The Force-Length Curves of the Human Rectus Femoris and Gastrocnemius Muscles in Vivo

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For a physiologically realistic joint range of motion and therefore range of muscle fiber lengths, only part of the whole muscle force-length curve can be used in vivo; that is, only a section of the force-length curve is expressed. Previous work has determined that the expressed section of the force-length curve for individual muscles can vary between subjects; however, the degree of intersubject variability is different for different muscles. This study determined the expressed section of both the rectus femoris and gastrocnemius—muscles with very different ratios of tendon slack length to muscle fiber optimum length—for 28 nonspecifically trained subjects to test the hypothesis that the value of this ratio affects the amount of variability in the expressed section. The force-length curves of the two muscles were reconstructed from moment-angle data using the method of Herzog & ter Keurs (1988). There was no relationship between the expressed sections of the force-length curve for the two muscles. Less variability was found in the expressed section of the gastrocnemius compared with the rectus femoris, supporting the hypothesis. The lack of relationship between the expressed sections of the two muscles has implications for motor control and for training muscle for rehabilitation.

Keywords: muscle, force, human

Various studies have shown that skeletal muscles often operate over only part of the force-length curve in vivo; that is, only part of the relationship characteristically seen in isolated preparations is expressed in whole muscles in vivo (e.g., Huijing, 1998; Lieber & Friden, 1998; Maganaris, 2001; Savelberg & Meijer, 2003). Here, the term expressed section of the force-length relationship refers to the section of the force-length curve that muscles operate over within the range of muscle lengths corresponding to a physiologically realistic joint range of motion. This expressed section can include all or any part of the force-length curve (e.g., Herzog & ter Keurs, 1988a; Maganaris, 2001; Savelberg & Meijer, 2003; Winter & Challis, 2008a).

Previous studies have demonstrated that subjects can vary in their expressed section of the force-length curve for certain muscles. For example, Herzog and ter Keurs (1988a) and Savelberg and Meijer (2003) have shown that there is a great deal of variability in the expressed section of the force-length relationship for the rectus femoris. However, studies on other muscles have not shown the same variability in the expressed section; for example, both Herzog et al. (1991b) and Winter and Challis (2008a) have shown that there is very little variation in the expressed section for the gastrocnemius, with most subjects operating over the ascending limb of the force-length curve. These studies all used the method of Herzog and ter Keurs (1988b), which permits the reconstruction of the force-length curve of biarticular muscles for individual subjects. This method assumes that for a biarticular muscle crossing two joints, A and B, the variation in the output at Joint A in response to a change in the angle of Joint B can only be due to the force-length properties of the biarticular muscle since the contribution of monoarticular muscles crossing Joint A would be constant. A sensitivity analysis was conducted to demonstrate the robustness of the technique of Herzog and ter Keurs (1988b) against typical in vivo sources of error using models of the triceps surae (Winter & Challis, 2008b).

The model-based validation of the method of Herzog and ter Keurs (1988b) involved building three models of the triceps surae such that each of the models contained a gastrocnemius operating over a different section of the force-length curve (ascending, plateau, and descending). In Winter and Challis (2008b), when building these models of the gastrocnemius, it was found that a critical model parameter in determining the proportion of the force-length curve used was the ratio of tendon slack length to muscle fiber optimum length ($L_{SLACK} : L_{OPT}$). When this ratio assumed a high value of more than 7 (representing a long tendon and short muscle fibers), it means that a much greater proportion of the force-length curve was used (more than a half). When this ratio
assumed a low value of less than 4 (representing a short tendon and long muscle fibers), a small proportion of the force-length relationship was used (less than a third). If a small proportion of the force-length curve is used then there is scope for much more variability in the expressed section of the force-length curve. If a large proportion of the force-length curve is used, then there is much less scope for variability in the expressed section, and given that a high value of $LT.SLACK : LF.OPT$ would generally be associated with a long, compliant tendon, the tendon extension would tend to shift the expressed section toward the ascending limb and plateau region of the force-length curve. This reasoning led to the hypothesis that low values of $LT.SLACK : LF.OPT$ would allow variability in the expressed section of the force-length curve, whereas high values of $LT.SLACK : LF.OPT$ would constrain variability. The values of other architectural and mechanical parameters would then determine the specific section expressed. The reported in vivo values of the would then determine the specific section expressed. The curve. This reasoning led to the hypothesis that low values of $LT.SLACK : LF.OPT$ would allow variability in the expressed section of the force-length curve, whereas high values of $LT.SLACK : LF.OPT$ would constrain variability. The values of other architectural and mechanical parameters would then determine the specific section expressed. The reported in vivo values of the $LT.SLACK : LF.OPT$ ratio are high for the gastrocnemius compared with other muscles due to the long Achilles tendon (e.g., rectus femoris 2.7, gastrocnemius 8.9, Hoy et al., 1990). This may explain why there is apparently greater variability in the expressed section in the rectus femoris (Herzog & ter Keurs, 1988a; Savelberg & Meijer, 2003) compared with the gastrocnemius (Herzog et al., 1991b; Winter & Challis, 2008a). However, it is difficult to make a direct comparison between these studies since they were conducted on different subjects. To reduce the effect of interindividual variability in the expression of the force-length relationship caused by environmental or training variations, it would be useful to compare the expressed section of these two muscles in the same subjects, and to collect data for a large number of subjects.

The purpose of this study was therefore to determine the force-length properties of the rectus femoris for a large group of untrained subjects and then to compare these results with the expressed section of the force-length curves obtained for the gastrocnemius (GA) in the same subjects (Winter & Challis, 2008a). The $LT.SLACK : LF.OPT$ ratio is a critical parameter in determining the section of the force-length relationship that a muscle operates over. Since the range of values that can be adopted for this parameter is wider for the rectus femoris than for the gastrocnemius, it would be expected that there would be more variability between subjects in the section of the force-length relationship that is expressed in the rectus femoris than for the gastrocnemius. Furthermore, since the difference in the value of this ratio between the muscles would be greater than the interindividual variation for a given muscle, there should be no relationship between the expressed sections of the two muscles for a given subject.

### Methods

Fourteen male and 14 female subjects (females: mass 60.9 kg ± 10.0, height 1.66 m ± 0.02; males: mass 86.1 kg ± 11.9, height 1.81 m ± 0.07) participated in this study. The subjects had not previously engaged in sports specific training, and had no history of injury of the right knee, ankle, or hip joints. Subjects gave written informed consent, and all procedures were approved by the Institutional Review Board at Pennsylvania State University.

To determine the force-length relationship of the rectus femoris, subjects performed maximal voluntary contractions on a Biodex III dynamometer using their right leg, at five knee angles (10, 30, 60, 90, and 110 degrees of flexion) for a given hip angle (see Figure 1 for definitions of joint angles). The hip angle was then changed and contractions were performed for the knee angles at the new hip angle. Knee extensions were performed at hip angles of 85, 70, 55, 40, 25, and 0° of flexion over two testing sessions. Subjects were allowed two efforts in each position and a 1-min rest between contractions. The order of all angles was randomized. The method of force-length curve reconstruction assumes—for example, on the rectus femoris—that for a given knee angle and set of hip angles the contribution of the biarticular muscle to the recorded joint moment varies, while the contribution of the monoarticular muscle remains constant. The validity of this method is discussed elsewhere (Winter & Challis, 2008b).

Measurement of the gastrocnemius force-length curve was performed on the same group of subjects using essentially the same experimental protocol, which was again performed over two days. The ankle joint was tested at five ankle angles (40, 30, and 15° of plantar flexion; 0 and 15° of dorsiflexion) for a given knee angle. The knee angle was then changed, and contractions at the same ankle angles were then performed at the new knee angle. Four knee angle positions were used (0, 50, 90, 115°, with 0° defined as full extension). Again, the order of presentation of the joint angles was randomized.

Before each trial in a given joint configuration, care was taken to ensure that the dynamometer axis was correctly aligned with the relevant joint axis. All bolts and moving parts on the dynamometer were checked and tightened, and restraining straps were used around the toes, ankle, heel, knee, thigh, and trunk. Before each contraction, a baseline recording was taken to account for any passive moment exerted on the dynamometer. Testing was performed on two separate days, four to ten days apart. The Biodex output was sampled at 100 Hz and filtered at 20 Hz. The passive moment was subtracted from the peak moment in each position to give the active moment.

The method used to reconstruct the force-length curves was based on the method of Herzog and ter Keurs (1988b). This method is explained in detail elsewhere for the reconstruction of the gastrocnemius force-length curves (Winter & Challis, 2008a); however, a brief description follows here for the reconstruction of the rectus femoris force-length curves. Muscle lengths and muscle moment arms were computed for each subject using regression equations based on cadaver data (Hawkins & Hull, 1990). The force in the patellar tendon was computed from the active moments and appropriate moment arms. Use of other regression equations (e.g.,
Visser et al., 1990) produced equivalent results. The change in the normalized rectus femoris muscle length was computed as a change from the reference position, defined as a fully extended knee and a 0° hip angle. This means that a muscle length shorter than the length of the muscle in the reference position is reported here as a negative length, and a length that is longer than the reference position length is reported as a positive length.

Robust regression techniques (Huber, 1996) were used to fit first- and second-order polynomials to each set of forces measured at the same knee angle, but at different hip angles. Sections of the force-length curve of muscle are either linear or concave down curves (Gordon et al., 1966). A second-order polynomial was used as long as it produced a concave down curve, this was the case for 27 of the 28 subjects; otherwise, the first-order polynomial was chosen. The polynomial for the first data set was used to predict the force value of the first data point in the second set, and the force difference was then subtracted from all the data points in this second set. This procedure was repeated for all subsequent sets. Following this alignment, second-order polynomials were fitted to the entire data set.

As a measure of goodness of fit, $r^2$ values were computed for each reconstructed curve. The expressed section of the force-length curve for a given muscle for an individual subject was identified using the location of the peak force within the analyzed range of fiber lengths. A muscle was identified as operating on the ascending limb if the peak force occurred at more than 60% of the way through the fiber lengths, a muscle was on the descending limb if the peak force occurred up to 40% of the way through, and a muscle was identified as operating on the plateau region if the peak force occurred between 40 and 60% of the range of fiber lengths. To test the hypothesis that the subjects would operate on the same portion of their force-length curve for both muscles, Fisher’s exact test for associations was used and a one-sided $p$-value calculated (Fisher, 1922). For this statistical analysis, only the plateau and descending limb categories were collapsed to form one category due to low cell counts in these categories for the gastrocnemius.

**Results**

For the rectus femoris, 14 subjects operated on the ascending limb of the force-length curve, 7 operated over the plateau region, and the remaining 9 subjects operated on the descending limb. For the rectus femoris, the mean and standard deviations of the subjects working on the ascending, plateau, and descending region of the force-length curve are presented (Figure 2). For the gastrocnemius, 24 subjects operated on the ascending limb of the force-length curve, 1 operated over the plateau region, and the remaining 3 subjects operated on the descending limb (Figure 3). For the gastrocnemius, the mean and standard deviation is presented for the subjects working on the ascending limb (Figure 3a); the data for the subject operating on the plateau is presented (Figure 3b); and the remaining three subjects operated on the descending region of the force-length curve, so here the median curve is presented for this group due to the low number of subjects (Figure 3c). The $r^2$ values for the reconstructed curves were generally high (>0.80). Statistical comparisons of the number of subjects falling into each category showed no relationship between expressed section of the force-length curve for the gastrocnemius and the rectus femoris ($p = .356$).
Discussion

The gastrocnemius showed a great deal of consistency across subjects in the expressed section of the force-length relationship: 24 subjects operated over the ascending limb, 1 subject over the plateau, and 3 over the descending limb. The distribution of expressed section for the rectus femoris was similar to that found by Herzog and ter Keurs (1988a). For the rectus femoris, there was a nearly equal distribution across the three sections with around a third of the subjects operating over each section. There was no relationship between the expressed sections of the two muscles; that is, for individual subjects, the expressed section for the gastrocnemius had no correlation or relationship with the expressed section of the rectus femoris. These results show that there is greater variability in the expressed section of the force-length curve for the rectus femoris than the gastrocnemius. These two muscles are very different in the ratio of their tendon slack length to fiber optimum length \( \frac{L_{\text{TSLLACK}}}{L_{\text{TOPT}}} \); rectus femoris 2.7, gastrocnemius 8.9; Hoy et al., 1990). These results support the hypothesis that the \( \frac{L_{\text{TSLLACK}}}{L_{\text{TOPT}}} \) ratio is important in determining a given muscle’s scope for variability in the expressed section.

The \( \frac{L_{\text{TSLLACK}}}{L_{\text{TOPT}}} \) ratio seems to constrain the scope of variability in the expressed section of the force-length curve because it affects the proportion of the force-length curve that is used over the physiological joint range of motion. However, variation in the \( \frac{L_{\text{TSLLACK}}}{L_{\text{TOPT}}} \) ratio can also affect the particular section of the force-length curve that is expressed. Increasing the ratio shifts the expressed section toward the descending limb since the short muscle fibers tend to reach their maximum length, and decreasing the ratio shifts the expressed section toward the ascending limb since the longer fibers tend not to reach their maximum length. As the typical \( \frac{L_{\text{TSLLACK}}}{L_{\text{TOPT}}} \) ratio is already high for the gastrocnemius, raising it even a small amount would make the muscle fibers so short that they reach their maximum length before the limit of the range of motion of the joints. However, decreasing the ratio leads to longer muscle fiber lengths than are typically seen in vivo (e.g., Maganaris et al., 2006); therefore, this ratio seems constrained for the gastrocnemius. This constraint means that most subjects would tend to express similar sections of the force-length relationship, and the specific section expressed would then be determined by other architectural and mechani-
cal properties of the muscle-tendon complex. For the gastrocnemius, the long compliant tendon would mean that the expressed section is shifted to the ascending limb for most subjects. In contrast, the rectus femoris has a low $L_{\text{SLACK}} : L_{\text{OPT}}$ ratio, meaning that a much smaller proportion of the force-length relationship is used. At lower values of the ratio, there is much more scope for small interindividual variation in the specific value of the $L_{\text{SLACK}} : L_{\text{OPT}}$ ratio to have an effect on the particular section of the rectus femoris force-length curve that is expressed for a particular subject. The particular section expressed would also be affected by the value of other parameters, such as the joint angle at which the optimum length occurs.

A number of studies have shown changes in sarcomere number as a consequence of different demands being placed on muscle (e.g., Koh & Herzog, 1998; Williams et al., 1999). It has been shown, in animal studies, that even adult muscle is able to change the serial number of sarcomeres (e.g., Tabary et al., 1972; Williams & Goldspink, 1978; Williams et al., 1999). In animal studies, there is evidence that the nature of the exercise regimen influences muscle force-length properties. When Lynn et al. (1998) had rats exercise either on an inclined or a declined treadmill, the shape of the force-length curve changed depending on the treadmill incline. The number of sarcomeres in series in the vastus intermedius was greater in muscle fibers from decline-trained animals. Previous studies in humans have found that there is a difference in the force-length properties of the rectus femoris between cyclists and runners (Herzog et al., 1991a; Savelberg & Meijer, 2003). The cyclists tended to be stronger at short rectus femoris lengths (a negative gradient to the force-length curve, indicating that they operated over the descending limb), whereas the runners were stronger at longer rectus femoris lengths (a positive gradient to the force-length curve, indicating that they operated over the ascending limb). This apparent specialization may be due to a training adaptation, or it may be that individuals with specific force-length properties gravitate toward sports for which they are adapted. Nevertheless, it would seem that for muscles such as the gastrocnemius, where the value of the $L_{\text{SLACK}} : L_{\text{OPT}}$ ratio is constrained, such specialization is not possible.

The results in this study were for nonspecifically trained subjects. Nonspecifically trained subjects chosen since specialized training could affect the relationship between the two muscles in terms of the expression of the force-length relationship. It is possible that some kind of chronic functional demand exists even in nonspecifically trained subjects, and for this reason a large group of 28 subjects was examined. However, there was no consistent relationship between the expressed section of the two muscles. The finding that there was no relationship between the two muscles in terms of their expressed section has implications for the coordination of complex movements. For example, if a subject operated over the ascending limb for the rectus femoris, they did not necessarily operate over that limb for the gastrocnemius.

These two muscles are involved in the sequential extension of joints in the lower limb in many activities, such as running and jumping. As different subjects have different gradients of their force-length curves for the same muscle (positive versus negative), this may indicate the requirement for different activation strategies to produce optimally coordinated movement. The tests conducted here were under maximal conditions, but most daily activities occur at submaximal levels. During submaximal contractions, muscle force will be reduced and therefore also tendon stretch, so for a given joint angle configuration, muscle fibers would be longer under submaximal conditions than under maximal conditions. This means, for example, that muscles identified as operating on the ascending limb would shift to longer lengths toward the plateau and descending limb.

Some studies have also attempted to determine the expressed section of the force-length relationship for monoarticular muscles (e.g., Sale et al., 1982; Gravel et al., 1987; Ichinose et al., 1997; Maganaris, 2001). However, the methods used to determine the expressed section of monoarticular muscles often involve assumptions that would preclude variability in the expressed section being observed. For example, Maganaris (2001) averaged moment-angle data across subjects in determining the expressed section of the soleus in vivo; this treatment assumes that all subjects have the same expressed section. Ichinose et al. (1997) determined the expressed section of the force-length relationship for the vastus lateralis by assuming that the vastus lateralis contributes 34% of the knee extension moment; however, this assumes in turn that all four muscles of the quadriceps group have the same expressed section for all subjects. Sale et al. (1982) assumed that the gastrocnemius would be slack if the knee were placed at a 90° angle, allowing the determination of the expressed section of the soleus. However, this in turn makes an assumption about the expressed section of the gastrocnemius (that it operates over the ascending limb) and assumes that it is the same for all subjects. The method of Herzog and ter Keurs (1988b) allows subject-specific determination of the force-length relationship because it does not involve such generic assumptions. Nevertheless, the method does assume the following: maximum efforts are produced during the voluntary contractions, co-contraction is absent, the moment arm is appropriate, and the dynamometer records the moment correctly. The validity of these assumptions has been discussed elsewhere (Herzog & ter Keurs, 1988b; Winter & Challis, 2008b), but briefly, Winter and Challis (2008b) showed that the reconstruction method is robust to variations in the assumed moment arm, and to random and systematic noise such as that occurring due to random instances of incomplete activation or some systematic fatigue.

Data collection from the Biodex requires careful experimental protocols to ensure accurate results; the results in the present study produced maximum moment levels and strength curves typical of those in the literature (Kulig et al., 1984). There is evidence in the literature
that high reliability can be obtained with the type of testing performed here (e.g., Callaghan et al., 2000; Suter et al., 1996). Pilot work showed that six normally active but nonspecifically trained subjects were able to perform the required number of contractions in this study with a coefficient of variation of 4–7% for 20 maximum voluntary contractions performed in the same position. These subjects also showed no large increase in the peak moment as a result of familiarization once three to four practice contractions had been performed. Fatigue and or learning effects could have influenced the measured joint moments and therefore the reconstructed force-length curves. Since testing took place over two days, the joint configurations tested at the start of the first session were repeated both at the end of the first session and during the second session to examine the influence of learning or fatigue. In 18% of sessions, there was a decrease of 10% or more in the measured moment at the end of the session compared with the beginning of the session. To examine the influence of such changes, the experimental data for each subject were perturbed randomly by 10% and 20% of their existing value, but the identified section of the force-length curve remained the same. It has previously been shown that the reconstruction method is robust against such noise (Winter & Challis, 2008b). Problems with the use of the Biodex have been highlighted by Arampatzis et al. (2005), who found that the Biodex-measured plantar flexion moment differed from that obtained using a motion analysis system and a pressure distribution insole. For the present analysis, the systematic errors these authors identified are not important since they would affect all of the data points equally, and therefore would not alter the identified section of the force-length curve.

The study has highlighted that different subjects exploit different portions of the force-length curves in vivo. The source of such variation warrants further study. An understanding of the expression of this muscle property in vivo can provide important insights into muscle function and has implications for motor control (Feldman & Latash, 2005), the success of tendon transfer surgery (Orendurff et al., 2005), and the advancement of science: recent attempts to falsify the equilibrium point hypothesis. Experimental Brain Research, 161, 91–103.


References


