others, star-shaped. They possess one, and sometimes two or three clear, ovoid nuclei, with distinct nucleoli. On the addition of acetic acid the cells disappear but the nuclei are unaffected. It is impossible to give any accurate measurements of the cells, on account of their great variations in size. The appearance of the connective tissue, with a few cells and nuclei, is represented in Fig. 153.

Between the muscles, and in the substance of the muscles, between the bundles of fibres, there always exists a greater or less quantity of adipose tissue in the meshes of the fibrous structure.

Blood-vessels and Lymphatics.—The muscles are abundantly supplied with blood-vessels, generally by a number of small arteries with two satellite veins. The capillary arrangement in this tissue is peculiar. From the smallest arterioles, capillary vessels are given off, arranged in a net-work with tolerably regular, oblong, rectangular meshes, their long diameter following the direction of the fibres. These envelop each primitive fasciculus, enclosing it completely, the artery and vein being upon the same side. The capillaries are smaller than in any other part of the vascular system.

The arrangement of the lymphatics in the muscles has never been definitely ascertained. There are lymphatics surrounding the large vascular trunks of the extremities and of the abdominal and thoracic walls, which, it would appear, must come from the substance of the muscles; but they have never been traced to their origin. Sappey has succeeded in injecting lymphatics upon the surface of some of the larger muscles, but he has not been able to follow them into the muscular substance.

Connection of the Muscles with the Tendons.—The primitive muscular fasciculi terminate in little, conical extremities, which are received into corresponding depressions in the bundles of fibres composing the tendons; but this union is so close that the muscle or the tendon may be ruptured without a separation at the point of union. In the penniform muscles this arrangement is quite uniform. In other muscles it is essentially the same, but the perimysium seems to be continuous with the loose areolar tissue enveloping the corresponding tendinous bundles.

Chemical Composition of the Muscles.—The most important nitrogenized constituent of the muscles is myosine. This resembles fibrin, but it presents certain points of difference in its behavior to reagents, by which it may be readily distinguished. One of its peculiar properties is that it is dissolved at an ordinary temperature by a mixture of one part of hydrochloric acid and ten of water. The muscular substance is permeated by a fluid, called the muscular juice, which contains certain coagulable albuminoid substances. Combined with the organic constituents of the muscular substance are mineral salts in great variety, which can not be separated without incineration. Certain excrementitious matters have also been found in the muscles; and probably nearly all of those eliminated by the kidneys exist here, although they are taken up by the blood as fast as they are produced and are consequently detected with difficulty. The muscles also contain inosite, inosic acid, lactic acid and certain volatile acids of fatty origin. During life the muscular fluid is slightly alkaline, but it becomes acid soon after death. The muscle itself, during contraction, has an acid reaction. The muscular juice is alkaline or neutral after moderate exercise as well as during complete repose; but when a muscle is made to undergo excessive exercise, the lactic and other acids exist in greater quantity and the reaction becomes acid.

Physiological Properties of the Muscles.

The important general properties of the striated muscles are the following: 1. Elasticity; 2. Tonicity; 3. Sensibility of a peculiar kind; 4. Contractility, or excitability. These are all necessary to the physiological action of the muscles. Their elasticity is brought into play in opposing muscles or sets of muscles; one set acting to move a part and to extend the antagonistic muscles, which, by virtue of their elasticity, retract when the extending force is removed. Their tonicity is an insensible and a more or less constant contraction, by which the action of opposing muscles is balanced when both are in the condition of what is called repose. Their sensibility is peculiar and is expressed chiefly in the sense of fatigue and in the appreciation of weight and of resistance to contraction. Their contractility or excitability is the property which enables them to contract under stimulation. All of these general properties strictly belong to physiology, as do some special acts that are not necessarily involved in the study of ordinary descriptive anatomy.

Elasticity of Muscles.—The true muscular substance contained in the sarcolemma is eminently contractile; and although it may possess a certain degree of elasticity, this property is most strongly marked in the accessory anatomical elements. The interstitial fibrous tissue is loose and presents a certain number of elastic fibres; and the sarcolemma is very elastic. It is probably the sarcolemma that gives to the muscles their retractile power after simple extension.

It is unnecessary to follow out in detail all of the many experiments that have been made upon the elasticity of muscles. There is a certain limit, of course, to their perfect elasticity—understanding by this the degree of extension that is followed by complete retraction—and this can not be exceeded in the human subject without dislocation of parts. It has been found by Marey, that the gastrocnemius muscle of a frog, detached from the body, can be extended about $\frac{1}{50}$ of an inch (0·5 mm.) by a weight of a little more than 300 grains (20 grammes). This weight, however, did not extend the muscle beyond the limit of perfect elasticity. The muscle of a frog of ordinary size was extended beyond the possibility of complete restoration, by a weight of about seven hundred and fifty grains (48·6 grammes). Marey also showed that fatigue of the muscles increased their extensibility and diminished their power of subsequent retraction. This fact has an application to the physiological action of muscles; for it is well known that they are unusually relaxed during fatigue after excessive exertion, and they are at that time more than ordinarily extensible.

Muscular Tonicity.—The muscles, under normal conditions, have an insensible and a constant tendency to contract, which is more or less dependent upon the action of the motor nerves. If, for example, a muscle be cut across in a surgical operation, the divided extremities become permanently retracted; or if the muscles of one side of the face be paralyzed, the muscles upon the opposite side insensibly distort the features. It is difficult to explain these phenomena by assuming that tonicity is due to reflex action, for there is no evidence that the contraction takes place as the consequence of a stimulus. All that can be said is that a muscle, not excessively fatigued, and with its nervous connections intact, is constantly in a state of insensible contraction, more or less marked.

Sensibility of the Muscles.—The muscles possess that kind of sensibility which gives an appreciation of the power of resistance, immobility, and elasticity of substances that are grasped, or which, by their weight, are opposed to the exertion of muscular power. It is by the appreciation of weight and resistance that the force required to accomplish muscular acts is regulated. These properties refer chiefly to simple muscular efforts. After long-continued exertion there is a sense of fatigue that is peculiar to the muscles. It is difficult to separate this entirely from the sense of nervous exhaustion, but it seems to be to a certain extent distinct; for when suffering from the fatigue that follows over-exertion, it seems as though a nervous stimulus could be sent to the muscles, to which they are for the time unable to respond.

When the muscles are thrown into tetanic contraction, a peculiar sensation is produced, which is entirely different from painful impressions made upon the ordinary sensory nerves. In the cramps of cholera, tetanus, or the convulsions from strychnine, these distressing sensations are very marked.

If the muscles possess any general sensibility, it is very slight. A muscle may be lacerated or irritated without producing actual pain, although contraction produced by irritants and the sense of tension when the muscles are drawn upon can always be appreciated.

Muscular Contractility, or Excitability.—During life and under normal conditions, the muscles will always contract in obedience to a proper stimulus applied either directly or through the nerves. In the natural action of the organism, this contraction is induced by nervous influence either through volition or reflex action. Still, a muscle may be living and yet have lost its contractility. For example, after a muscle has been for a long time paralyzed and disused, the application of the most powerful stimulus will fail to induce contraction; but when examined with the microscope, it is found that the nutrition of the muscle has become profoundly affected, and that the contractile substance has disappeared. Muscular contractility persists for a certain time after death and in muscles separated from the body; and this fact has been taken advantage of by physiologists in the study of the properties of the muscular tissue. A muscle detached from the living body continues for a time to respire, and it undergoes some of the changes of disassimilation observed in the organism. So long as these changes are restricted within the limits of physical and chemical integrity of the fibre, contractility remains. As these processes are very slow in the cold-blooded animals, the excitability of all the parts persists for a considerable time after death.

In the human subject and the warm-blooded animals, the muscles cease to respond to a stimulus a few hours after death, although the time of disappearance of excitability is very variable. Nysten, in a number of experiments upon the disappearance of excitability in the human subject after decapitation, found that different parts lost their contractility at different periods, but that generally this depended upon exposure to the air. With the exception of the right auricle of the heart, the striated muscles were the last to lose their excitability. In one instance, certain of the voluntary muscles that had not been exposed retained their contractility seven hours and fifty minutes after death. Longet and Masson found that an electric shock, sufficiently powerful to produce death instantly, destroyed the excitability of the muscular tissue and of the motor nerves.

The experiments of Longet (1841) presented almost conclusive proof of the independence of muscular excitability. He resected the facial nerve and found that it ceased to respond to mechanical and electric stimulus, or in other words, lost its excitability, after the fourth day. Operating, however, upon the muscles supplied exclusively with filaments from this nerve, he found that they responded promptly to mechanical and electric stimulation, and that this continued for more than twelve weeks. In other experiments it was shown that while the contractility of the muscles could be seriously influenced through the nervous system, this was effected only by modifications in their nutrition. When the mixed nerves were divided, the nutrition of the muscles was generally disturbed; and although muscular contractility persisted for some time after the nervous excitability had disappeared, it became very much diminished at the end of six weeks. Some varieties of curare destroy the excitability of the motor nerves, leaving the sensitory filaments intact. If a frog be poisoned by introducing a little of this agent under the skin, stimulation, electric or mechanical, applied to an exposed nerve, fails to produce muscular contraction; but if the stimulus be applied directly to the muscles, they will contract vigorously. In this way the nerves are, as it were, dissected out from the muscles; and the discovery of an agent that will paralyze the nerves without affecting the muscles affords conclusive proof that the excitability of these two systems is distinct. If a frog be poisoned with potassium sulphocyanide, precisely the contrary effect is observed; that is, the muscles will become insensible to excitation, while the nervous system is unaffected. This fact may be demonstrated by apply-

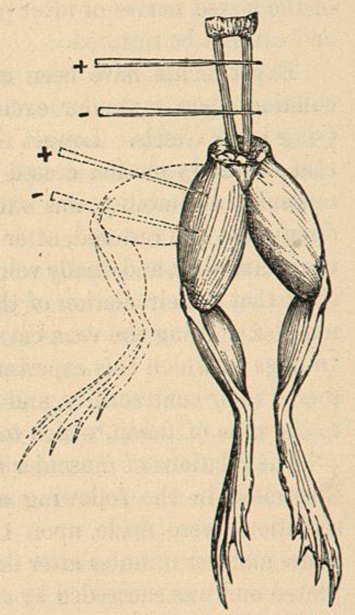

FIG. 154.—*Frog's legs prepared so as to show the effects of curare* (Bernard). Faradization of the nerves in this animal, which has been poisoned with curare, has no effect; while the stimulus applied directly to the muscles (see dotted lines) produces contraction.

ing a tight ligature around the body in the lumbar region, involving all the parts except the lumbar nerves. If the poison be now introduced beneath the skin above the ligature, only the anterior parts are affected, because the vascular communication with the posterior extremities is cut off. If the exposed nerves be now stimulated, the muscles of the legs are thrown into contraction, showing that the nervous excitability remains. Reflex movements in the posterior extremities may also be produced by irritation of the parts above the ligature. These experiments leave no doubt of the existence of an inherent and independent excitability in the muscular tissue (Bernard). Contractions of muscles, it is true, are normally excited through the nervous system, and artificial stimulation of a motor nerve is the most efficient method of producing the simultaneous action of all the fibres of a muscle or of a set of muscles; but electric, mechanical, or chemical irritation of the muscles themselves will produce contraction, after the nervous excitability has been abolished. The conditions under which muscular contractility exists are simply those of normal nutrition of the muscular tissue. When the muscles have become profoundly affected in their nutrition, as the result of section of the mixed nerves or after prolonged paralysis, their excitability disappears and can not be restored.

Experiments have been made with regard to the influence of the circulation upon muscular excitability, chiefly with reference to the effects of tying large vessels. Longet tied the abdominal aorta in five dogs and found that voluntary motion ceased in about a quarter of an hour, and that the muscular excitability was extinct in two hours and a quarter. When the circulation was restored, after three or four hours, by removing the ligature, the excitability, and finally voluntary movement, returned. These experiments show that the circulation of the blood is necessary to the contractility of the muscles. Tying the vena cava did not affect the excitability of the muscles. In dogs in which this experiment was performed, the lower extremities preserved their contractility, and the voluntary movements were unaffected up to the time of death, which took place in twenty-six hours.

The relations of muscular excitability to the circulation have been farther illustrated in the following experiments by Brown-Séquard: The first observations were made upon two men executed by decapitation. Thirteen hours and ten minutes after death, when the muscular excitability had disappeared and was succeeded by cadaveric rigidity, a quantity of fresh, defibrinated venous blood from the human subject was injected into the arteries of one hand and was returned by the veins. It was afterward re-injected several times during a period of thirty-five minutes. The whole time occupied in the different injections was ten to fifteen minutes. Ten minutes after the last injection, and about fourteen hours after death, the excitability was found to have returned in a marked degree in twelve muscles of the hand. There were only two muscles out of the nineteen, in which the excitability could not be demonstrated. Three hours after, the excitability still existed, but it disappeared a quarter of an hour later. The second observation was essentially the same, except that defibrinated blood from the dog was used and the experiments were made upon the muscles of the arm. The excitability was restored in all of the muscles, and it persisted, the cadaveric rigidity having disappeared, twenty hours after decapitation.

Muscular Contraction.

The stimulus of the will, conveyed through the conductors of motor impulses from the brain to a muscle or set of muscles, excites the muscular fibres and causes them to contract. In muscles that have been exercised and educated, this action is regulated with great nicety, so that the most delicate and rapid as well as powerful contractions may be produced. Certain movements, not under the control of the will, are produced as the result of unconscious reflection from a nervous centre, along the motor conductors, of an impression made upon sensory nerves. During this action certain important phenomena are observed in the muscles themselves. They change in form, consistence, and to a certain extent, in their constitution; the different periods of their stimulation, contraction and relaxation are positive and well marked; their nutrition is for the time modified; they develop galvanic currents; and in short, they present a number of general phenomena, distinct from the results of their action, that are more or less important.

The most prominent of the phenomena accompanying muscular action is shortening and hardening of the fibres. It is necessary only to observe the action of any well developed muscle to appreciate these changes. The active shortening is shown by the approximation of the points of attachment, and the hardening is sufficiently palpable. The latter phenomenon is marked in proportion to the development of the true muscular tissue and its freedom from inert matter, such as fat. It is the muscular substance alone which has the property of contraction; and this action increases the consumption of oxygen and probably of other matters, the formation of carbon dioxide and some other excrementitious products, and develops heat.

Notwithstanding the marked and constant changes in the form and consistence of the muscles during contraction, their actual volume undergoes modifications so slight that they may practically be disregarded. The exceeding slight change which has been observed in recent experiments (Valentin, Landois) is a diminution in volume.

Changes in the Form of the Muscular Fibres during Contraction.—All physiologists are agreed that in muscular contraction there is an increase in the thickness of the fibre, nearly compensating its diminution in length. This has been repeatedly observed in microscopical examinations, and the only points now to determine are the exact mechanism of this transverse enlargement, its duration, the means by which it may be excited, and its physiological modifications. These questions have been made the subjects of investigation by Helmholtz, Du Bois-Reymond, Aeby, Marey and others; and although it is hardly necessary to follow these experimenters through all the details of their observations, many important points have been developed, particularly by the methods of registering the muscular movements.

One essential condition in the study of the mechanism of muscular contraction is to imitate, in a muscle or a part of a muscle that can be subjected to direct observation, the force that naturally excites it to contraction. The application of electricity to the nerve is the most perfect method that can be employed for this purpose. In this way a single contraction may be produced, or by employing a rapid succession of impulses, so-called tetanic action may be excited. While the electric current is not identical with the nervous force, it is the best substitute that can be used in experiments upon muscular contractility, and it has the advantage of affecting but little the physical and chemical integrity of the nervous and muscular tissues.

There are two classes of phenomena that may be produced by electric excitation of motor nerves: 1. When the stimulus is applied in the form of a single discharge, it is followed by a single muscular contraction. 2. Under a rapid succession of discharges, the muscle is thrown into a state of permanent, or tetanic contraction. It will facilitate a comprehension of the subject to study these phenomena separately and successively.

Mechanism of a Single Muscular Contraction.—If an electric discharge, even very feeble, be applied to a motor nerve connected with a fresh muscle, it is followed by a sudden contraction, which is succeeded by a rapid relaxation. Under this stimulation, the muscle shortens by about three-tenths of its entire length. The form of the contraction, as registered by the apparatus of Helmholtz, Marey and others who have applied the graphic method to the study of muscular action, presents certain peculiarities.

According to Helmholtz, the whole period of a single contraction and relaxation of the gastrocnemius muscle of a frog is a little less than one-third of a second. The muscles of mammals and birds contract more rapidly, but with this exception, the essential characters of the contraction are the same. The following are the periods occupied by these different phenomena in the gastrocnemius of a frog:

Interval between stimulation and contraction (latent period)............	0″·020
Contraction......	0″·180
Relaxation...	0″·105
	0″·305

The latent period in man is 0·004 to 0·01 of a second, the contraction occupies 0·03 to 0·4 of a second, and the period of relaxation is a little shorter than the period of contraction. The duration of the electric current is only 0″·0008. This description represents the contraction of an entire muscle, but it does not indicate the changes in form of the individual fibres, a point much more difficult to determine satisfactorily. It is well established, however, that a single fibre, with its excitability unimpaired, becomes contracted and swollen at the point where the stimulation is applied. The question now is whether, in normal contraction of the fibres in obedience to the natural nervous stimulus, there be a uniform shortening of the whole fibre, a shortening of those portions only that are the seat of the terminations of the motor nerves, or a peristaltic shortening and swelling, rapidly running the length of the fibre.

The experiments of Aeby, which have been repeated and extended by Marey, have shown that when one extremity of a muscle is excited, a contraction occurs at that point and is propagated along the muscle, in the form of a wave. The estimated rapidity of this wave is 33 to 43 feet (10 to 13 metres) per second (Hermann). Applying this principle to the physiological action of muscles, Aeby proposed the theory that shortening of the fibres takes place wherever a stimulus is received, and that this is propagated in the form of a wave, which meets in its course another wave starting from a different point of stimulation. Although this view of the physiological action of the muscular fibres is very probable, it can not be assumed that it has been absolutely demonstrated; but it is certainly more satisfactory and better sustained by experimental facts than any other theory that has yet been advanced.

Mechanism of Tetanic Muscular Contraction.—By a voluntary effort a muscular contraction may be produced, of a certain duration and of a power, within certain limits, proportionate to the amount of force required; but after a time the muscle becomes fatigued, and it may become exhausted to the extent that it will no longer respond to the normal stimulus. This normal muscular action in obedience to impulses conveyed by motor nerves may be closely imitated by electric stimulation. When a single electric discharge is applied to a nerve, there is a single muscular contraction; but a rapid succession of discharges produces a persistent contraction, which is called tetanic.

During the passage of a feeble galvanic current through a nerve, there is no contraction in the muscles to which the nerve is attached; and it is only when the circuit is closed or opened that any action is observed. The interrupted galvanic current, the induced current, or a succession of discharges of statical electricity, when they do not follow each other too rapidly, produces a corresponding succession of muscular contractions. As the rapidity of these electric impulses is increased, the individual contractions become less and less distinct, until finally the contraction is persistent. Distinct single contractions occur with ten excitations per second, a partial fusion of the different acts takes place with twenty per second, and a complete fusion, or tetanus, with twenty-seven per second (Marey). When the contraction becomes continuous, there is an elevation of the line marked on a registering apparatus, showing increased power as the excitations are more and more rapid. This is artificial tetanus; but it probably is the kind of contraction that occurs in the physiological action of the voluntary muscles.

It is probable that the normal nervous stimulus in voluntary muscular action is a succession of impulses, which produce a power of muscular contraction that is proportionate to their rapidity. Vibrations, which are more or less regular, actually occur during the contraction of muscles (Wollaston, Haughton, Helmholtz). Helmholtz, indeed, has recognized a musical note produced by contracting muscles, which exactly corresponds to the number of excitations per second applied to the nerve. This can be heard in the temporal and masseter muscles by filling the ears with wax and causing these