Chapter I

GENERAL CHARACTERS OF MUSCULAR TISSUE

§ I. *TYPES OF MUSCLE*

A muscle consists essentially of a bundle of elongated fibres, each of which may be considered as a syncytium of cells and each of which is functionally a single unit. Generally each fibre is functionally distinct from its neighbours so that any one fibre can be excited by itself without the excitation spreading beyond that fibre. The characteristic sign of the special function of muscular tissue consists in shortening and developing tension on excitation by an appropriate stimulus and in subsequent relaxation to the original length and tension. Other functions may be superimposed upon this kind of response, but it may be treated as the type.

Different muscles differ *morphologically* with respect to:

(1) Their origin in the embryo;
(2) Their anatomical position and structure;
(3) Their histological appearance;
(4) Their chemical composition;
(5) Their nerve supply;

functionally with respect to:

(6) The type of stimuli to which they are sensitive;
(7) The type of response to stimulation.

(6) and (7) might be further subdivided. Thus muscles may differ in their time scale, as for example insect's wing muscles and tortoise's heart muscle. More important still, they may differ according to whether they are spontaneously active, that is, whether internal changes may act as stimuli, or not, as for example frog's heart muscle and skeletal muscle.

In attempting to classify muscles it is convenient to consider first vertebrate muscle, particularly mammalian muscle, about which we have considerable knowledge, and consider two strongly contrasted types; then it will be found that most types of muscular tissue in the animal kingdom resemble one or other type or are intermediate. First then consider two types of mammalian muscle which we may call *skeletal* and *visceral*. These are distinct embryologically and anatomically, if we confine our attention to typical cases and neglect doubtful or intermediate ones. They are also distinct according to the other criteria enumerated.

SKELETAL MUSCLES OF HIGHER VERTEBRATES

Taking *skeletal* muscle first, as it is found in the body. A Mammal or any other *walking* animal is mechanically an articulated girder structure, of which the skeleton forms the system of *compression members* and the muscles (along with certain other structures) the *tension members*. The muscles are not only the *prime movers* of the body but also the *tension members* on which the body as a static structure depends. That is to say, they are necessary to maintain bodily posture in the gravitational field. The muscular tensions, *tonus*, by which posture is maintained, are smaller than the tensions developed during movement, but they are maintained for long periods with small expenditure of energy. In considering skeletal muscle, and any other sort of muscle, the function of maintaining *tone* cannot be neglected. Mammalian skeletal muscles differ in type among themselves, are not homogeneous structures (excluding non-muscular material such as tendon and blood vessels), and lastly are part of a highly specialized neuro-muscular system. Taking these points in order, muscles have been distinguished as red and white, and the distinction is found to correspond more or less to the amount of use the muscle has, as for example the wing muscles of fowl and pigeon or the leg muscles of hare and rabbit, and also to certain histological differences. The differences are not constant; for instance, wild rabbit's muscle is redder than tame and it is said that among men, the muscles of athletes are redder than those of old or sedentary individuals. Further, histologically all mammalian muscles are seen to be mixed, and the increase that follows use is seen to be due to hypertrophy of existing cells not to growth of new ones. Continual use apparently tends to bring about an increase in the "sarcoplasm" of the muscle fibre and among other things an increase of haemoglobin, the red pigment. Though one may still ask, Why are the frog's leg muscles white and the tortoise's red?

COMPLEX STRUCTURE OF SKELETAL MUSCLES

This brings us to another point, that histologically mammalian skeletal muscle is complex, as is nearly all muscle of similar character. Fibres, usually thin, with a granular appearance, can be distinguished from large, more translucent ones. The former are usually more pigmented and are more numerous in typical red muscle. There is a certain degree of correlation between pigmentation, granular fibres and constant use. Generally also the red type is more slowly moving (see Knoll, 1891; D. M. Needham, 1926). It must be pointed out however that Greene (1926) finds that the dark (red) muscles under the skin of the Pacific king salmon (*Onchorynchus tschawytschia*) are functionally degenerate compared with the pale (pink) muscles, but are full of fat and apparently act as fat depôts. Probably the dark muscle of other fishes is similar. Altogether too much stress should not be laid upon the distinction between red and white muscle or the two types of muscle fibre, except to recognize the fact that the muscle is a complex tissue.

In addition to the two types of fibre already mentioned there is a third most important structure belonging to the muscle tissue proper, the *muscle spindle*. This, as Sherrington has shown, is a sense organ developed in connection with a specialized muscle cell (see Cobb, 1925). The special significance of these structures in relation to muscle *tone* will be referred to later, suffice to say at present that it is characteristic of mammalian skeletal muscle to have no spontaneous activity apart from stimulation through its motor nerves. The reflex response of the muscle to passive tension is regulated by means of the muscle spindles as *affector organs*. Whereas visceral muscle represents an unspecialized, possibly primitive, system which is to a large extent self-regulating and only casually dependent on the central nervous system, the skeletal muscle is entirely bound up with it. This of course explains the fact that the isolated skeletal muscle only reproduces some of the activities of the intact organ; by isolating it we have destroyed the *afferent* side of the system of sense organ, nerve and muscle which exists in the body.

A further point to be mentioned is the still-vexed question of the *autonomic nerve supply* to skeletal muscle, on which subject see Hines (1927) and Fulton (1926, Chap. XVI). The nerve supply to a muscle carries (*a*) *myelinated fibres* which are *efferent* and come from the *anterior nerve root*, (*b*) *myelinated fibres* which are *afferent* from the *spindles* and go through the *posterior root* into the cord. In addition there are (*c*) *non-myelinated fibres*, not only those going to blood vessels but almost certainly to the muscle fibres themselves and ending in special types of nerve ending. Their function is still a matter of controversy, some workers suggesting that they are responsible for the maintenance of *tone* (see Cobb, 1925).

HISTOLOGY OF SKELETAL MUSCLES

A histological feature of skeletal, and some other muscles, to which much attention has been drawn in the past, is the appearance of *cross striation* in the fibres. The fact that many muscles are not cross striated shows that the structures giving this appearance, whatever they are, are not a necessary part of the contractile mechanism. They are more probably a special modification of the contractile mechanism for special functions. We may therefore dismiss all theories of muscular contraction based, as many have been, on the detailed microscopic appearance of the cross striation of certain kinds of muscle. It must be remembered too that the details of the cross striated structure are of a size near the limits of microscopic vision so that the visible appearances may be delusive. Haycraft (1891) was able to obtain all the appearances of cross striated structure, except those depending on the birefringence of the muscle, by taking casts in collodion from the surface of muscles. He considered that the various structures described by histologists were the optical results of a very fine surface varicosity of the fibres. These observations have been ignored by most histologists, but they seem to merit serious consideration.

In general, cross striation is most conspicuous in the most rapidly moving muscles, such as insect's wing muscles. The most plausible suggestion yet made is therefore that of Hill (1926) that cross striated muscle has an arrangement comparable to "baffle plates" set across the length of the fibre to reduce the amount of flow of the semi-liquid contents. Loss of energy by internal friction in the muscle is the chief source of lowered mechanical efficiency when the rate of movement is increased. If the muscle fibre were like a hollow tube with the walls thickened at intervals, this would account for the cross striated appearance and be compatible with Haycraft's observations, supposing there was a swelling corresponding to the "baffle plates". For further information as to the histology of muscle the reader should consult Schafer (1912).

FUNCTIONAL CHARACTER OF SKELETAL MUSCLES

Functionally it is characteristic of skeletal muscles in contrast to other types to show no spontaneous activity when denervated. They are not very extensible, and stretching does not act as a stimulus. They are stimulated by electric currents of short duration but require fairly high potentials to excite them; in particular they are more readily excited by single shocks from an induction coil than any other type of muscle. They have a short *refractory period* so that repeated stimulation of suitable frequency gives rise to fused contractions (*tetanus*). They can develop high tensions and their response to stimulation is rapid. In the last respect muscles from different animals and even different muscles from the same animal vary greatly, for example, the rapid twitch of frog's leg muscles and the much slower response of the muscles of the abdominal wall.

VISCERAL MUSCLES OF HIGHER VERTEBRATES

The visceral muscles are contrasted with the skeletal muscles in nearly every respect. The muscular tissue of the alimentary canal may be taken as the type. This consists of sheets or layers of contractile cells forming part of the wall of a tube or sac. The muscle cells in different layers may run longitudinally, circularly or diagonally. The general effect of their contraction is to exert pressure on the contents of the organ and change its shape. The muscles of this type are distinct from the skeletal muscles also in their origin in the embryo and their histological character; they are not cross striated. They have generally a double nerve supply which consists of *non-medullated* fibres of the *autonomic system*. They are nearly always spontaneously active apart from nervous stimulation, with a tendency to rhythmical movements and also to tonic contraction; some muscles produce one type of effect, rhythmic or tonic, more markedly than the other. Spontaneous activity and double innervation must be closely connected. Skeletal muscle which is inert by itself needs only excitation and therefore one set of nerve fibres. Spontaneously active muscle if it is to be controlled needs both inhibition and augmentation, therefore, two sets of fibres.

It is not necessary to decide whether the spontaneous activity of the musculature of the alimentary canal is really a function of the muscle fibres themselves or, as is possible, of the nerve net found in close contact with the layers of muscular tissue. The important point is that the organs and the experimentally separable parts of the organs are spontaneously active apart from external stimulation, nervous or otherwise. The minor question as to the exact *locus* of the self-excitatory process cannot be settled except by the actual separation of muscular and nervous elements.

A peculiarity of some visceral muscles is that conditions which excite when relaxed (passage of gas bubbles, mechanical stroking of surface, some kinds of electrical stimuli, adrenaline) produce relaxation when the muscle is in a state of tonic contraction (Evans, 1926, 2). This may be a consequence of double innervation, depending upon the inhibitor nerve endings being more excitable during prolonged activity and the augmentor nerve endings during rest. Compared with skeletal muscle the visceral muscular tissue is usually more extensible, and stretching acts as a stimulus, or at least increases excitability. Electric currents need to be of longer duration to stimulate, the response is generally more prolonged, and the tensions developed are much smaller.

So far we have been considering typical skeletal and visceral muscles of a Vertebrate, more particularly a Mammal, and emphasizing the differences; but there are a good many muscles in the body of an intermediate type. As Cobb (1926) says, "In fact it seems that no sharp lines can be drawn between the different types of muscle. *Smooth muscle* and *striated muscle* seem different enough but when one considers the muscles of the eyeball, larynx, tongue, diaphragm and heart it is difficult to see where to draw the dividing line between two obviously different extremes". And he goes on to quote some other authorities for his views. The view which will be maintained in what follows is that there is no *fundamental* difference between any muscles, but that the differences are differences of degree. The muscles of vertebrate limbs are specialized for rapid movement, the production of large tensions, complete central control and considerable delicacy of control, as witness the control of the human fingers. The muscles of the intestine are specialized or perhaps they are primitive, but at any rate they carry out slow movements involving small stresses, they are automatic for the most part and only controlled in a general way by the central nervous system. That is to say, the central nervous system augments or inhibits but the actual type and course of movement is dictated by local conditions and largely by the state of the tissue itself. Therefore we may say that muscles differ chiefly in respect to:

Time scale—rapidity of response as determined by time relations for electrical stimulation, latent period, refractory period, duration of the two phases of the mechanical response.

Intensity of response—measured by tension developed per unit cross section with maximal stimulation, or amount of chemical change per unit mass.

Degree of automaticity—including not only tendency to spontaneous activity but the kind of connection with the central nervous system.

Histological and other structural characters may be considered as of minor importance unless they are diagnostic of functional character. It must be remembered that muscles of widely different functional character are grouped together as "smooth muscle" for no better reason than mere absence of visible cross striation.

The vertebrate heart is an interesting and highly specialized type of muscle intermediate in character between the skeletal and typical visceral muscle. An important feature of heart muscle is that the whole organ is functionally a *syncytium*, so that the excitation of one part tends to excite the whole organ. At the same time different regions contain muscle cells of very different physiological character as regards excitability and type of response—compare the spontaneously active tissue of the *sinu-auricular node* of the mammalian heart with the *ventricular* tissue.

The *retractor penis* of the dog is an unstriated muscle of an interesting type approaching that of skeletal muscle (Winton, 1927).

MUSCLES OF INVERTEBRATES

Leaving the vertebrate group of animals we find that the musculature of the Arthropods presents no great difficulty in classification, their limbs are moved by typical skeletal muscles and the intestines by typical visceral muscles, and there are intermediate types. The heart muscle in particular shows interesting variations. The heart of *Limulus* shows in its loss of automaticity an approximation to the skeletal type, while the crustacean heart, like that of the Vertebrate, approximates more to the visceral type. Outside these two great Phyla we find classification more difficult. The body muscles of the Cephalopods among the Molluscs and the adductors of the shell of the Lamellibranchs may be considered as skeletal and the rest visceral. When we consider the Annelid Worms there is little to go upon. The earthworm for instance possesses no skeleton and none of its muscle is striated. We might either (1) on general morphological grounds treat the body muscles as skeletal and the gut muscles as visceral, or (2) on histological grounds treat them all as visceral, or (3) consider that they all represent more primitive undifferentiated types. Without more complete investigations a choice cannot be made between these alternatives.

§ II. *CHEMISTRY OF MUSCULAR TISSUE*

The chemical composition of muscles is fairly characteristic, and in certain cases at least functional differences between different muscles can be correlated with differences in chemical composition. On the other hand, the chemistry of many substances found in muscles is imperfectly known and many constituents have no recognized function.

Muscular tissue of the mammalian skeletal type is composed, as regards main constituents and in round numbers, as follows:

Water	75%
Soluble material (not protein or carbohydrate)	3–5%
Carbohydrate	1%
Fatty acid (minimum)	½–1%
Protein	18–20%

In many muscles the fat contents will be higher owing to storage fat. *Cholesterol* in small amounts is always present. In visceral vertebrate muscle there is more water and less protein, and as little as 12 per cent. protein in some Invertebrates.

INORGANIC CONSTITUENTS

The inorganic salt content varies in different animals according to the general level of salt content. For instance, the muscles of marine Invertebrates will be isotonic with sea water and have an osmotic pressure about five times that of frog's muscle. As in most tissues, the potassium content of muscle is high and the sodium relatively low. In Table 1 are given some figures for the ash analysis of various vertebrate muscles. They are taken from a review of the chemical composition of muscle by Costantino (1923). In skeletal vertebrate muscles hardly any of the phosphorus is present as inorganic phosphate. Part is ether-soluble, probably *phosphatide* phosphorus; the rest, which is water-soluble, is "organic phosphate", partly phosphate esters. In vertebrate visceral and some invertebrate muscles there is relatively more inorganic phosphate.

Table 1

Inorganic Constituents of Vertebrate Muscle
mg. per 100 gm.

Species	Tissue	K	Na	Ca	Mg	Fe	P	Cl	S	
Ox (*Bos taurus*)	Skeletal (Beef steak)	366	65	2	24	25	170	57	187	(1)
	Smooth (*Retractor penis*)	267	109	9	12	2	113	128	217	(2)
Fowl (*Gallus indicus*)	Skeletal white	410	89	—	—	—	251	26	—	(3)
	Skeletal red	373	77	—	—	—	241	33	—	(3)
	Stomach	356	72	—	—	—	182	84	—	(3)
Frog (*Rana catesbiana*)	Skeletal	350	54	28	30	10	155	66	141	(4)
	Smooth	325	73	4	13	0·7	137	120	161	(4)

References: (1) Katz, 1896; (2) Costantino, 1911; (3) Costantino, 1912; (4) Meigs and Ryan, 1912.

The organic extractives are a miscellaneous group of water-soluble substances mostly of unknown function. Among them *creatine* is conspicuous in vertebrate muscle, which may contain

1 per cent. In the elasmobranch Fishes nearly 2 per cent. of *urea* is present. For the special problems concerned with creatine the reader should consult Hunter's review (1922), and book (1928). It is conceivable that the functions of the living cell call for a certain concentration of diffusible non-electrolytes and that creatine, urea, and the other soluble innocuous organic substances found in muscles fulfil this need. The creatine, however, is partly combined and may have special functions (see p. 11). Among the organic extractives *lactic acid* is sometimes included, but this substance is present during life in minimal quantities, is related to the carbohydrates, and has a special function which will be discussed later.

Inositol is generally present, and may be connected with the carbohydrates (see pp. 50, 51 and also J. Needham, 1926).

CARBOHYDRATES

Of the carbohydrates *glycogen* is the most important and abundant. It has been found in every type of muscle that has been properly investigated. Cases are reported in the literature where glycogen appears to be absent in muscle, but these results are almost certainly due to workers not realizing the rapidity of *post mortem* glycogenolysis, and to the difficulties of analysis where low concentrations are concerned. The amount varies from about 0·1 to 1 per cent. in most muscles. In vertebrate muscle there is a rough correlation between normal glycogen content and degree of muscular activity. In some Invertebrates as in bivalve Molluscs and Nematode Worms considerable quantities (2–3 per cent.) of glycogen are found in muscles and other tissues. The high glycogen content is not connected with excessive muscular activity but is storage material; these animals store glycogen rather than fat and have no specialized tissue or organ for the purpose. Among Crustacea glycogen is stored in the muscles in preparation for the moult and is used up in the process (the muscle tissues as a whole seem to degenerate also). As glycogen is not a well-characterized substance it is difficult to decide whether it is identical throughout the animal kingdom, but Harden and Young (1902) in their very careful work could find no evidence of difference between specimens from yeast, oysters and rabbit's liver.