

Theoretical determination of force-length relations of intact human skeletal muscles using the cross-bridge model

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Abstract. The purpose of this study was to determine force-length relations of selected human skeletal muscles, based on the theoretical foundations of the cross-bridge model and to calculate a strength curve for knee extension from these relations. Force-length relations were determined for the rectus femoris, vastus lateralis, vastus medialis, vastus intermedius and gastrocnemius muscles, using sarcomere/fiber length data from both legs of four cadavers and sarcomere geometry data reported in the literature. It appears that the two-joint muscles investigated in this study are not able to produce force throughout their full anatomical range of motion, whereas the one-joint muscles can. The strength curve for knee extension was determined as the sum of the force-length relations of the individual knee extensor muscles and showed good agreement with experimentally obtained knee extensor strength curves.

Key words: Force-length relations – Cross-bridge theory – Human skeletal muscle

Introduction

Force-length relations, or the observation that muscles can exert more force at some lengths than at others, were first reported almost a century ago (Blix 1891). Although these relations have been well documented for investigations performed on single muscle fibers of animals (e.g. Gordon et al. 1966), they have only been studied on rare occasions for intact human skeletal muscles (e.g. Herzog and ter Keurs 1988). This lack of information on intact human skeletal muscles is primarily due to the difficulty of isolating an individual muscle from a whole muscle group and determining its force as a function of its length.

Force-length relations of muscles are defined in this paper as the relationship that exists between the *maximal*

active isometric force that muscles can exert and the *average* length of their fibers. In tests on intact human skeletal muscles, *maximal* forces are associated with maximal voluntary contractions. Such contractions may depend on the emotional state of the subject and other non-controllable variables and, therefore, may not always be the same. In tests on isolated animal muscles, maximal forces are produced using externally controlled tetanic stimulations. These stimulations are constant and, in contrast to the intact muscles, involve all motor units of a muscle.

Active forces are associated with the forces produced in the contractile elements of a muscle and require metabolic energy. In contrast, passive forces of a muscle do not require metabolic energy and are associated with the forces produced in elastic elements which are arranged in parallel with the contractile elements. *Isometric* force is associated with a contraction during which the average length of the muscle fibers remains constant. Such a contraction may be achieved by keeping the joint configuration and muscular force constant for a period of time during the contraction. This definition of isometric contraction is different from the commonly used one, according to which the joint configuration but not the muscular force is kept constant. In this latter definition, the fibers of a muscle may undergo length changes (Wagemans et al. 1988) and thus affect the maximal force recorded (Hill 1938).

The cross-bridge model of muscular contraction is based on the theory that there are »cross-bridges« extending from the thick filaments towards the thin filaments of a sarcomere (Huxley 1957). During contraction, these cross-bridges are believed to attach to the thin filaments, exert force on them and produce a sliding of the thin past the thick filaments. It is assumed that these cross-bridges are arranged in a periodic way on the thick filaments, that they are independent of one another, and that each of them is associated with the same ability to produce force. Under these assumptions, the force that a sarcomere can exert is a linear function of the overlap between thick and thin filaments for sarcomere lengths twice the thin filament length or longer. Experimental evidence on single animal muscle fibers (e.g. Gordon et al. 1966) has lent support to the idea of the cross-bridge

model as the mechanism underlying maximal isometric force production in skeletal muscles.

If one accepts the cross-bridge model, theoretical force-length relations of skeletal muscles may be calculated knowing: (a) the sarcomere geometry, in particular the thick and thin filament lengths and the width of the bare zone (i.e. the midportion of the thick filament where there are no cross-bridges); (b) the length of the sarcomeres at one given fiber length; and (c) the maximal active isometric force of a muscle.

The purpose of this study was to determine force-length relations of selected human skeletal muscles based on the theoretical foundations of the cross-bridge model and to calculate a strength curve for knee extension from these relations. Strength curves are defined here as the relations which are obtained as the sum of the force-length relations of all muscles of a synergistic group. Since the muscles in a synergistic group have different fiber lengths, these relations are typically expressed in terms of force (moment) as a function of joint angle.

Methods

Muscles. Four unembalmed human cadavers of three women and one man, all of whom had died between the ages of 60 and 88 years, were used to determine fiber and sarcomere lengths for the rectus femoris muscle (RF). Four different unembalmed human cadavers of two men and two women who had died between the ages of 83 and 87 years, were used to determine the fiber and sarcomere lengths for the vastus lateralis (VL), vastus intermedius (VI), vastus medialis (VM), lateral gastrocnemius (LG) and medial gastrocnemius (MG) muscles.

For RF, fiber and sarcomere lengths were determined for the proximal, middle and distal sections of the muscle, which were obtained by dividing the muscle belly into three segments of equal length. For the remaining muscles, fiber and sarcomere lengths were determined for a typical superficial fiber with no distinction given to location. Fiber lengths for VI were obtained from the literature (Wickiewicz et al. 1983) because of the difficulty of defining fiber lengths in this muscle without using techniques to either isolate individual fibers or being able to trace them through the muscle.

Fiber length. Fiber lengths were measured *in situ* for configurations approximating the anatomical position. The muscles were exposed by dissection, and fiber bundles were selected and marked with sutures at the origin and insertion points of the fiber bundles. The origin and insertion of a fiber bundle were defined as the first indication of tendinous material observed at the proximal and distal ends of the fiber bundle, respectively. Fiber lengths were measured along the paths of the fibers between the two sutures, using strings which were fixed onto the selected fiber bundles and calipers to measure the length of the strings. Each fiber bundle was measured three times *in situ*, and the mean value was recorded as the fiber length. Variations in repeated fiber length measurements were about ± 1 mm for each person and ± 2 mm between two people. In order to assess whether the fibers of the proximal part of RF were different from those of the middle and distal parts (as one group), a *t*-test ($\alpha = 0.05$) was performed.

The "anatomical position" of the cadavers was associated with slightly varying hip, knee, and ankle joint angles, which were defined as the included angles between the trunk and thigh, thigh and shank, and shank and foot, respectively. For the purpose of joint angle measurements, trunk, thigh and shank segments were represented with straight lines connecting the hip and shoulder joints, the lateral femoral condyle and greater trochanter, and the lateral malleolus and fibular head, respectively. The foot segment was represented with a straight line approximating the lateral part of the sole.

In order to compare fiber and sarcomere lengths of the same muscles from different cadavers, length measures were normalized

with respect to hip, knee and ankle joint angles of 180° , 180° , and 142° , respectively. Changes in fiber lengths as a function of joint angle were determined using an adaptation of the regression equations reported by Herzog (1985) and Grieve et al. (1978) for the knee extensor and gastrocnemius muscles, respectively. The regression equations reported by Herzog (1985) were determined from a series of lateral knee and hip radiographs of one male subject who was asked to contract the knee extensor muscles maximally in each knee/hip joint configuration. The regression equations reported by Grieve et al. (1978) were obtained from muscle length measurements at varying knee/ankle joint configurations of eight human cadavers.

Sarcomere length. A section of the muscle containing the marked fiber bundle was dissected out and fixed in a 10% buffered formalin solution for 48 h. The fiber bundle was then dissected free from the rest of the muscle, keeping the sutures intact, and further fixed in a 10% buffered formalin solution for 24 h. After the formalin bath, the length of the fiber bundle was measured again to account for any change in length that might have occurred during the fixation process. Changes in length were found to be less than 5% in all cases and were accounted for in the sarcomere length calculations. For example, a piece of tissue that had shrunk by 3% during the fixation process was assumed to have average sarcomere lengths of 97% of those it had before the fixation process. Decreases in VI length were assumed to be 3%, as this was the average change in length of the piece of tissue dissected out. Three small pieces (approximately 1 cm in length) of each muscle fiber were dehydrated and embedded in plastic for microtomy. No measurable length changes occurred during this process. Sections of $4 \mu\text{m}$ thickness were cut and stained with phosphotungstic acid hematoxylin. Sarcomere lengths were determined using a light microscope with a total magnification of 800X. For each sample, the length of 20 sarcomeres was measured three times in five different locations. The sarcomere lengths were then determined as the mean of these 15 measurements divided by 20 (number of sarcomeres) and multiplied by the calibration factor of the micrometer and the shrinkage factor due to fixation. Errors in the determination of fiber and sarcomere lengths were estimated to be ± 2 mm and $\pm 0.1 \mu\text{m}$, respectively.

Determination of theoretical force-length relations. Once the sarcomere and fiber lengths were determined, it was necessary to obtain measures of sarcomere geometry for human skeletal muscles. The following measures were used: (a) thick filament length – $1.60 \mu\text{m}$, (b) thin filament length – $1.32 \mu\text{m}$, (c) bare zone – $0.17 \mu\text{m}$ (Walker and Randolph-Schrodt 1973).

According to the cross-bridge model, the active isometric force of a muscle is maximal when a maximal number of cross-bridge attachments between thick and thin filaments can be made. This is the case for sarcomere lengths ranging from $2.64 \mu\text{m}$ (i.e. twice the thin filament length) to $2.81 \mu\text{m}$ (i.e., $2.64 \mu\text{m}$ plus the width of the bare zone) in human skeletal muscles (Fig. 1) and is commonly referred to as the "optimal length." The force associated with this optimal sarcomere length is the maximal isometric force which will be assigned a normalized value of 1.0 (Fig. 1).

At sarcomere lengths of more than $2.81 \mu\text{m}$, the number of potential cross-bridge attachments between thick and thin filaments decreases in direct relation to thick and thin filament overlap. According to the cross-bridge model, the maximal force decreases in the same way, up to the point where thick and thin filaments cease to overlap. At this length ($4.24 \mu\text{m}$ i.e. thick filament plus twice the thin filament length) the force that a sarcomere can exert is believed to be zero (Fig. 1). This phenomenon is sometimes referred to as the »passive insufficiency« of a muscle (Steindler 1977).

At sarcomere lengths of less than $2.64 \mu\text{m}$, the maximal force that a sarcomere can exert has been shown to decrease (e.g., Gordon et al. 1966). The reasons for this decrease in force are not known. However, two basic mechanisms are often associated with it. The first mechanism relates to a decrease in the force producing ability of the cross-bridges due to changes in lateral spacing of thick and thin filaments and/or due to interference of the thin filaments with each other at these short sarcomere lengths. The second mechanism is associated with an increase in internal forces opposing the contractile forces. These internal

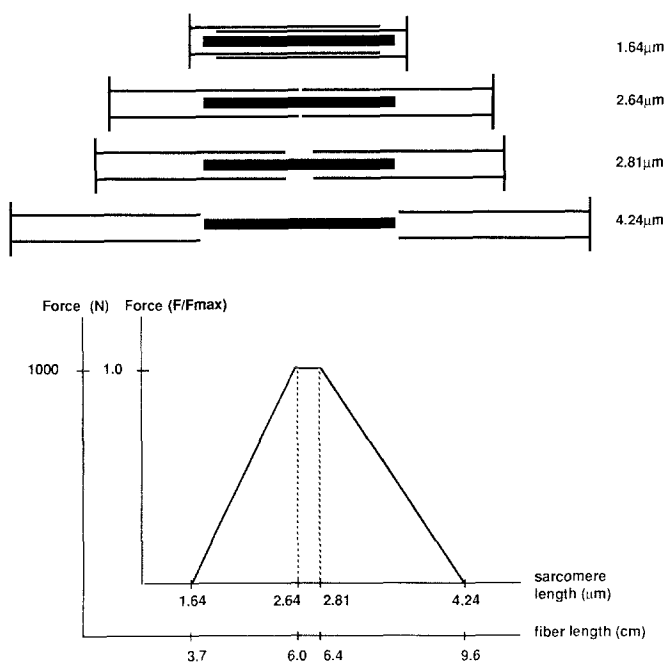


Fig. 1. The cross-bridge model and the theoretical relationship between sarcomere and fiber length and force production in human skeletal muscle. The thick and thin filaments are represented by the *thick* and *thin horizontal lines* in the top part of the figure, respectively. The bare zone is indicated by the gap between the thin filaments in the middle of the sarcomere at the sarcomere length of $2.81 \mu\text{m}$. See text for detailed explanation of cross-bridge model. Theoretical force-length relation of a muscle (*lower panel*). A sarcomere length of $2.64 \mu\text{m}$ was assumed to be associated with a fiber length of 6.0 cm and maximal active isometric force was taken to be 1000 N

forces are typically believed to be related to changes in osmotic pressures within the muscle fiber when the fiber changes its length, or they are associated with the compression of thick and thin filaments.

Since the precise mechanisms underlying the decrease in force below optimal sarcomere lengths are not known and since no experimental data for this part of the force-length relation are available for human skeletal muscles (or muscle fibers) an assumption had to be made. It was assumed that the decrease in force for sarcomere lengths below $2.64 \mu\text{m}$ was linearly related to sarcomere length. The point of zero force production (i.e., "active insufficiency") was taken to occur at a sarcomere length of $1.64 \mu\text{m}$, which is 60% of the length of a sarcomere at optimal length ($2.73 \mu\text{m}$) for human skeletal muscle. This value of 60% corresponds to findings on isolated fibers of frog skeletal muscle (Gordon et al. 1966), but the absolute values of optimal length in frog skeletal muscle (about $2.10 \mu\text{m}$) and zero force production ($1.27 \mu\text{m}$) do not coincide with those of human skeletal muscle because of the differences in thin filament lengths.

In order to obtain a force-length relation of a muscle, it was assumed that sarcomere lengths are linearly related to fiber lengths and that they are uniform within muscle fibers, and are the same between muscle fibers. Figure 1 shows an example in which a sarcomere length of $2.64 \mu\text{m}$ was associated with an arbitrarily selected fiber length of 6.0 cm and the maximal active isometric force was taken to be 1000 N .

For muscles with distinctly different fiber lengths [e.g. proximal, middle and distal parts of RF (Abrahamse et al. 1988)], force-length relations were determined for individual parts separately and then added together for corresponding joint configurations to obtain the force-length relation of the whole muscle. It was assumed in this that each part of the muscle can exert the same maximal isometric force and that changes in fiber length as a function of changes in joint configurations are the same for all parts of the muscle.

Table 1. Fiber and corresponding sarcomere lengths for selected human skeletal muscles

Muscle type	<i>n</i>	Mean fiber length (cm)	SD (cm)	<i>n</i>	Mean sarcomere length (μm)	SD (μm)
RF proximal	8	7.9	0.55	8	2.29	0.10
RF middle	8	7.2	0.69	8	2.34	0.13
RF distal	8	6.9	0.74	8	2.33	0.09
MG	7	4.9	0.60	7	2.75	0.54
LG	7	5.3	1.21	6	2.67	0.36
VL	8	7.9	1.46	8	1.92	0.23
VI	—	—	—	8	1.90	0.25
VM	8	8.0	1.15	8	1.86	0.27

RF = Rectus femoris; MG = medial gastrocnemius; LG = lateral gastrocnemius; VL = vastus lateralis; VI = vastus intermedius; VM = vastus medialis

Determination of strength curves. In order to determine strength curves, the force-length relations of synergistic muscles were added together for corresponding joint configurations. For the specific case of the strength curve for knee extension, the relation between changes in fiber lengths and changes in joint configurations was determined using an adaptation of the regression equations reported by Herzog (1985). The mean fiber length of VI at a fully extended knee position was assumed to be 6.8 cm (Wickiewicz et al. 1983). In order to account for the differences in the maximal active isometric force of the knee extensor muscles in the calculation of the knee extensor strength curve, the maximal active isometric force of each muscle was normalized relative to that of VL. The normalized values for RF, VL, VM, and VI were found to be 0.92 , 1.00 (by definition), 0.72 and 0.64 , respectively (Herzog 1987). These values were obtained based on the assumption that the maximal active isometric force of a muscle is linearly related to its physiological cross-sectional area.

Results and discussion

RF

The mean fiber and sarcomere lengths determined in this study are shown in Table 1. It was found that the fibers of the proximal part of RF were significantly longer than those of the middle and distal parts. The corresponding sarcomere lengths were similar. The force-length relations of the proximal, middle and distal parts of RF are shown in Fig. 2. The forces were normalized relative to the maximal force generated by each part and the fiber lengths are given in such a way, that they correspond to the same joint configurations. The ranges of fiber lengths over which forces can be observed are 8.9 , 8.1 , and 7.7 cm for the proximal, middle and distal parts, respectively. These differences in the range of active force production are directly related to the differences in fiber lengths. »Active« and »passive insufficiency« of the entire muscle, and thus the range of joint positions over which active force production of the entire muscle can occur, are determined by the fibers of the proximal part of RF.

The force-length relation of the whole RF muscle is shown in Fig. 3. This curve is the sum of the curves from Fig. 2, normalized to the maximal force of the entire muscle. The curves in Fig. 2 are not as smooth as that in Fig. 3. This is due to the non-uniform fiber lengths of the different parts

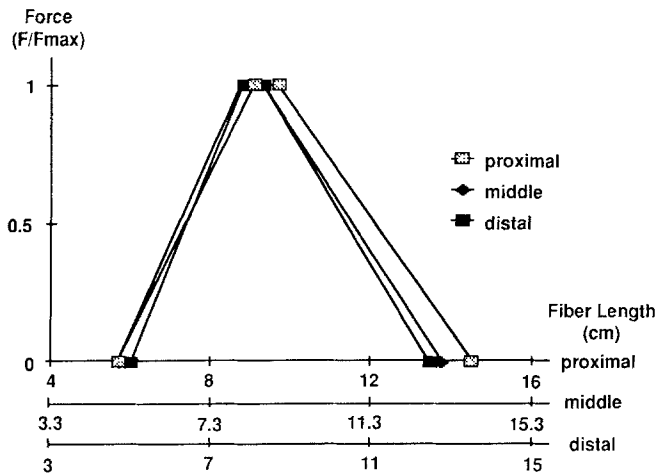


Fig. 2. Theoretical force-length relations of the proximal, middle and distal parts of human rectus femoris muscle. The forces were normalized relative to the maximal force generated by each part (f/f_{max})

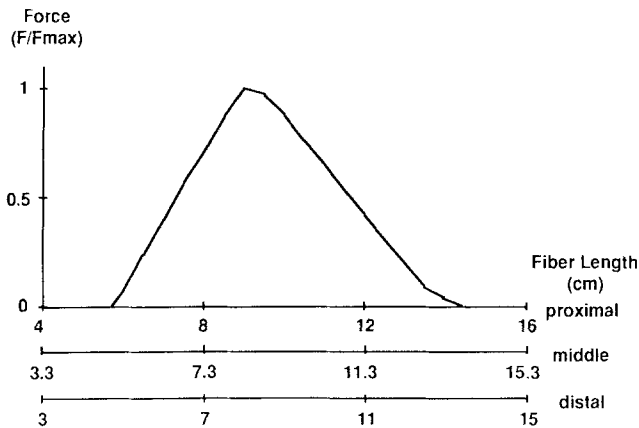


Fig. 3. Theoretical force-length relation of a whole human rectus femoris muscle. This curve is the sum of the curves shown in Fig. 2, normalized to the force generated by the whole muscle

of the muscle. If the force-length relation of the entire muscle was calculated summing the force-length relations of each individual fiber within that muscle, the non-uniformity of the fiber lengths would probably produce a perfectly smooth curve. In addition, if the non-uniformities in fiber lengths were more pronounced than is the case for RF, then the force-length relation of the entire muscle could theoretically be of a completely different shape than the one obtained using the cross-bridge model for one mean length of muscle fibers.

According to the cross-bridge theory, the maximal range of active force production of RF is 8.9 cm. Assuming that the average change in fiber length is governed by the regression equations reported by Herzog (1985), RF can exert force over a range of hip/knee joint angles of about 178° . The total range of motion at the hip and knee joints is approximately 260° (120° at the hip and 140° at the knee) and corresponds to a change in length of RF of about

13.0 cm. (Herzog 1985; Steindler 1977; Fick 1910). Since the range of motion of RF appears to be larger than its range of active force production, it may be assumed that there are joint configurations where the active force production of RF is zero. This phenomenon has been referred to as »active/passive insufficiency« of a muscle and has been described particularly for multi-joint muscles (e.g. Steindler 1977). Most recently, »active insufficiency« has been found experimentally in intact cat gastrocnemius muscles in our laboratory.

Gastrocnemius muscle

The mean fiber and sarcomere lengths of MG and LG are similar (Table 1). For the joint configuration investigated (knee angle of 180° , ankle angle of 142°), sarcomere and thus fiber lengths were optimal (i.e., sarcomere lengths were between $2.64 \mu\text{m}$ and $2.81 \mu\text{m}$), and correspond to some intermediate length of the in-situ muscle. The force-length relations of MG and LG and of the entire muscle are shown in Figs. 4 and 5, respectively.

According to the cross-bridge model, the maximal range of active force production of the whole gastrocnemius muscle is about 5.5 cm. The range of length changes of the in-situ gastrocnemius is believed to be about 8.8 cm (Grieve et al. 1978). Therefore, if the assumptions made above are correct, then there are knee/ankle joint configurations where the gastrocnemius muscle is not able to produce active force.

Active and passive insufficiencies of the gastrocnemius muscle are limited by the fibers of MG and LG, respectively. According to the cross-bridge model, active insufficiency of a relaxed gastrocnemius muscle is reached at joint angles of 180° and 166° at the knee and ankle, respectively, or at any combination of the two angles that keeps the gastrocnemius at the length (or shorter) corresponding to these two joint angles. Passive insufficiency of the gastrocnemius is reached at joint angles of 180° and 106° at the knee and ankle, respectively, or any combination of the two angles that keeps the gastrocnemius at the length (or longer) corresponding to these two joint angles. At joint configurations where passive insufficiency of the gastrocnemius is reached, the muscle may still be able to exert force due to passive elastic structures of the muscle that are arranged parallel to the active contractile elements (e.g., Wilkie 1968).

Vasti muscles

The sarcomere lengths of the VL, VM and VI and the fiber lengths of VL and VM are similar (Table 1). The fiber length of VI was taken from data reported by Wickiewicz et al. (1983) and appeared to be shorter (6.8 cm) than those of VL and VM obtained in this study. Wickiewicz et al. (1983) reported fiber lengths for joint angles corresponding to the anatomical position. This implies that the knee angle was 180° or slightly smaller. If the values of Wickiewicz et al. (1983) were obtained at a knee angle of precisely 180° , then they may be directly compared to those in Table 1. If the knee angle was smaller than 180° , the fiber lengths of VI

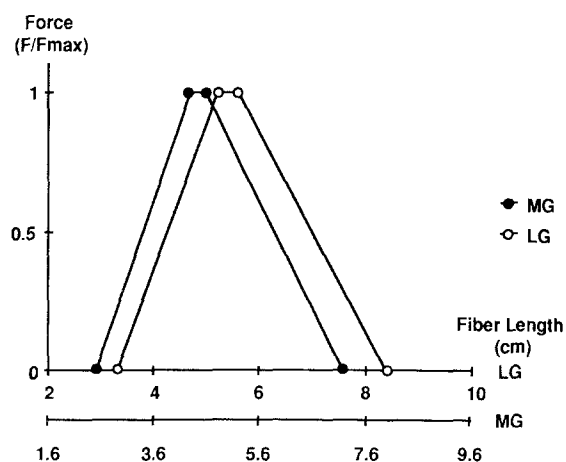


Fig. 4. Theoretical force-length relations of the medial and lateral parts of human gastrocnemius muscle. *MG* (●) and *LG* (○) represent the medial and lateral parts of the gastrocnemius muscle, respectively. Force is normalized to the maximal force generated by each part (f/f_{max})

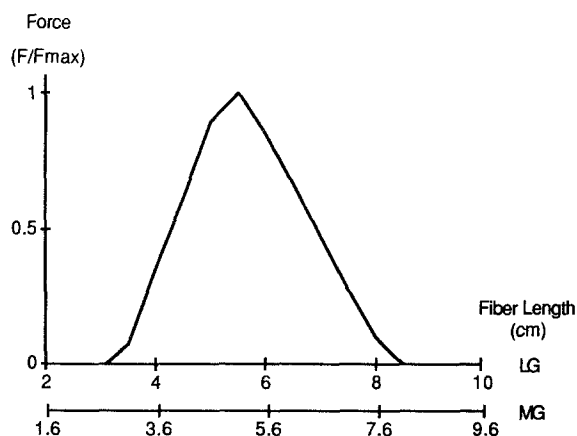


Fig. 5. Theoretical force-length relation of human gastrocnemius muscle. Force is normalized to maximal force generated by the whole muscle (f/f_{max})

would be overestimated compared to the values in Table 1. Therefore, it appears safe to assume that the fiber lengths of *VI* are shorter than those of *VL* and *VM*.

The theoretical force-length relations of the three vasti muscles are shown in Fig. 6. The fiber lengths on the horizontal axis are plotted such that they correspond to the same knee joint configuration. The maximal force of each muscle was normalized relative to the maximal force of *VL*. The range of active force production was determined to be 10.7, 11.2, and 9.3 cm for *VL*, *VM*, and *VI*, respectively. Therefore, all three muscles appear to be able to produce active force throughout the full range of motion of the knee joint. *VL* seems to be the most favorable muscle for force production at short muscle lengths, i.e. near full knee extension, whereas *VM* seems to be the most favorable muscle as muscle lengths increase, i.e. near full knee flexion. The range of optimal lengths of the three vasti muscles appears to be at similar knee joint configurations but different fiber lengths.

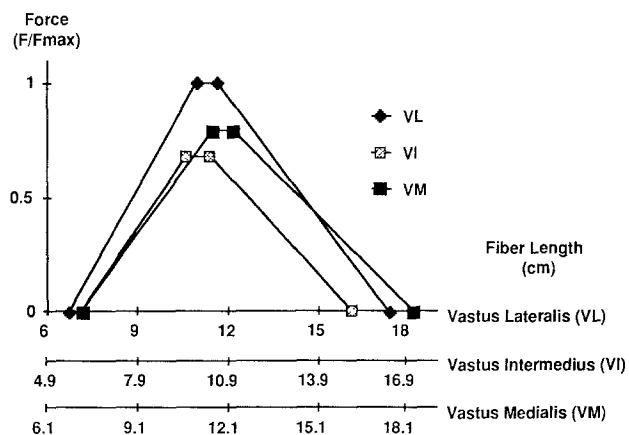


Fig. 6. Theoretical force-length relations of human vastus lateralis (*VL*), vastus medialis (*VM*), and vastus intermedius (*VI*) muscles. Force is normalized to the maximal force generated by (f/f_{max})

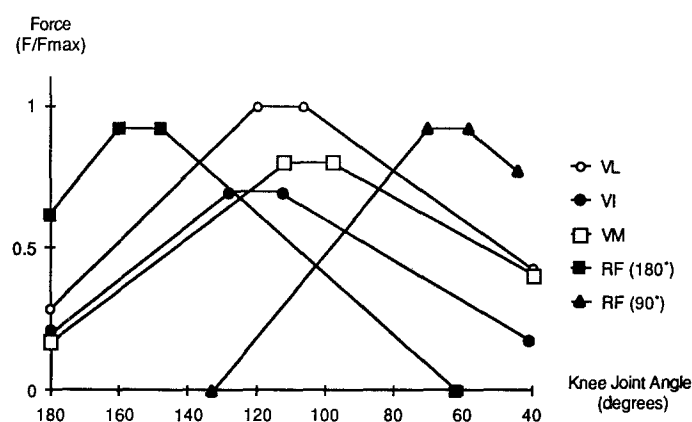


Fig. 7. Theoretical force-length relations of the individual knee extensor muscles. Length measures are given as a function of knee joint angle and the relation of the rectus femoris muscle is given for hip joint angles of 90° and 180°. Force is normalized to the maximal force generated by *VL*. *VL*, *VM* and *VI* are described in legend to Fig. 6; *RF*, rectus femoris muscle

Knee extensor strength curve

The maximal active isometric forces of all four knee extensor muscles are shown as a function of the knee joint angle and normalized to the maximal force of *VL* in Fig. 7. Since *RF* is a two-joint muscle, its force production depends on the hip and knee joint angles. The force production of *RF* is shown here for hip angles of 180° and 90°. When the hip is extended at 180° (i.e., lengthening of *RF* at the hip), active force production of *RF* is predicted to be zero before full knee flexion is reached. When the hip is flexed at 90° (i.e., shortening of *RF* at the hip), active force production is predicted to cease before full knee extension is reached. All three vasti appear to be able to produce active force throughout the full range of knee joint motion. The results in Fig. 7 suggest that the strength curve of the knee extensor muscles depends on the hip joint angle. This point is illustrated in Fig. 8, for hip joint angles of 180° and 90°.

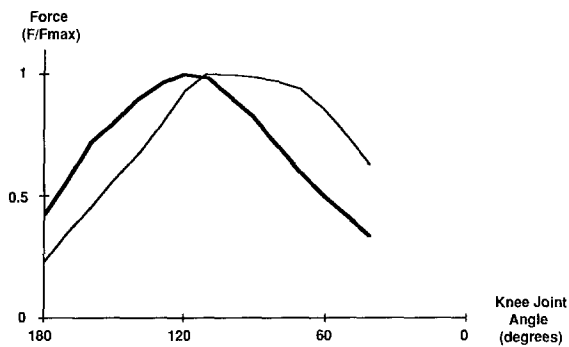


Fig. 8. Theoretical strength curves of the knee extensor muscles for hip joint angles of 90° (thin line) and 180° (thick line). Curves are the sums of force-length curves for individual knee extensor muscles, at 90° and 180° . Force is normalized to the maximal force generated

With the hip joint angle at 90° , the maximal force of the knee extensor muscles is predicted to occur at knee angles which are 10° – 20° smaller (i.e. the knee is more flexed) than with the hip joint angle at 180° . Also, the average decrease in force with increasing knee flexion is smaller with a hip joint angle of 90° than with one of 180° . As a consequence, the force of the knee extensor muscles is larger at full knee flexion (i.e. 40°) and the hip joint at 90° than at full knee flexion and the hip joint at 180° . The opposite is predicted at full knee extension.

The shape of the strength curves shown in Fig. 8 is similar to corresponding strength curves reported in a review article by Kulig et al. (1984) and our own findings (unpublished results). Also, maximal forces for strength curves of knee extensor muscles were reported for knee joint angles between 115° and 124° (Carpenter 1938), between 105° and 125° (Clarke et al. 1950), at 120° (Williams and Stutzmann 1959), between 80° and 120° (Campney and Wehr 1965), and at 120° (Lindahl et al. 1969). All these values are close to the occurrence of peak forces (110 – 120°) shown in Fig. 8.

The knee extensor strength curves in Fig. 8 show the force of the knee extensor muscles as a function of knee joint angle. However, strength curves typically relate an external force or moment to the joint angle (Kulig et al. 1984), thus including the effects that changes in moment arms of the muscles about a joint may have on this relation. For nearly constant moment arms of the muscles throughout the range of joint motion, this difference is not important; for highly variable changes in moment arms this difference may cause corresponding strength curves to have different shapes. According to Herzog (1985), moment arms of all knee extensor muscles are 17% to 42% larger at full knee extension than they are at knee joint angles below 120° . Therefore, it is speculated that a »moment vs joint angle« curve of the knee extensor muscles would be of similar shape as that shown in Fig. 8 for knee angles ranging from 40° to 120° whereas the curve may be slightly flatter than that in Fig. 8 for knee angles between 120° and 180° .

In this study force-length relations of human skeletal muscles were determined using sarcomere and fiber geometries obtained from cadaver studies and the cross-bridge model. In order to do this, some non-trivial assumptions

about the uniformity of sarcomere/fiber anatomy and the dynamics of fiber shortening were required. Also, the cross-bridge model of muscular contraction is based on several assumptions which have been questioned seriously (e.g. Iwazumi 1978). In addition, the theoretical considerations made here assume constant stimulation of the muscles; possible excitatory/inhibitory mechanisms due to proprioception and/or muscular synergism are not included. Therefore, it may well be that these theoretical force-length relations bear little meaning if one is interested in the actual force-length relations of in vivo human skeletal muscles. In order to test whether or not the force-length relations obtained in this study represent meaningful relations, an investigation has been undertaken in which force-length relations were determined experimentally for selected in vivo human skeletal muscles.

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References

- Abrahamse SK, Herzog W, and ter Keurs HEDJ (1988) Considerations regarding force-length relations of human rectus femoris muscle. Proceedings of the Canadian Society for Biomechanics Ottawa, pp 30–31
- Blix M (1891) Die Laenge und die Spannung des Muskels. Scand Arch Physiol 3: 295–318
- Campney HK, Wehr RW (1965) An interpretation of the strength differences associated with varying angles of pull. Res Q 36: 403–412
- Carpenter A (1938) A study of the angles in the measurement of the leg lift. Res Q 9: 70–72
- Clarke HH, Elkins EC, Martin GM, Wakim KG (1950) Application of muscle power to movements of the joints. Arch Phys Med Rehabil 31: 81–89
- Fick R (1910) Handbuch der Anatomie des Menschen, vol 2. Fischer, Stuttgart
- Gordon AM, Huxley AF, Julian FJ (1966) The variation in isometric tension with sarcomere length in vertebrate muscle fibers. J Physiol (London) 184: 170–192
- Grieve DW, Pheasant S, Cavanagh PR (1978) Prediction of gastrocnemius length from knee and ankle posture. Biomechanics VI-A. University Park Press, Baltimore, pp 405–412
- Herzog W (1985) Individual muscle force prediction in athletic movements. Thesis, University of Calgary Printing
- Herzog W (1987) Determination of muscle model parameters using an optimization technique. Biomechanics X-B, pp 1175–1179
- Herzog W, ter Keurs HEDJ (1988) Force-length relation of in-vivo human rectus femoris muscles. Pflügers Arch 411: 642–647
- Hill AV (1938) The heat of shortening and the dynamic constants of muscle. Proc R Soc Lond Biol 126: 136–195
- Huxley AF (1957) Muscle structure and theories of contraction. Prog Biophys Biophys Chem 7: 255–318
- Iwazumi T (1978) Molecular mechanism of muscle contraction: another view. In: Baan J, Nordergraaf A, Baines J (eds) Cardiovascular system dynamics. MIT Press, Cambridge, Mass. pp 11–21
- Kulig K, Andrews JG, Hay JG (1984) Human strength curves. Exercise and sport sciences reviews, vol 12. The Collamore Press, Lexington, pp 417–466

- Lindahl O, Movin A, Rindgrist I (1969) Knee extension measurement of the isometric force in different positions of the knee joint. *Acta Orthop Scand* 40: 79–85
- Steindler A (1977) *Kinesiology of the human body*. Thomas, Springfield
- Wagemans E, Leemputte M van, Willems E (1988) An ultrasound method to determine muscle structure. *Proceedings of the American Society of Biomechanics, 12th Annual Meeting*. pp 208–209
- Walker SM, Randolph-Schrodt G (1973) I-segment lengths and thin filament periods in skeletal muscle fibers of the Rhesus monkey and the human. *Anat Rec* 178: 63–82
- Wickiewicz TL, Roy RR, Powell PL, Edgerton VR (1983) Muscle architecture of the human lower limb. *Clin Orthop* 179: 275–283
- Wilkie DR (1968) *Studies in biology 11. Muscle*. Arnold London
- Williams M, Stutzmann L (1959) Strength variation through the range of joint motion. *Phys Ther* 39: 145–152