	More phosphatids and cholesterol than in others.
6. Inorganic	Na/K—1/3. Ca++.	About same.	Na/K—1/2, i.e., more Na. Ca++.
Action of Ions			
1. Sodium	Excitation.	Probably same.	Initiates and maintains heart beat.
2. Calcium	Presents mostly in sarcoplasmic reticulum and stimulates ATP-*ase* activity during muscular contraction.	Same as skeletal.	Increases strength of contraction and duration of systole.
3. Potassium	Reduces excitability and hastens fatigue.	Probably same.	Inhibits contraction and produces relaxation.
Metabolism			
1. Carbohydrates			
(a) Lactic acid	Oxidised less easily than glucose and often incomplete.	Oxidised less easily than glucose and often incomplete.	Completely and more readily than glucose.
(b) Glycogen	Reduced in Starvation and Diabetes Mellitus.	Reduced in Starvation and Diabetes Mellitus.	Increased.
2. Blood supply and O_2 consumption	Moderate.	Less.	High.
Distribution	Skeletal.	Hollow viscera, capsules, skin, etc.	Only in heart.
Control	Under the *will*, so voluntary.	Not so, involuntary	Not so, involuntary.
Nerve Supply	Somatic with special nerve endings.	Autonomic with ganglia and free nerve terminals.	Same as in involuntary.

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1. Skeletal—striated voluntary (FIG. 59).
2. Cardiac—striated involuntary (FIG. 60).
3. Visceral—non-striated (plain or smooth) involuntary (FIG. 61).

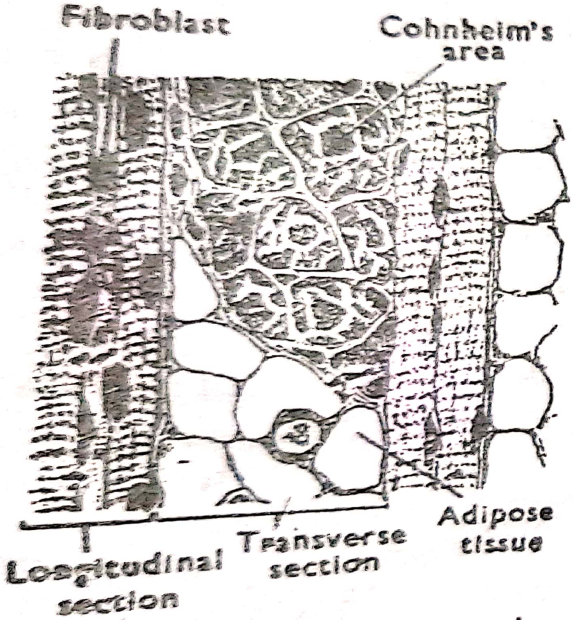

FIG. 59. Diagrammatic representation of skeletal muscle.

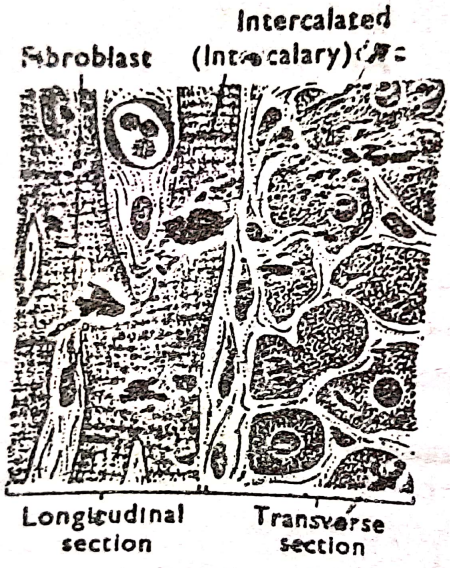

FIG. 60. Sectional view of cardiac muscle (diagrammatic).

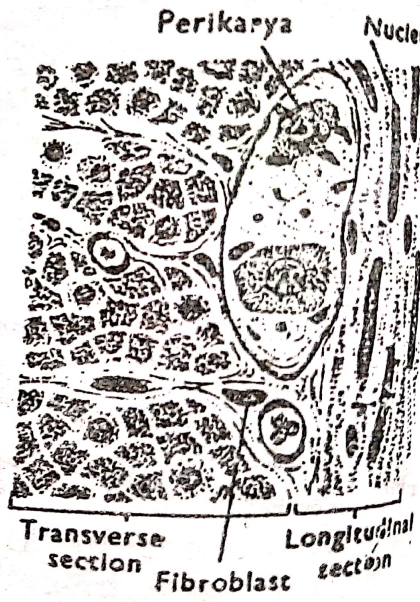

FIG. 61. Diagram depicts the sectional view of visceral muscle.

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