PROCEEDINGS OF THE NUTRITION SOCIETY

FORTY-EIGHTH SCIENTIFIC MEETING

ROYAL SOCIETY OF MEDICINE, LONDON

17 JULY 1948

THE NUTRITION OF ATHLETES

Chairman: PROFESSOR J. R. MARRACK, *London Hospital Medical College, Whitechapel, London, E.* 1

The Neuro-Muscular Mechanism

By P. EGGLETON, *Department of Physiology, University of Edinburgh*

The neuro-muscular mechanism is a very large subject to talk about in the half hour I have at my disposal, and it would be impossible in the time, even if I had the knowledge, to do justice to the whole subject. I shall accordingly speak in the main about voluntary muscles, which have been the subject of by far the greatest amount of work, and leave hardly touched the field of work on the co-ordination of movement in the cerebellum, which is very intimately concerned in athletics.

The structure of muscle

The neuro-muscular mechanism is certainly a highly elaborate structure. Basically its unit is a muscle fibre anything up to 2–3 cm. long, characterized by alternate bands of substance distinguishable in polarized light as isotropic and non-isotropic, respectively. Several million of these go to make up a muscle, and the chemist would regard his work as finished if he could describe the events occurring within a single fibre during and after a bout of activity. But a complete description of the function of the muscle entails reference to considerably more architecture than this. First there is the blood supply, entering by an artery which divides and divides to form a capillary bed. The whole muscle is permeated by capillaries so fully that in an active muscle no capillary is farther than 20μ. from its nearest neighbour. Correlated with this circulation is the lymphatic drainage about which considerably less is known definitely because of the extreme difficulty of identifying the smaller lymph channels in the tissue. Then there is the nerve supply. The motor nerve trunk divides on entering the muscle until fibres reach every muscle fibre. Each nerve fibre ends in a neuro-muscular junction and, according to present-day beliefs, an incoming stimulus causes the production of acetylcholine at this junction, which in turn initiates the contraction in that part of the fibre to which it is attached; but no less important to the survival of an animal is the sensory nerve trunk also ramifying within the muscle and ending in the stretch receptors which estimate the state of elongation or strain in the muscle and convey the information to the central nervous system. The motor nerve is indeed always in direct reflex connexion with these proprioceptive sensory endings. This proprioceptive mechanism has no access to consciousness; it is limited to spinal and cerebellar pathways. A different set of sensory fibres registers pain, and we should not overlook the sympathetic nerve fibres, serving the purpose of controlling the calibre of the arterioles in the muscle substance and thus controlling the supply of blood. Each one of these systems, muscle fibres, blood vessels, motor and sensory nerve fibres, lymphatics, is ramified through the muscle, so that within any cu. mm. of the muscle tissue can be found elements of each. Finally, the whole is set in a matrix of connective tissue which provides the necessary mechanical continuity.

The mechanism of muscular exercise

Physiological studies on the mechanism of muscular exercise fall into three clear-cut categories. First, there is the work on intact animals, including man. Such work is almost entirely restricted to the dog and man, for it generally entails conscious co-operation on the part of the subject. There is, indeed, no finer guinea-pig for the study of exercise in the intact animal than a volunteer athlete. Such work is, of course, limited to measurements that can be made without pain or injury, that is to say, principally to respiratory measurements, urine and blood analyses, nutrition studies and mechanical measurements of work done. The second category of work consists of studies of isolated muscles and nerves, and for this the mammal is not generally suitable, because of the difficulty of maintaining the isolated tissue in a good condition without so much necessary apparatus that the preparation is apt to be buried under a pile of iron-mongery. We find, however, that such studies can be made on the muscles and nerves of cold-blooded animals which in favourable cases can survive many hours after isolation, and of such preparations the leg muscles of the frog are, for economic reasons, usually chosen, though some valuable work has been done on preparations such as the foot muscle of the snail, *Helix pomatia*, and the muscles of certain marine shellfish. From the standpoint of the present meeting all such work suffers from the disadvantage that the results may not be applicable without some modification to the human case. One such difference, for example, between the frog and the mammal appears to be the site of resynthesizing of glycogen from lactic acid, and another difference is that invertebrates appear to have no creatine in their muscles. The amino-acid, arginine, appears to serve the same purpose. The last category of work consists in the study of extracts of muscle and nerve tissue used as mixed enzyme systems. Muscles from almost any source can be used for such work; the pectoral muscle of the pigeon and the leg muscles of the frog have both been extensively used, and the relevance of the results so obtained to the problem of human exercise is even more risky, for the occurrence of some process in a disorganized tissue extract is no proof that this process is a normal chemical concomitant of the original tissue—in the remains of a smashed-up motor car a number of chemical processes might well occur, such as the solution of the tyres in the petrol, which have no place in the normal metabolism of a motor car.

Nevertheless, it is a matter for congratulation that, in point of fact, the findings of the workers in these three fields of research combine to produce a picture of the neuro-muscular machine, which comes nearer to the physiologist's ideal, a description of physiological phenomena in terms of chemistry and physics, than has been achieved in respect of any other branch of physiology, save perhaps the transport of gases by the blood.

Food and energy output

To take first the results of studies on the intact human being: it is a matter of economic consequence that a manual labourer requires more food in proportion to his output of work, the upper limit being a food intake some three times the requirement usually referred to as basal or characteristic of a completely resting individual. It was the experience of administrators in the Ruhr district during the past 2 years or so that the coal raised by miners was a simple function of the amount of food they could get to eat, and although this relationship is almost certainly not a simple matter of thermodynamics, but involves the questions of psychology as well, yet it would be interesting to have figures for the relation between food intake and mechanical work done in such an industrial setting. Much evidence, however, goes to indicate that a robust man can metabolize an extra 4000 Cal. of food in a working day, and a performance of manual labour on this scale raises the interesting question whether one variety of food is better than another in making up these 4000 Cal. There is much evidence derived from work on muscles and muscle extracts to indicate that carbohydrate is the main fuel of exercise, but there is also evidence that such manual labourers do not in fact choose to eat carbohydrates, but show a decided preference for fat and protein. Indeed, the firm belief, fixed in the minds of athletes as well as labourers, that meat is of great value in the performance of muscular work, must be taken into account; for whereas it may prove to be a psychological error, a survival perhaps of sympathetic magic, yet it may have justification in the sense, for example, that meat is a good source of vitamins of the B group, and one of these at least is essential to the metabolism of carbohydrates; or it might be a source of creatine (see p. 253). A liking for fatty food on the part of manual labourers and all the inhabitants of very cold countries may be related to its high energy content and the limited size of the human stomach.

Oxygen intake and energy output

Whatever be the optimum mixture of foodstuffs, the limit to the abilities of our muscular mechanism regarded as an engine is about 4000 Cal./day, and if this effort is spread over 12 hr. it implies an energy development of 5–6 Cal./min. Now it was found by A. V. Hill and his associates that men, running at a pace which they could keep up without getting into mounting respiratory difficulties, utilized oxygen at the rate of about 4 l./min., the calorific equivalent of which is more like 20 than 5 or 6 Cal. Hill's experiments, however, were almost all confined to periods of minutes, and it is clear that, although 4 l. of oxygen can be pumped into the body by the heart each minute, when necessity drives, this cannot be maintained indefinitely, and exercise which has to be maintained for hours must be kept down to a level more like 1 l./min. We have to remember that 'fatigue' is a word used to describe more than one physiological state. The credit for this sixteenfold increase in oxygen supply is partly due to the muscles themselves, which are capable of abstracting twice as much oxygen from each ml. of blood, when their need for oxygen is great enough. Thus the heart can increase its rate of pumping up to eight times the normal rate, though like any other organ it fatigues after some minutes of this effort, and for periods of hours it seems incapable of more than about four times its normal output of blood.

An athlete is capable of movement calling for an energy output considerably greater even than would be warranted by having a sixteenfold increase in the rate of oxygen usage. He can for short durations work at a rate which would demand a hundred times the combustion rate of a resting individual, and he achieves this in virtue of a store of energy kept in the muscle which can be used up more rapidly than food could be oxidized. The capacity thus to incur an oxygen debt—for the oxygen not used during exercise must be taken in afterwards in order to restore the reserve of mobilizable energy—is limited to the equivalent of about 16 l. of oxygen in a healthy athlete, or the equivalent of 4 min. supply at the heart's maximal rate of delivery. Thus it is only in athletic events of less than 4 min. duration, and in practice in events of less than 1 min. duration that this oxygen debt mechanism makes its presence felt. In the 100 yards sprint, which is run almost entirely on oxygen debt, the rate of output of energy of the runner is anything from 10 to 13 h.p., corresponding to an oxygen intake rate of 23 l./min., six times anything that the heart can in fact achieve. The question, what is the nature of this reserve of chemical energy, was attacked vigorously during the early part of this century by the schools of Hill, Meyerhof and Emden. It had been known since a century ago that lactic acid appears in the blood stream in the conditions we are considering, and a comparison of the heats of combustion of lactic acid and of glycogen indicates that a change from glycogen to lactic acid—which involves no oxidation—is one which must lead to the production of energy. The work of these men showed clearly that this reaction is at least the chief source of energy. Thus carbohydrate has the special peculiarity that some of its energy can be tapped—milked off as it were—without the use of oxygen, whereas a similar dodge seems not to be possible with either fat or protein. The amount of lactic acid which accumulates in the body of an athlete in extreme conditions may be as much as 100 g., an amount capable of financing an oxygen debt in the neighbourhood of 12 l.; but this does not seem to be quite the whole story for, as Margaria, Edwards & Dill (1933) showed, small oxygen debts occasioned by very brief outbursts of severe exercise are not accompanied by the appearance of lactic acid. The explanation of this part of the total oxygen debt appears to lie—though the point has not been proven—in the creatine phosphate content of the skeletal muscle. Creatine phosphate is a reserve of non-oxidative energy which we must imagine to be still more rapidly mobilizable than the glycogen molecule. It can be tapped more rapidly, and it is also the first to be restored after the exercise is over. This element of the mechanism is, however, one that could not be studied in the intact animal.

The chemistry of muscle contraction

The different elements of the neuro-muscular mechanism seem to have been elaborated in the course of evolution at very different dates. Even on the, as yet scanty, information available, we can form a picture of the way in which this device was elaborated. The power of mobility is possessed by a number of single-celled organisms. Usually it takes the form of the possession of some appendage such as a flagellum, but it may also take the form of pseudopodia or even, as with *Amoeba proteus*, the entire plasma of the cell is involved in what appears to be a cyclic process of liquefaction and gelation. In this latter case Pantin (1930) showed (by necessarily indirect evidence, since the quantity of the amoeba that can be obtained in culture is so small that some chemical process allows the organism to move for a while without oxygen; the amoeba can go into oxygen debt.

The basis of the process is a protein which changes its physical state according to the local atmosphere of ions. The use of adenosine triphosphoric acid (ATP) as the immediate source of the energy required seems also to be an ancient device, for it is found, not only in muscles of all kinds, but in tissues other than muscular, and even in organisms other than animal; yeast is an excellent source of ATP. The device of obtaining energy from carbohydrate without oxidation is extremely ancient, but the existence of a reserve of energy in the form of high-energy phosphoguanidine derivatives is largely restricted to muscle tissues.

An early invention of this type was arginine phosphate, found to-day in the muscles of all invertebrates; but a change was made at the time of the evolution of the early vertebrates, for the place of arginine was taken by the new chemical substance, hitherto, it seems, not known in the world, the amino-acid, creatine, also a substituted guanidine. Whether this substitution of creatine for arginine has a survival value in itself, or whether it was the accidental result of some other genetic change with which it was associated, we cannot tell, but it appears to be the case that all vertebrates at present living utilize creatine, and not arginine, for this purpose. Creatine has been shown by Schoenheimer, du Vigneau and others (Bloch & Schoenheimer, 1940; du Vigneau, Chandler, Cohn & Brown, 1940) to be synthesized in the mammalian body from arginine (together with glycine and methionine), so our dependence upon arginine is not lessened.

It is also the case that the muscles of vertebrates contain considerable amounts of the two dipeptides, β-alanylhistidine and β-alanylmethylhistidine, neither of which appears in the muscles of any invertebrate so far examined. It is odd that these substances should be associated strictly with the vertebrate type of architecture.

Once the principal mechanism of a contractile organ had been evolved, its subsequent elaboration for very different functions is no matter for surprise. We may divide muscles into 'fast' and 'slow' and—a totally different basis of distinction—into 'isometric' and 'isotonic'. Muscles with rapid reaction time, that is to say, for which a single twitch is a brief phenomenon lasting only a fraction of a second, are incapable of maintaining contraction for any length of time. The low internal viscosity which enables them to contract rapidly militates against an economical maintenance of contraction, for a maintained contraction, i.e. a tetanus, is, in fact, the same as a series of twitches, and the more rapidly each twitch passes off the more twitches must be initiated each second to keep up the contracture. Thus we meet in, say, the rabbit, the soleus muscle which anatomically serves the same purpose as the gastrocnemius, but is distinguished from the latter by being slow in response and highly economical in maintenance of posture. A still more remarkable differentiation is to be found in the shellfish, *Pecten*, which has two muscles for closing its bivalve shell; one of them snapping the jaws together, but fatiguing very soon, and the other, a slowly contracting muscle having the appearance more of a tendon than a muscle, which can hold the jaws together for some hours without fatiguing. In man there are no contrasting types of skeletal muscle such as are found in the rabbit and some other animals, and one must suppose that each skeletal muscle is an all-purpose organ presumably not too good at either of the two types of contraction. The slow viscous skeletal muscle of the soleus type is characterized by red pigmentation and perhaps by a somewhat smaller content of available energy components than the fast-moving type, but the essential chemistry appears to have nothing individually characteristic about it. It is this viscosity of the muscle which militates against high-speed working, and, in fact, sets the limit to the speed with which an athlete can perform tasks of short duration.

Our other basis of classification is between muscles whose anatomical position is such that they produce great tensions with comparatively little change in length, such as, for example, our own gastrocnemius muscle, and those which have little force to overcome but must change considerably in length. The so-called plain or unstriated muscles are in this category, and the heart muscle may be regarded also in this category in so far as the volume of the heart changes from diastole to systole by a very substantial amount in exercise and the length of each fibre of the myocardium changes in similar degree. It is customary on histological grounds to distinguish sharply between plain and striated muscle in the body, but I am inclined to wonder whether this categorization has all the justification it appears to have. Of the four categories of muscles I have indicated, i.e. fast isotonic, fast isometric, slow isotonic and slow isometric, we find that so-called plain or unstriated muscle frequently comes into the category of slow isotonic, thus having a function which entails very considerable slow changes of length, but against comparatively little resistance. At the other end of the scale are the muscles of the eyelid which have to work very rapidly and against considerable mechanical disadvantage so that, although the eyelid moves a considerable distance, the muscles change little in length. From the one extreme to the other all types and gradations of muscle are found, each to its special task.

The heart muscle

The heart muscle, which occupies so central and important a position in the neuromuscular mechanism, deserves a brief comment to itself. The heart muscle is peculiar in that it makes little or no use of any 'oxygen-debt' mechanism. Its supply of creatine phosphate is low, and its blood supply—the coronary circulation—is very generous. A. J. Clark and his collaborators (Clark, Eggleton & Eggleton, 1932), who made an intensive study of the amphibian heart, found that it could survive and beat in the total absence of oxygen, and that it carries enough creatine phosphate to last five to ten beats, but the mammalian heart does not work in anaerobic conditions for any length of time.

Athletic abilities

There has been some discussion in athletic and sporting circles concerning the reasons for the apparently increasing athletic abilities of the human race, or such parts of it as indulge in athletics, during the present century. Thus if we consider the 100 yard sprint and confine ourselves to British records, we find that the record stood in 1886 at 10 sec., and it was not altered until the turn of the century when Duffey brought it down to 9·8. Another 20 years and Liddell reduced it to 9·7 sec., and in 1947, Macdonald Bailey brought the figure to 9·6 sec. where it still stands. The 1500 m. was run by Kiviat in 1912 in 3 min. 56 sec., and the seconds have been nibbled off this figure fairly steadily since 1924, until the present figure of 3 min. 43 sec. was reached by Strand last year. This represents a fairly steady reduction of time of 0·5 sec./year.

A second matter of some discussion, more relevant to the interests of the present meeting, is the question, whether the not very excellent performance of English athletes during the past few years is related to changes in dietary habits necessitated by the war. To take the first of these questions first: I am very doubtful if there has really been any change in human abilities during the present century of the magnitude that seems to be indicated by the athletic statistics. It would be very interesting to know what were the abilities of the Ancient Greeks in the field of athletics, but, unfortunately, very little information is available. The Greeks had no accurate measure of time less than a day, and were content in the matter of athletics merely to acclaim the winner without any objective measure of his performace. In athletic events which did not involve time or speed in their measure of success, some comparison with Ancient Greece might be possible, but this depends on the accuracy of the Ancient Greek measures and the correctness of our estimate of them in metric or English units.

As Gardiner (1910) has written: 'We have no means of estimating the performances of Greek runners or comparing them with those of our own times. The Greeks kept no records. We hear of a runner who would outpace and catch hares, of another who raced a horse from Coronea to Thebes and beat it. Various feats of endurance are recorded. Herodotus tells us how Pheidippides ran from Athens to Sparta in 2 days, a distance of 150 miles. It was the same Pheidippides who is said to have brought to Athens the news of the victory of Marathon, a story commemorated in the modern Marathon race which is, of course, a purely modern event unknown to the ancients. But all this is too vague to be of any value for comparison. Such scanty evidence suggests that the Greeks generally attained a high standard of running, especially in long distances.'

So far as modern records are concerned, few of these date from earlier than 1880, when an interest in athletic events arose first in England and, later, on the Continent. The first annual Oxford and Cambridge Boat Race was held in 1856; the first modern Olympic Games were held at Athens in 1896; the first ascent of the Matterhorn was made by Whymper in 1865; and Captain Webb swam the Channel in 1875.

In those earlier days, athletes and sportsmen were a very picked population, for only the wealthy could afford to indulge such tastes. In this country, it was probably only the better-off 5% of the population who had such opportunities, and this means that athletes were drawn from a population of half a million people—for we must exclude children and all females from the count. With an increasing interest in sport generally, and a number of social changes, which, in the last 50 years, have eased the position of lower income groups and altered the attitude of women to athletics, the number of people able to indulge a taste for athletics is increasing considerably, perhaps to as much as 2 or 3 million, and such an increase may well be critical, since a really first-class athlete is a rare phenomenon, turning up perhaps once in a million or so. If this view is correct, it means we may expect to see records broken over a few years yet, but with diminishing frequency until, for each nation, a set of figures is reached, representing—though not in a way of much scientific interest, since science is more concerned with averages than with extremes—the abilities of that nation in the field of athletics. Subsequently, even this set of figures might be expected to show slow improvement, but in this connexion, we should take warning from the observation made by A. V. Hill in 1927, that the speeds of race-horses, which have been officially recorded for nearly two centuries in this country, have not improved at all in this interval despite the fact that it represents the results of forty or fifty generations of selective breeding (using as much money, incidentally, as might have founded and maintained several excellent institutes of genetics). Where the human population is concerned, with a complete absence of selective breeding, changes in intrinsic athletic ability in any calculable number of generations are out of the question, and the only improvement which it is reasonable to expect would be an improvement attributable to improved nutrition—for which there is plenty of scope.

On the second question, whether British athletic prowess has fallen off because of dietary restrictions, I have no opinion to offer. It would, indeed, be presumptuous of me in such a gathering, but I think we should remember that the war had other effects upon our youth than that upon diet. Much time that might otherwise have been devoted to athletics was spent in a different kind of training; the playing fields of Eton had indeed remarkably little to do with the winning of this war, but perhaps in a few years of peace they may produce once again a crop of first-class athletes.

REFERENCES

Bloch, K. & Schoenheimer, R. (1940). *J. biol. Chem.* **134**, 785.
Clark, A. J., Eggleton, M. G. & Eggleton, P. (1932). *J. Physiol.* **75**, 332.
Gardiner, E. N. (1910). *Greek Athletics, Sports and Festivals.* London: Macmillan.
Margaria, R., Edwards, H. T. & Dill, D. B. (1933). *Amer. J. Physiol.* **106**, 689.
Pantin, C. F. A. (1930). *Proc. roy. Soc.* B, **105**, 538.
Vigneau, V. du, Chandler, J. P., Cohn, M. & Brown, G. B. (1940). *J. biol. Chem.* **134**, 787.

Chemical Aspects of Muscular Contraction

By DOROTHY M. NEEDHAM, *Biochemical Laboratory, University of Cambridge*

In the biochemistry of muscle contraction, two lines of work, followed independently for some 50 years and only recently coming together, must be considered. One is the nature of the muscle machine, the other the nature of the essential fuel.