CHAPTER 8

SOME GENERAL CONSIDERATIONS

Certain excellent works on the myology of birds have been referred to at various places in the present studies and their importance in the study of muscle homology has also been stressed. In such studies, however, main emphasis is laid on the complex problem of muscle homology and fuller information regarding the working of the muscle could hardly be expected. Usually in myological studies the action of the muscle is determined by exerting a pull on one end of the muscle in a preserved animal. Howell(1946) pointed out the limitations of such a method and stressed the importance of electrically stimulating the muscle of the anaesthetised animal in order to obtain a better interpretation of muscle function. Fisher (1946), in his excellent work on the locomotor apparatus of new world vultures, made a special study of muscle volume to determine the relative functional importance of different muscles in different birds having close phylogenetic affinity and correlated such differences with the flying habits of those birds. Nair (1952, 1954a &b) was one of the few to study ~~the~~ avian flight muscles from mophological as well as biochemical points of view. He determined the chemical composition of the pectoral muscles of several Indian birds, and emphasised the variations as an index of muscle power (1952) and brought to light certain morphological differences between the wing musculature of flapping and soaring birds(1954a).

He (1954b) also studied the relation between body weight and the weight of the pectoral muscles in birds exhibiting different modes of flight and advanced ? put forth some interesting ideas regarding muscle power in birds. Marey's approach (1893) to the functional aspects of the flight muscles was a direct one. He used elaborate instruments attached to flying birds and recorded movements of some muscles during flight. Brown (1948, ~~&~~ 1953), with the help of cinematographical pictures of flying birds, studied the different successive steps in bird flight and made some comments on the role of different flight muscles in the successive phases of flight. Numerous apparatus devised for direct studies in cursorial and aquatic animals are, however, of little use for similar studies on birds. In this respect Marey's approach, though remarkable, could not be followed by later workers, owing to innumerable difficulties associated with handling such instruments.

Studies on the structure of muscles other than those of birds have yielded considerable information on (muscles) function. The present study, though confined to a single muscle, has shown some ? (evinced sufficient) promise of fruitful possibility in such an approach to the study of the functional aspects of avian flight muscles. Like the *pectoralis major*, other flight muscles ~~too~~, have undergone structural modifications according to their individual requirements. In the pigeon the important and well developed muscles of the pectoral girdle — *supracoracoideus*, *coracobrachialis posterior*, *subscapularis*, *dorsalis scapulae* and serratus posterior (terminology adopted from Fisher, 1946) and all the muscles of the upper arm except brachialis are mixed muscles. On the other hand, all the muscles of the forearm except extensor metacarpi radialis have only one type of fibres (red) with remarkable uniformity in fibre diameter.

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On the Similarly other hand, all the flight muscles of the kite, excepting those used merely for the movements of feathers, consists of only red fibres, with less variation in average diameter. In short, ~~the structure of the~~ other flight muscles, have undergone structural modifications similar to those of the pectoralis major, and these ~~structural~~ modifications can be correlated with function, if those of the pectoralis are correctly understood.

It is always advantageous to study the structure of a single muscle in many different birds rather than of many muscles in a few birds. The advantage of such an approach is obvious, when we consider~~ing~~ the fact that no two muscles in the animal body are ~~for~~ identical in function and mode of action. On the other hand, the homologous muscles of different animals (provided they all belong to a single natural group) have the same function, the only difference being the manner in which the work load is handled. With one variable, such as the function of the muscle thus eliminated, the study of the action of the other variables, namely the structure of the muscle, could be studied ~~with~~ to better advantage. The study of the pectoralis major, as presented in this work, if extended further to many more birds and a similar study if conducted on the other

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flight muscles also, should go a long way in our understanding of the functional aspect of flight. The possible chances of success in such an enterprise could also be realised from the work of Burger (1956) on the structure of the *expansor secundariorum* of birds.

From the present findings, it appears that the diameter of the fibres plays a more important role than hitherto realised and that for stability as well as mechanical efficiency an optimum size for the fibres is necessary. Bigger diameter, evidently, gives mechanical advantage to the contractile mechanism. On the other hand, in fibres with smaller diameter, the rate of diffusion of dissolved substances is comparatively higher and such fibres are of great advantage in long and sustained action. The pectoralis of flying birds in general should be powerful and at the same time adapted for sustained action, but there is considerable variation with regard to these two important aspects of muscle action in birds differing in their mode of flight. In birds exhibiting soaring and flapping types of flight a compromise appears to have been reached in the structure of the pectoralis to get maximum efficiency out of these two divergent functional aspects of muscle action; the fibres of the pectoralis of these birds have neither too big large nor too small a diameter, the rate of increase of which with the increase in the weight of the muscle, is low. In the first chapter it has been shown that the fibres in the pectoralis of kite are large. ~~and~~ On the basis of the study under in chapter five, the large size of the fibres could be attributed to the bigger larger size of the animal.

In the birds exhibiting shooting type of flight the rate of increase in the fibre diameter per increase in gram weight of the muscle, is higher. In the flight of these birds, a phase of quick wing strokes alternates with a short phase during which the wings are flexed and the bird looses its altitude, which is then regained only with the commencement renewal ? of the first phase. That is why the wing strokes are quicker and more powerful in these types of birds than w those of the flapping type of fliers, whose wing beats are regular and altitude is gained with every down stroke of the wings (Brown, 1948). Thus in shooting types of fliers more emphasis ~~is~~ is laid on quick and powerful action. The Heavier the bird, the greater the need for powerful strokes (is all the more greater), ~~and~~ for which an increase in fibre diameter per increase in gram weight of the muscle is of distinct advantage. With the increase in fibre diameter the decrease in the rate of diffusion of soluble substances in the pectoralis of these birds seems to have been compensated for by the second phase of having the wings flexed. But in this type of bird~~s~~, if with increase in the size of the muscle and an increase in the diameter of the fibres a bird with the size of a kite were to perform the shooting type of flight, muscle fibres of enormous size would have been required. This would have enforced such great limitations on the diffusion of substances in the muscle fibres that a short period of recovery, such as could be achieved

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during the second phase of the shooting flight when the wings are flexed, would not have been sufficient. Perhaps this may be one of the reasons why this type of flight is exhibited only by small-sized birds.

The fowl and partridge, when chased, take short low flights during which the wing strokes are heavy and quick (and thus so that in the pectoralis major, fibres with bigger diameter are of distinct advantage. The rate of increase in the diameter of the fibres per increase in gram weight of the muscle is ofcourse low. Lower concentration of the oxygen carriers like myoglobin and cytochromes and slow rate at which the lactic acid is removed (due to greater fibre diameter) during contraction, should prevent sustained action in these fibres.

However, nothing is known about the nature of the fibres in the breast muscle of non-flying water birds, which use their wings as paddles working in unison with their legs to propell them through water. In these birds the manner in which the work load is handled by the pectoralis major is considerably different from that during flight; the wing strokes in these birds are no longer comparable with those which make the flying bird air-borne. In the Ratitae too, the wing flaps during running on the ground are only to give a forward accleration. In this respect they too also differ very mush from the gallinaceous birds.

The validity of the common practice of classifying muscles as 'red' and 'white' has been put to extensive test during these investigations, and it can now be said that such a classification indicates nothing except the colours of the muscle fibres. Among red fibres themselves two types are met with, one in which there is high amount of fat but little ~~of~~ glycogen (e.g. the red fibres of the pigeon pectoralis), and ~~the~~ an other type, in which both glycogen ~~as well as~~ and fat are present in large amounts (e.g. the fibres in the superficial layer of the kite pectoralis). An alternative scheme of classification of muscle on the basis of certain histophysiological properties is suggested as follows:

a. Muscles having only white fibres with high or moderate amounts of glycogen (load) but with negligible fat inclusions for ~~the~~ quick contractions of short duration, e.g. fowl.

b Muscles with only red fibres having a large amount of fat inclusions but little ~~of~~ glycogen, primarily for sustained isometric contractions, e.g. parakeet.

c Muscles with red fibres having glycogen as well as fat in large amounts, for tonus action thus well equipped for sustained isotonic contrations, e.g. kite.

d Mixed type of muscles having white, glycogen-loaded, and red, fat-loaded fibres occurring side by side, e.g. pigeon.

The problem of the mixed type of muscle in which distinctly different types of fibres coexist as parts of a single system and working in unison as units of an integrated organ seems to be of paramount importance, not only with respect to the study of muscles of birds but also for a closer understanding of the general problem of muscular contraction. The mixed type of pectoralis, as well as pectoralis with only one type of fibres, occurs in birds with diverse flying habits. However, one could reasonably expect something in common about the mode of action of the pectoralis of birds like the hawk, kingfisher, and pigeon in having the mixed type of pectoralis, even though they differ widely in their mode of flight. But we have no means of knowing it at present. However, the present work has yielded some very encouraging results, which have brought this baffling problem of mixed type of muscles to the forefront in a new perspective. The pectoralis of the pigeon and dove with red and white fibres of sharply divergent types forms an excellent material for studying the various aspects of this problem. The high amount of fat and mitochondrial inclusions in the narrow fibres and higher glycogen content and extreme low amount of fat and mitochondria in the white fibres and their implications on muscle physiology have already been discussed. George and Scaria (1958) showed that the activity of dehydrogenases is very high in narrow fibres but in the broad ones they are hardly detectable with histochemical methods. Lipase and alkaline phosphatase too are concentrated primarily in the narrow fibres. ~~The~~ Alkaline phosphatase probably plays an important role in fat metabolism (Montagna, 1956). George and Pishawikar (unpublished) showed that creatine phosphate, ATP and ATPase, are present in very high concentrations in the broad fibres in comparision to the narrow ones. Inorganic phosphate and certain free amino acids like glutamic acid too, are in high concentration in narrow fibres (George and Pishawikar, unpublished).

On stimulation, creatine phosphate in broad fibres gets depleted very rapidly with the result that in the stimulated muscle the red and white fibres show no difference in the concentration of the creatine phosphate (George and Pishawikar, unpublished). In the light of these ~~above~~ observations, the negligible dehydrogenase activity in the white fibres of the pigeon and dove pectoralis presents a complex problem, as to how the energy-rich phosphates are built up in them in such high concentration for which the Krebs cycle enzyme systems including the dehydrogenases are so far known to be absolutely necessary. The present work does not provide a solution to this problem but nevertheless suggests some possibilities which might be of help to future research in obtaining satisfactory answers. Perhaps the energy-rich phosphates in the white fibres may regenerate in any one of the following ways:

1. Probably dehydrogenases in the white fibres, even if in small amounts, may be sufficient for building up a high amount of energy-rich phosphates during the period of rest. Since the rate of regeneration of energy rich phosphates in these fibres should be very low, once the reserve store

of energy in the form of energy-rich phosphates is depleted during the process of contraction, these fibres can no longer contract and cope up with the narrow fibres. In the narrow fibres, though the energy-rich phosphates are not built up in large amount during the period of rest, the chemical processes that regenerate these energy sources are very well organised so that they can be regenerated continuously in sufficient amount during the process of contraction. This leads to the conclusion that only during the initial phase of flight, that is, during the take off from the perch when the wing strokes are heavy and of maximum amplitude, the broad fibres take part in active contraction and once the energy-rich phosphates are depleted they remain passive in a state of (somewhat akin to) fatigue, and the narrow fibres alone undergo the process of contraction till the broad fibres are once again fit to contract.

2. Another possibility is that, due to bigger size, the broad fibres have a greater mechanical advantage and a higher dynamic power per gram weight than the narrow fibres. Following this assumption, which is based on the work presented in this thesis, it can be visualised that for the same amount of work done, the broad fibres have a lower energy consumption than that ~~of~~ do the narrow fibres, and thus in these fibres the rate of regeneration of the energy-rich phosphates, even if low, may be sufficient for the sustained contraction.

3. Yet another possibility is the presence of an alternate pathway for the regeneration of energy-rich phosphates

in broad fibres. At present the energy rich phosphates are known to regenerate only through the Krebs cycle enzyme system, in which dehydrogenases form important links. This assumption presupposes the presence of an alternate pathway, in which various dehydrogenases are not absolutely necessary for the regeneration of the energy-rich phosphates. So far, no such pathway has ever been reported in any living system. This suggestion is ~~rather~~ more philosophical than scientific, and is merely a reflection of our lack of knowledge.

The problem is indeed a complex one. Our tools of research have to be prudently employed in obtaining the right answers. Often our methods are unable to give a true picture of the actual processes and from the data obtained, we are led to visualize certain functions of the machinery without having any idea at all, as to what exactly happens in the living system. In concluding, I can do no better than quote Green as follows; " A sufficiently ingenious mechanic could separate the parts of a baby Austin and use them to make a perambulator or a pressure pump or a hair-dryer of sorts. If the mechanic was not particularly bright and was uninformed as to the source of these parts, he might be tempted into believing that they were infact designed for the particular ends he happened to have in view. The biochemist is presented with a similar problem in the course of his reconstructions. The materials of the cells offer unlimited possibilities of combinations and interactions, but only a few of these possibilities are realised in the cell under normal conditions. There is thus a grave element of risk in trying to reason too closely from reconstructed systems to the intact cell. The reconstruction can have no biological significance until some difinite counterpart of these events is observed *in vivo*." (as referred by Baldwin, 1957)