THE LAWS OF MUSCLE AND TENDON GROWTH

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WOOLLARD in his *Recent Advances in Anatomy* states that the preliminary phases of development are "succeeded by a final period of functional differentiation and co-ordination of the elements of the organism," and that "this correlation takes place through hormones, through the nervous system, by atrophy and hypertrophy, and by the mutual interaction of parts with one another (4)." Remarkably little is known of these processes. This paper is an attempt to unravel what appears to be the easiest group of problems of this period, that of the later development of muscles and their associated tendons. The attempt has been made along purely morphological lines, but it is hoped that other investigators will eventually confirm or disprove the conclusions by experimental research.

A problem is often most easily studied in its more extreme aspects, so in this case the plantaris, the muscle possessing the longest tendon in the human body, may serve as an introduction to our problem (fig. 1). In the normal adult figured the belly, measuring 110 mm., gives origin to a tendon 200 mm. in length. This discrepancy between flesh and sinew is still further emphasised by the separation of an individual macroscopic element of the belly (fig. 1, *P.*) which measures only 52 mm.

But when the same dissection is carried out on the gastrocnemius, the element so isolated (fig. 1, *G.*) measures precisely the same, 52 mm., though the gastrocnemius is a normally proportioned muscle. The apparent fleshiness is due to the greater distribution of the contractile tissue over the body of the muscle.

The identity in the lengths of the fibres taken from these two muscles suggests at once a common cause: the very similar origin and insertion at the femur and calcis, giving a similar range of movement.

If now the lengths of the fibres of the plantaris and soleus are compared (fig. 2) the elements of the soleus are seen to be even shorter than those of the gastrocnemius and plantaris, measuring only 34 mm. in the specimen studied. This may be correlated with the origin of the soleus from the bones of the leg, so that it acts only on the ankle joint and not on the knee as well.

It is clear that the short length of the fibres is mechanically the most economical arrangement possible, for the range of movement between the origins and insertions of the muscles is limited by the nature of the bones and joints to which they are attached, and the fibre length is adequate to bring this range of movement about. Should the length of any fibre be doubled, then the extra half of the fibre would never be able to contract at all. In the case of a muscle whose origin and insertion can move to and fro through a long distance, the fibres of that muscle are correspondingly long, as in the sartorius of Man.

This correlation of fibre length with mobility is confirmed by a study of a club foot (fig. 3) showing an abnormally limited movement of congenital origin. The lengths of the fibres are rather less than one-third those of the normal specimen (fig. 4), corresponding to the very small amount of movement allowed in such feet.

In strong contrast to the condition of the muscles in this congenital immobility stands the condition in an amputation stump resulting from an operation carried out in adult life (fig. 5). The tendo Achillis is firmly bound to the lower end of the tibia by new fibrous tissue, so that the gastrocnemius passing from femur to tibia could still act on the knee joint, but the soleus, now passing from one part of the tibia to another part of the same bone could have no action whatever. Yet in this condition of acquired immobility it is still fleshy and the fibres are of normal length. Thus it is clear that a process of growth is necessary for the fibres of a muscle to become suited in length to the work they perform. If the same amputation had been performed on a boy, the resultant adult specimen would show no muscular substance in the soleus.

The growth of muscle and tendon is an ill-understood subject. In the lower Vertebrates it is thought that the muscle is of myotomic origin, whereas the tendon is developed *in situ* from the mesenchyme of the developing limb bud. In the higher Vertebrates the myotomic origin of the limb muscles is less certain, and muscle and tendon are often held to be independent in development. It is noteworthy, however, that failure of junction of a muscle with its tendon is quite unknown, whereas it would be expected on the theory of independent development that such failure would occur as often as, say, failure of junction of the parts of the face. The absolute absence of any such anomaly suggests a closer relation between the developing muscle and tendon.

It may be noted that the combined length of the muscle and tendon is always such that at any age and in any individual the muscle is slung between its origin and insertion, so that it is neither taut nor loose. In the short muscular Bushman (fig. 6), for instance, the muscles are arranged just as efficiently as in the tall spare Bantu (fig. 1), so that they are neither torn when stretched nor slack when contracted, and this applies even to the anomalous muscles of the Bushman (fig. 6, X and Y).

Now this condition might be brought about by a system of genes in the individual cells of the bones and muscles, causing each part to be modelled in proportion to the others, or by a system of nervous impulses or hormones, keeping each part in touch with the parts around it. But either of these mechanisms would be much too complex to work in practice, particularly with the invariable perfection seen even in the case of anomalies (fig. 6) and congenital disturbances (fig. 3), so a more simple mechanism must be sought, one that will apply to all muscles and one that cannot go wrong.

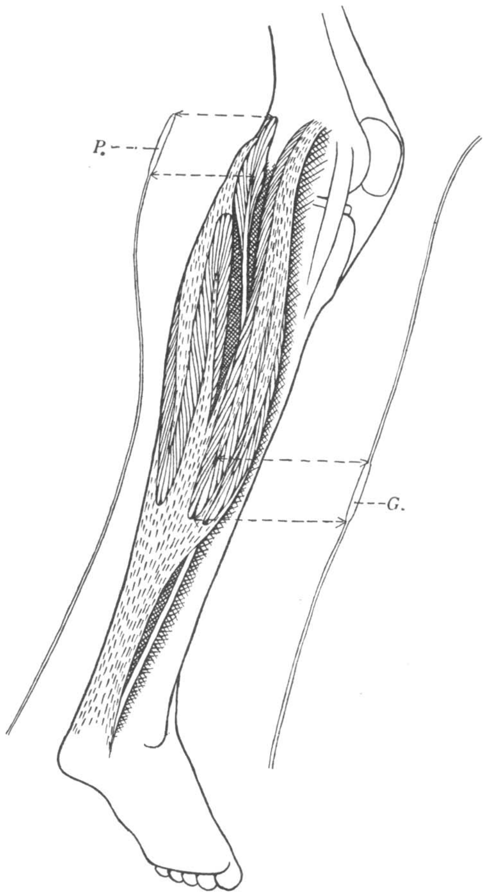

Fig. 1.

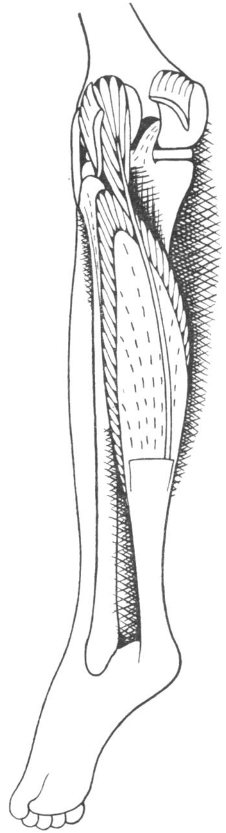

Fig. 2.

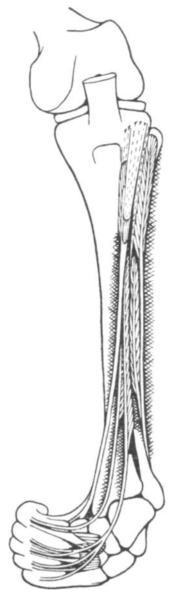

Fig. 3.

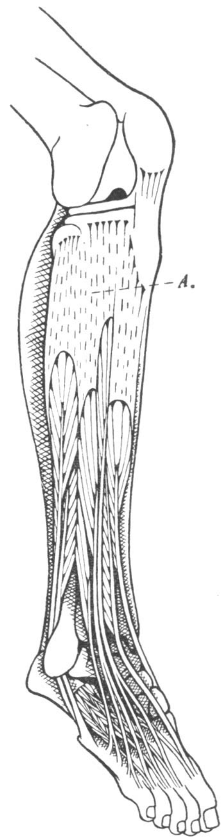

Fig. 4.

Fig. 1. Plantaris and gastrocnemius of Bantu.
Fig. 3. Anterior tibial muscles in a case of club foot.

Fig. 2. Plantaris and soleus of Bantu.
Fig. 4. Anterior tibial muscles of Bantu.

It is well known that the skin overlying a tumour becomes stretched, and this implies growth by traction, not only of the skin itself but also of the arteries and nerves supplying it. Growth of muscle is of precisely the same nature; that is to say, it grows in response to traction at its origin and insertion. This throws the control of the lengths of the muscles of the limbs on to the bones to which they are attached. If the bones grow, the muscles are stretched and grow to a length compatible with them.

This is not the only mechanism at work in muscle growth, for it does not explain the phenomena of muscle creep or muscle migration, but it is the most important mechanism, especially in the limbs, where migration is at a minimum.

The late foetal musculature is very similar to that of the adult, but there is relatively more muscle and less tendon. An extreme case of this is found in the serratus posterior superior of the eight months' foetus (fig. 7, *S.P.*) compared with that of the adult (fig. 8). Assuming that the adult in question passed at eight months through a stage comparable to that of the foetus shown, the amount of tendon is immensely increased. The part of the muscle inserted on the second rib has increased in fibre length from 20 to 30 mm., but the part inserted into the fourth rib has actually decreased from 20 to 17 mm. This diminution suggests that the tendon is lengthened at the expense of the muscular substance. Whether the tendon is formed from the muscle fibres themselves or from the connective tissue surrounding them cannot be decided by macroscopic examination, but in either case muscle is replaced by tendon.

Of the growth of tendon, once formed, little is known. There is some evidence that it can decrease in length, for no other explanation can be given of the condition of the soleus in the amputation stump (fig. 5) where the lower muscular fibres have been reversed in direction so that they now pass proximally from their origin to their insertion, apparently owing to contraction in the aponeurosis of insertion.

But of any interstitial increase in length, that is an increase otherwise than by accretion at either end from muscle or periosteum, there is no evidence. Though this point can only be settled by experimental work, it seems highly probable that tendons are to be classed with those organs, such as the bones, nails, yolk of eggs, the lens of the eye, teeth, etc., that cannot increase by interstitial growth. It increases by metamorphosis of muscle only.

The stimulus to tendon formation appears to be the limitation of the range of movement of the muscle by the conformation of the bones and joints. How the muscle fibre becomes sensible to its own inability to contract and perform work throughout its entire length is unknown, but Fenn has shown that certain processes only occur in the muscle if contraction actually occurs, and not if the muscle is not allowed to shorten (isometric contraction) (1). It may be that the absence of one of these changes gives the necessary stimulus.

Thus starting with a muscle tendon complex in a developing animal of any age after movement has once begun, the length of the complex keeps pace with the bones to which it is attached by growing in response to the traction

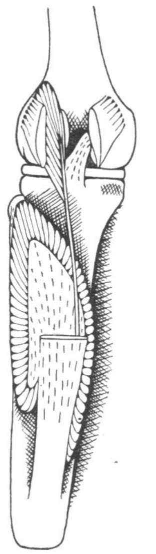

Fig. 5. Plantaris and soleus in an amputation stump.

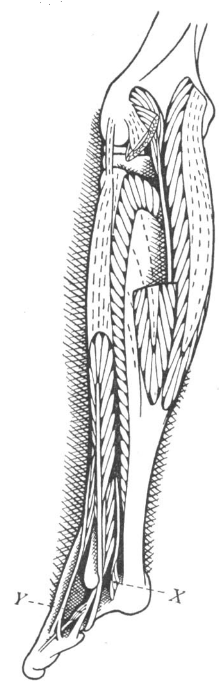

Fig. 6. Calf muscles of Bushman.

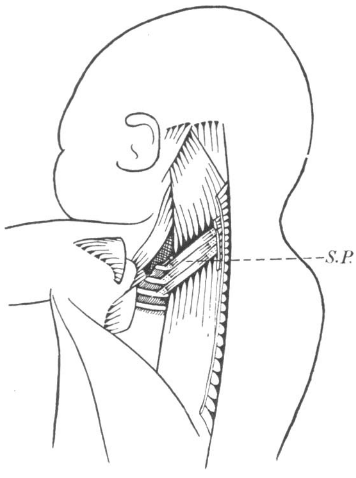

Fig. 7. Serratus posterior superior of eight months' foetus.

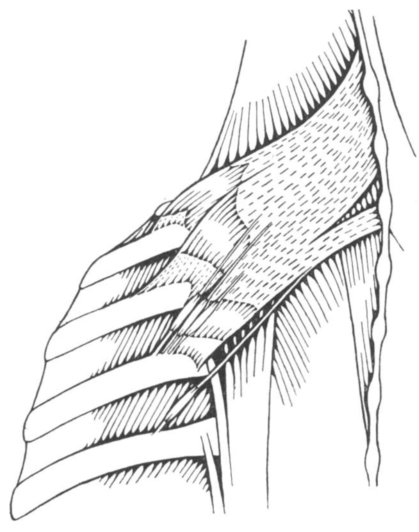

Fig. 8. Serratus posterior superior of adult.

set up within it, but growing only in its muscular part. This growth of muscle substance is counterbalanced by tendon formation in those parts which fail to contract owing to the limitation of possible movement.

There has been one previous important attempt to correlate development with function—that of Julius Wolff (3)—who claimed that the osteoblasts of a developing bone build according to the stresses and strains to which they are subjected. This noble theory was proved invalid by a study of the bones in foetal life, where the forces are different to those in the adult, but the bones show much the same structure, and by the fact that the theory implied interstitial growth in bone. The grounds for a mechanical explanation of the growth of muscle and tendon appear somewhat more secure, as the foetus is known to carry out muscular movements from an early age.

A neat example of the working of these theories is seen in the coccygeus muscle and the sacro-spinous ligament (fig. 9). It is generally acknowledged that the ligament is formed from part of the muscle, but no accurate description of the metamorphosis has been offered.

The ligament, however, is found to pass from the ischial spine to the immovable sacrum, while the muscle passes from the spine to the mobile coccyx. The response of the fibres to the limitation of movement between spine and sacrum has been complete tendinification.

In the lower animals, for instance in the baboon (fig. 10), the muscle has no insertion on the sacrum, which here consists of but three pieces. All the fibres pass to the basal vertebrae of the tail. The fibres are, as would be expected on the traction and limitation hypotheses suggested above, entirely muscular. Should any ape be found in which the coccygeus reaches the sacrum, that ape will be found to possess a sacro-spinous ligament.

The application of these theories to the field of Vertebrate evolution are immense. In the specialisation of limbs which has played a part in so many orders of Mammals, including that in which Man himself is to be found, it is no longer necessary to postulate complex co-ordinating mechanisms to govern the sizes of the muscles, nor a vast series of genes to suit the muscles to their work. Given in the developing organism a basic plan of musculature, the effects of traction and limitation will suit each mass to the cursorial limb of a horse, the specialised limb of a rabbit, or the familiar leg of Man (figs. 4, 9).

One point that has hitherto clouded an appreciation of the structure of muscles is the confusion between connective tissue and tendon; that is, between fascia and aponeurosis. If the representation of the anterior tibial muscles in fig. 4 is compared with that in any ordinary text-book of anatomy (2), it will be noted that the muscles are shown in my figure taking origin by a common superficial aponeurosis (fig. 4, *A.*) formed by their conjoined tendons of origin from the heads of the tibia and fibula. This structure, which may be named the aponeurosis cruris, is removed in ordinary dissection as "deep fascia" and is so represented in the text-books. But, being tendinous, it cannot be homologous to the deep fascia which covers the gastrocnemius or the

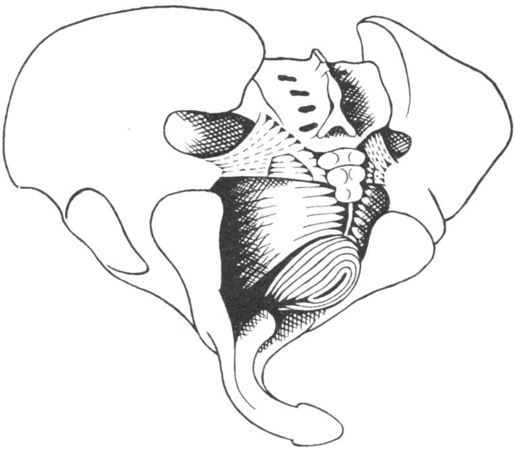

Fig. 9. Coccygeus muscle and sacrospinous ligament of Man.

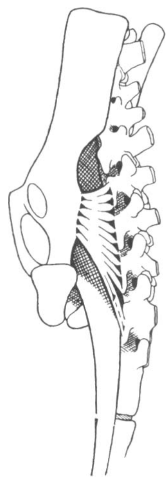

Fig. 10. Coccygeus muscle of baboon (*Papio*).

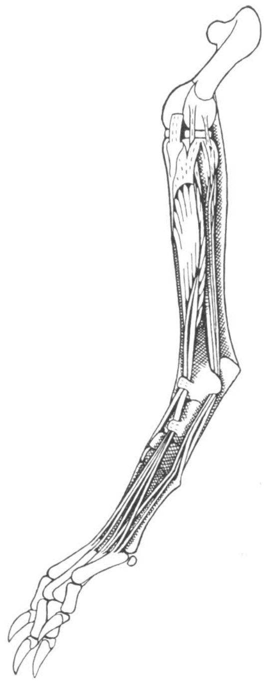

Fig. 11. Anterior tibial muscles of rabbit.

lower part of the leg. The true fascia lata is to be found as fibrous tissue covering the superficial surface of the aponeurosis in the same way as the areolar deep fascia of the thigh covers the subjacent muscles.

Similar structures are to be found wherever muscles are commonly said to arise from or to be inserted into fasciae or intermuscular septa, both of which are built up of connective tissue and are not constituted to take the strains of muscle pull. Every muscle fibre, apart from those belonging to the skin musculature, such as those of the face, perinaeum, etc., either directly or through tendon, takes origin from bone and is inserted into bone.

SUMMARY

It is attempted along morphological lines to substantiate the following laws of muscle and tendon growth:

(1) That the length of the fibres of any muscle bears a constant proportion to the distance through which its origin and insertion can be approximated.

As corollaries to this:

That muscles contracting through the same distance have fibres of equal length, and

That all the fibres of a single narrow muscle are of the same length.

Bringing about this correlation:

(2) That muscle fibres grow along their whole length in response to *traction* set up by the growth of the bones to which the muscle is attached.

(3) That tendon is lengthened by metamorphosis of muscle tissue in response to a *limitation* of the range of possible contraction determined by the nature of the attachments of the muscle.

As a result of these mechanisms:

(4) That muscle can adapt itself to the changing shapes of limbs in an evolving phylum without any necessary alteration in the genetic make-up of the constituent species.

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REFERENCES

(1) FENN (1923). *J. Physiol.* vol. LVIII, p. 180.
(2) GRAY, H. (1926). *Anatomy*, 3rd ed. fig. 618.
(3) WOLFF, J. (1870). "Ueber die innere Architektur der Knocken." *Virchow's Arch. f. pathol. Anat. u. Physiol.* vol. I.
(4) WOOLLARD, H. (1929). *Recent Advances in Anatomy*, p. 73.