J. Anat. (1988), **160**, pp. 79–88
With 4 *figures*
Printed in Great Britain

The range of sarcomere lengths in the muscles of the human lower limb

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(*Accepted* 21 *December* 1987)

INTRODUCTION

Although it is well known that the length of the sarcomeres in vertebrate striated muscle influences the force that can be exerted by that muscle (Gordon, Huxley & Julian, 1966), little work has been carried out to determine the working range of sarcomere lengths. Published data on sarcomere length refer to the muscles of the jaw in rats (Nordstrom & Yemm, 1972; Nordstrom, Bishop & Yemm, 1974) and rabbits (Weijs & van der Weilen-Drent, 1982; Hertzberg, Muhl & Begole, 1980), with a few studies on limb muscle lengths in the rabbit (Dimery, 1985), the cat (Rack & Westbury, 1969) and some bird species (Cutts, 1986). The lack of information relating to sarcomere lengths in human muscle is even more striking. A length–tension curve for human muscle has been produced (Walker & Schrodt, 1973) and the sarcomere lengths have been investigated with respect to determining the number of sarcomeres in series in a muscle fibre, in order to evaluate the relationship between force and velocity according to the Hills equation (Wickiewicz *et al.* 1982). A pilot study has been carried out with a view to producing a survey of the range of sarcomere lengths of the muscles of the human leg (Cutts, 1987).

METHODS

Sarcomere lengths in the anatomical position

Sarcomere lengths were determined for the anatomical position using muscle samples taken from the limbs of three cadavers fixed in an embalming fluid comprising 17 parts by volume 90% industrial methylated spirit, 2 parts liquid phenol, 2 parts glycerine and 1 part 40% formalin. Small samples of muscle were taken from five distinct regions of each of the following muscles: rectus femoris, vastus medialis, vastus lateralis, vastus intermedius, biceps femoris (short head), semimembranosus, semitendinosus, tibialis anterior, gastrocnemius, soleus (deep surface). From these samples, thin layers of muscle fibres approximately 1 fibre thick, with several fibres lying side by side, were teased out and set in glycerol jelly on microscope slides. Three such slides were prepared for each muscle sample. The lengths of the sarcomeres were determined using a diffraction method described by Dimery (1985) and Cutts (1987).

Muscle length variation with limb position change

The muscle lengths were measured in the intact cadaver using a length of string, which was marked at positions corresponding to the origin and insertion of each muscle. The entire muscle length, then the length of the tendinosus portion only, were

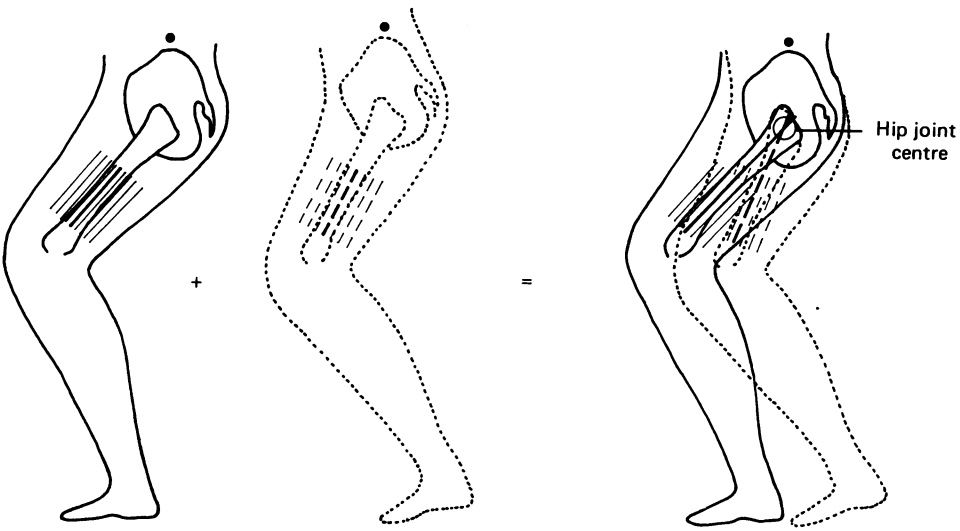

Fig. 1. A simplified explanation of determining the centre of rotation of a ball and socket joint (in this case the hip), using the Moiré fringe technique. A photograph is taken of the leg with the plate of parallel lines attached, then the leg (not the hip) is moved slightly and a second photographic exposure made on the same frame. The transparency is projected to life size, and the central parallels extrapolated to their point of intersection. This point of intersection describes the centre of rotation. A full explanation is given by Shoupe & Steffen (1974).

measured, allowing the proportion of the muscle which is contractile tissue to be evaluated.

A healthy young male volunteer of average height and build was selected and X-rays taken of the lower part of his leg from a distance of approximately 2 m, to give a life size image. For ethical reasons, the pelvic area could not be X-rayed, so the centre of rotation of the hip was determined using the Moiré fringe technique (see Fig. 1). A plate of material covered in parallel lines, with a heavier central line, was attached to the thigh. A double exposure photograph was taken of the leg in two slightly different positions; this was then projected to life size and the central lines of the plate extrapolated to the point of intersection, which describes the centre of rotation of the hip. The theory of Moiré fringe is described fully by Shoupe & Steffen (1974). The procedure was fully explained to the volunteer, and the risks of the X-ray outlined.

Using the information relating to the hip joint centre and the X-rays of the lower part of the leg, a life size cardboard model of the leg was constructed. The areas of attachment of the muscles were drawn on the model, their centroids determined and marked. Photographs of the subject in various positions were taken; these were projected to life size and the outlines traced on to large sheets of paper. The bone model was positioned within these outlines, and the muscle lines of action drawn in to join the centroids of the areas of attachment and origin. The lengths of the muscles were measured directly from the tracing, and the length of the contractile portion evaluated.

To simplify the calculations of predicted sarcomere lengths, we assume that all the fibres run the entire length of the contractile part of the muscle. In actual fact this may not be true, but we are using the fibre length as a measure of the length of a series of sarcomeres lying side by side. In the cases where more than one fibre runs the length of the contractile portion of the muscle, this length will be made up of n sarcomeres from the first fibre and m sarcomeres from the second. Since $n+m$ should approximately equal the number of sarcomeres in a single fibre running the entire length of the contractile portion, it is valid to make this assumption.

A further assumption is made regarding length change in the tendons. Even under the large forces exerted during, for example, running quickly, when a force of 0·5 tonne could be expected in the tendo calcaneus of a 70 kg man, the length change in the tendon would only be in the order of 3–5% (Alexander, 1984). In slow movements, this would be much less, and in the passive movements under consideration here the length changes in the tendons would be so small that we can equate them to zero.

Prediction of sarcomere length at varying limb positions

If, for any given position, both the length of the sarcomeres and the length of the contractile tissue of a muscle with parallel fibres are known, the number of sarcomeres in series can be calculated easily from

$$Sn = L$$

where S = sarcomere length, n = number of sarcomeres lying in series along the length of the muscle fibre and L = length of the contractile portion of the muscle. When the length of the muscle changes, n will remain constant, so we can calculate S for the new muscle length from

$$S = (L/n)$$

If the muscle is pennate in type, the angle of pennation must be taken into account. When the muscle lengths were measured, the angles of pennation were also determined for each muscle. The change in length of the sarcomeres will affect differently the long axis of the contractile portion of the muscle, which can still be determined by using the bone model in the required position. Consider Figure 2.

L_1 is the initial length of the contractile tissue along the line of action, L_2 is the length of contractile tissue along the line of action after contraction, l_1 and l_2 are the lengths of the muscle fibres before and after contraction respectively, and δ_1 and δ_2 are the angles of pennation of the muscle before and after contraction. The change in the angle of pennation during contraction is minimal, and as all the measured values of δ are between 0 and 20 degrees, then

$$0{\cdot}94 < \cos\delta < 1{\cdot}00.$$

We can write

$$L_1 - L_2 = (l_1 - l_2)\cos\delta$$

$$l_1 - l_2 = \frac{L_1 - L_2}{\cos\delta}.$$

Hence the relative change in fibre length

$$\frac{l_1 - l_2}{l_1} = \frac{L_1 - L_2}{l_1 \cos\delta}.$$

Since the relative change in fibre length is the same as the relative change in sarcomere length, sarcomere length after contraction can be calculated from

$$S_2 = S_1 - S_1 \frac{L_1 - L_2}{l_1 \cos\delta},$$

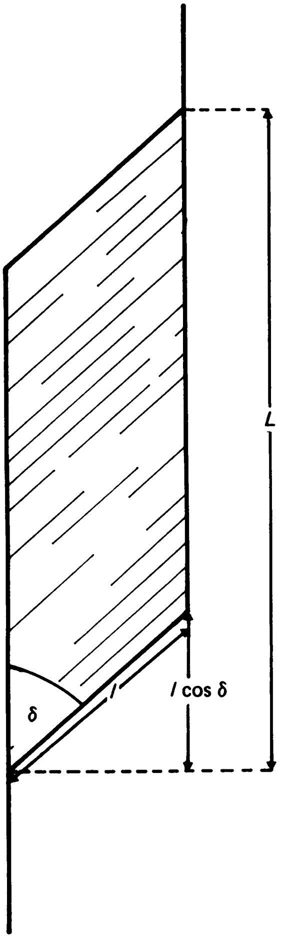

Fig. 2. Relationship of the fibre length, angle of pennation and length of contractile tissue along the line of action of the muscle.

where S_1 is the initial sarcomere length and S_2 is the new sarcomere length. The values for initial fibre length (anatomical position), as given by Wickiewicz, Roy, Powell & Edgerton (1983), are summarised in Table 1.

RESULTS

Table 2 shows the observed sarcomere lengths for the muscles in the investigation, with 95% confidence limits, and the predicted sarcomere lengths for the estimated longest and shortest muscle lengths. The positions used to estimate these muscle lengths are shown in Figures 3(*a*) and 3(*b*). The angles of pennation of the muscles, which were measured directly from the cadavers, used in making these predictions are shown in Table 3, with the results of Alexander & Vernon (1975) included for comparison. Muscle length in the anatomical position, and the theoretical minimum and maximum muscle lengths from which the sarcomere lengths were predicted, are shown in Table 4.

Table 1. *Lengths of muscle fibres in the muscles of the human leg*

Muscle	Length of muscle fibres* (mm)
Vastus medialis	70·3
Vastus lateralis	65·6
Vastus intermedius	68·3
Rectus femoris	66·0
Semitendinosus	158·0
Semimembranosus	62·7
Biceps femoris (short head)	139·3
Tibialis anterior	77·3
Soleus	19·5
Gastrocnemius	50·7

* Means of data presented by Wickiewicz *et al.* (1983).

Table 2. *Sarcomere lengths in the muscles of the human leg*

	Sarcomere length (μm)			
Muscle	Anatomical position	Mean (±95% confidence limits)	Theoretical longest position	Theoretical shortest position
Vastus medialis	2·048	±0·028	3·401	1·988
Vastus lateralis	2·173	±0·025	3·531	2·071
Vastus intermedius	1·970	±0·038	2·482	2·030
Rectus femoris	2·146	±0·063	2·541	1·365
Semitendinosus	2·987	±0·054	3·670	2·228
Semimembranosus	2·541	±0·045	4·406	1·482
Biceps femoris	2·281	±0·035	3·167	1·198
Tibialis anterior	3·007	±0·026	3·321	1·085
Soleus	2·033	±0·071	3·359	1·260
Gastrocnemius	2·733	±0·079	4·413	1·012

Table 3. *Angles of pennation in the muscles of the human leg*

	Angle of pennation of fibres (degrees)				
	Specimen				
Muscle	1	2	3	Mean	Alexander & Vernon
Vastus medialis	13	16	14	14·3	15
Vastus lateralis	12	13	13	12·7	13
Vastus intermedius	16	17	17	16·7	18
Rectus femoris	16	18	16	16·7	15
Semitendinosus	5	5	5	5	0
Semimembranosus	17	16	18	17	16
Biceps femoris (short head)	2	4	5	3·6	0
Tibialis anterior	7	8	7	7·3	8
Soleus	20	18	20	19·3	20
Gastrocnemius (lateral head)	10	12	10	10·7	8

Table 4. *Lengths of contractile portions of the muscles of the human leg*

Muscle	Length of contractile portion of muscle (mm) Theoretical maximum	Theoretical minimum	Anatomical position
Vastus medialis	254	207	209
Vastus lateralis	293	240	243
Vastus intermedius	204	189	187
Rectus femoris	326	278	301
Semitendinosus	242	166	206
Semimembranosus	353	274	299
Biceps femoris	357	237	303
Tibialis anterior	269	212	261
Soleus	365	296	313
Gastrocnemius	261	212	245

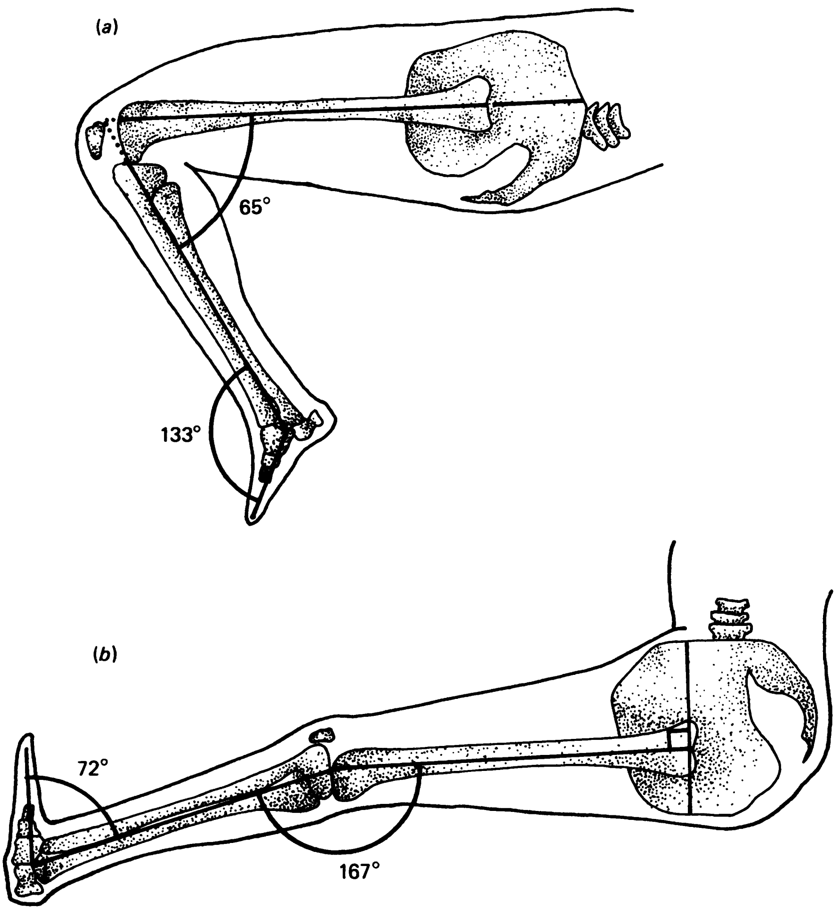

Fig. 3(*a–b*). The positions used to determine the extremes of muscle length used in sarcomere length prediction. Fig. 3(*a*) shows where the soleus and gastrocnemius muscles and the hamstring muscle group are at a minimum length, and the tibialis anterior and quadriceps muscle group are at a maximum length. In the position described in Fig. 3(*b*), the soleus, gastrocnemius and the hamstrings are at their maximum lengths, whilst the tibialis anterior and the quadriceps are at their minimum lengths.

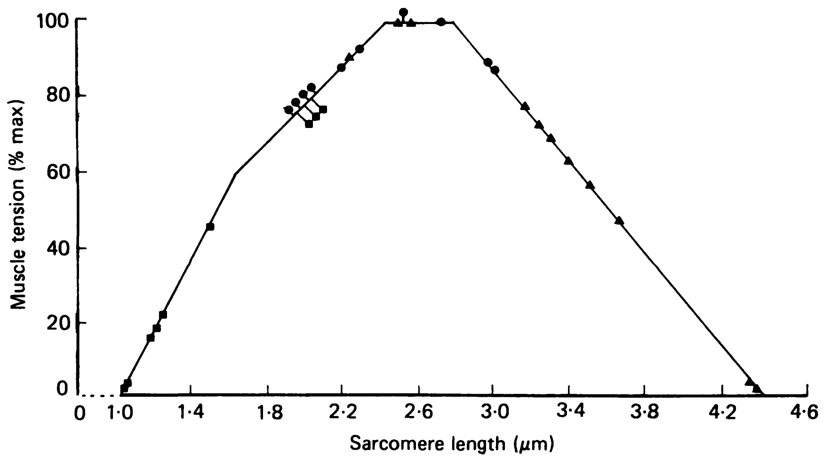

Fig. 4. Observed and predicted sarcomere lengths have been superimposed on a length–tension curve for human muscle prepared from the data of Walker & Schrodt (1973), to show the spread of sarcomere length from the longest theoretical muscle length to the shortest. Sarcomere lengths in the anatomical position are also shown. ●, Anatomical position muscle length; ■, theoretical minimum muscle length; ▲, theoretical maximum muscle length.

The results given are the means of a large number of observations for each muscle, with 95% confidence limits attached; for each muscle a total of 15 slides of myofibrils was prepared, and each of these was photographed three times. In order to test the repeatability of the measurements made, a muscle was chosen at random and the photographic negatives for all the slides were measured five times. Analysis of variance showed no significant difference between the five measurements ($F = 0{\cdot}017$, $P > F$). In order to establish that there was no significant difference between sarcomere length in the three cadavers, a further analysis of variance was done. This indicated that there was no significant difference between the three cadavers ($F = 3{\cdot}010$, $P > F$).

DISCUSSION

Experimental material

The observations reported here were made on the limb muscles of three human cadavers which had been embalmed according to standard practice; that is, the body was received within a few days of death, after having been kept under refrigerated conditions. By this time the muscles of the cadavers will have passed through the state of rigor mortis, during which the configuration of the muscle proteins is approximately the same as if an active contraction had brought the limb to its present position (White, 1970; Bendall, 1973). If the cadavers are not moved from this position after rigor has passed, we may assume that the muscles are still in a condition appropriate to that when the limb has been brought to that position by an active contraction, so it is most important that the cadavers are handled with extreme care. The legs must not be allowed to dangle freely, which would result in passive stretching of the muscles from their lengths when the body was laid out in the anatomical position. The fixing of the cadavers was carried out by experienced technicians, who maintained the body in the true anatomical position. Should any movement of the limbs have occurred, then errors will be present in the results presented here. This is a fairly serious drawback to the use of cadaveric material, but unfortunately there is no alternative human tissue available for experimental work. Much more reliably fixed specimens were used in other investigations of small vertebrates, where the specimen was killed, then arranged in the required position before immersing the whole animal or parts of it in fixative when rigor mortis had set in (Dimery, 1985; Cutts, 1986).

Experimental method

The experimental method for determination of sarcomere lengths has been discussed previously (Cutts, 1987). The sarcomere lengths obtained by using the diffraction method do not differ significantly from those obtained by counting the number of sarcomeres against a marker of known length (Dimery, 1985; Cutts, 1986, 1987).

The means of predicting sarcomere length from muscle length is based on measurements taken from a two dimensional model of the leg. In the muscles under investigation here this is reasonable, but if any muscle cannot be represented adequately by a two dimensional model, errors will be introduced. If any errors are present in the observed sarcomere lengths, these will be carried through to all predicted sarcomere lengths for the muscle in question. When observed and predicted sarcomere lengths have been compared in the past, discrepancies have occurred (Dimery, 1985; Rayne & Crawford, 1972), but there appears to have been no account taken of the angles of pennation of the muscles in predicting sarcomere length in either of these investigations.

Results

Figure 4 shows the length–tension curve for human muscle (prepared from the data of Walker & Schrodt, 1973); the data points superimposed on this curve represent the sarcomere lengths observed and predicted in this study. These values are for sarcomere length in fixed cadaveric tissue; an additional investigation (Cutts, 1988) into shrinkage of muscle fibres during fixation indicated that there is no significant length change as long as the muscles are fixed intact on the skeleton, so the same values will apply to living tissue.

In the anatomical position, the majority of these values occur on the upper part of the ascending limb and the plateau of the curve, with two cases on the upper part of the descending limb. In this region of the curve, a maximal amount of the tension potential can be realised. The predicted sarcomere lengths for the theoretical shortest muscle lengths all occur along the ascending limb of the curve. The spacing of the data points indicates that the muscle lengths are not all at their absolute minimum where force can still be generated; if this were so then all the sarcomere lengths would fall in approximately the same place. The muscles on this part of the curve all have different force producing capabilities, those approaching zero force being the shortest. Without some means of monitoring the force output of a muscle it is difficult to decide at what point the minimum functional length is achieved. The electromyographic signal may be a useful tool here, but the assumption would have to be made that the EMG signal is an indicator of muscle force rather than electrical excitation of the muscle cells. At this stage of the understanding of the EMG signal, such an assumption would be inappropriate. Again, with the estimated maximum lengths we have a range of sarcomere length and corresponding force-producing potential. If the positions chosen were all the absolute functional maximum lengths, all the data points would fall in this same place. It must be emphasised that these values relate to very extreme limb positions, out of the range of everyday movement.

It has been noted that at extreme positions in three jaw muscles of the rat, there was some disagreement between the lengths of the muscle fibres and the sarcomeres (Rayne & Crawford, 1972). Studies of locomotory sarcomere lengths in the rabbit (Dimery, 1985) indicate that the working range of sarcomere lengths is over the plateau of the curve and the upper part of both limbs, whilst in bird flight muscle the sarcomere lengths in locomotory positions extend only over the upper part of the ascending limb and the plateau (Cutts, 1986). It seems likely that the range of sarcomere length in everyday movements in human muscle will cover a similar portion of the curve. Edman, Elzinga & Noble (1978) suggest that the descending limb may be unstable and should therefore be avoided. If Edman *et al.* are correct, then from data so far available the muscles which operate over the nearest range of lengths to optimum are the flight muscles of birds.

Further evidence to suggest that the normal working range of sarcomere length is around the plateau of the length–tension curve is given by Pennycuick & Rezende (1984), who in their calculation of the power output of muscles assume that vertebrate striated muscle operates over a range of lengths, the minimum of which is 85% of the maximum. Rayne & Crawford (1972) report that it is generally accepted that, to ensure the tension exerted and speed of movement are sufficient to effect the full range of movement, the difference between the longest and shortest sarcomere lengths should be no more than 40% of the longest sarcomere length. If this is true for all the muscles here, then all the sarcomere lengths during normal movement are likely to be in the plateau region of the length–tension curve.

SUMMARY

The lengths of the sarcomeres of some muscles of the human leg were determined for the anatomical position, using a method based on diffraction. Measurements were made of the muscle lengths and angles of pennation from cadavers, and these were used to predict sarcomere lengths at other limb positions.

The measured and predicted sarcomere lengths were compared with the length–tension curve for human muscle, which showed the range of sarcomere length from both extremes of muscle length to cover the entire range of the length–tension curve.

I would like to thank the Arthritis and Rheumatism Council for Research for financial support, Professor R. McN. Alexander for discussion, advice and use of equipment, Dr L. Adams for providing cadaveric tissue samples, Mr R. Adkin for information regarding the embalming and storage of cadavers and Dr B. B. Seedhom and Professor V. Wright for discussion of the paper in general.

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