

## Effect of knee flexion angle on active joint stiffness

M. P. McHugh and D. E. Hogan

Nicholas Institute of Sports Medicine and Athletic Trauma, Lenox Hill Hospital, New York, USA

Received 18 July 2003,  
accepted 8 November 2003  
Correspondence: Malachy P.  
McHugh, Nicholas Institute of  
Sports Medicine and Athletic  
Trauma, Lenox Hill Hospital, 130  
East 77th Street, New York, NY  
10021, USA.

### Abstract

**Aim:** The purpose of this study was to determine if active joint stiffness measured during maximum voluntary knee extension contractions was affected by knee flexion angle.

**Methods:** Eighteen subjects volunteered (11 male, seven female). A stretch was imposed on isometric knee contractions performed at 30°, 50°, 70°, 90°, and 110° of knee flexion. Active joint stiffness was computed from the increase in torque relative to the change in knee flexion angle for the first 50 ms of the stretch (approximately 1.5°) and corrected for effects of gravitational component due to leg mass and passive tension.

**Results:** There was a plateau in knee extension torque between 70° and 90° with lower values at all other angles ( $P < 0.05$ ). Peak active joint stiffness occurred at 70° with lower values ( $P < 0.05$ ) at all other angles except 50°. Stiffness at 70° ( $441.1 \pm 189.9 \text{ Nm rad}^{-1}$ ) was 49% higher than at 30° and 45% higher than at 110°.

**Conclusion:** Active joint stiffness was dependent on knee flexion angle. Peak joint stiffness during maximal contractions occurred at, or prior to, the optimal angle for torque production for all subjects.

**Keywords** knee extension torque, length–tension relationship, muscle-tendon unit, passive stiffness.

When an isometrically contracted muscle is stretched there is an augmentation in contractile force. This response has been studied in animal models using single fibre (Rack & Westbury 1974, Malamud *et al.* 1996) and whole muscles preparations (Walmsley & Proske 1981), and in humans during voluntary or stimulated contractions (Sinkjaer *et al.* 1988, Blanpied & Smidt 1992, 1993). This response has been referred to as short-range stiffness (Rack & Westbury 1974, Walmsley & Proske 1981, Malamud *et al.* 1996), short-range tension (Whitehead *et al.* 2001), the short-range elastic component (Haugen & Sten-Knudsen 1981, Campbell & Lakie 1998), and intrinsic muscle or joint stiffness (Sinkjaer *et al.* 1988, Blanpied & Smidt 1992, 1993). In controlled animal experiments the measured stiffness is thought to reflect cross-bridge attachment strength or cross-bridge stiffness (Malamud *et al.* 1996, Whitehead *et al.* 2001) but tendon compliance also plays a role (Rack & Westbury 1974, Walmsley & Proske 1981). In the *in vivo* human studies, stiffness was shown to be a

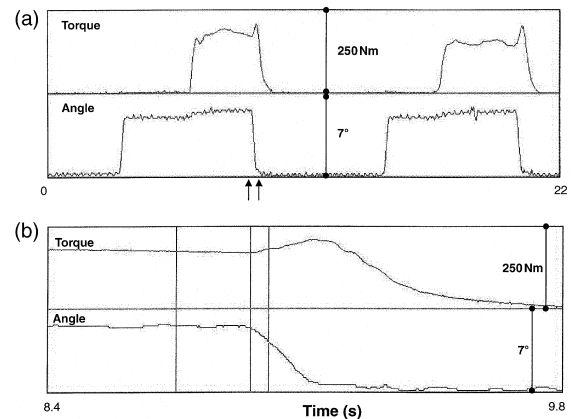
function of prestretch torque, with higher stiffness values with higher contraction intensities (Sinkjaer *et al.* 1988, Blanpied & Smidt 1992, 1993). Since the number of cross-bridges systematically increases with contraction intensity, it was concluded that *in vivo* measurement of stiffness also reflected the number of attached cross-bridges or cross-bridge stiffness. However, no additional evidence was provided to support such a conclusion.

The effect of muscle length on stiffness has been studied in animal models in relaxed and contracted states (Flitney & Hirst 1978, Haugen & Sten-Knudsen 1981, Whitehead *et al.* 2001). Of note, stiffness was decreased on the descending limb of the length tension curve in isometrically contracted frog sartorius muscles (Flitney & Hirst 1978). Since the number of cross-bridges is decreased on the descending limb of the length–tension curve (Huxley & Peachey 1961, Gordon *et al.* 1966) decreased stiffness was attributed to the decrease in the number of cross-bridges. The effect of

joint angle and, therefore, muscle length, on *in vivo* measurements of active joint stiffness during voluntary contractions is not well understood. Stiffness has been measured at different muscle lengths during voluntary contractions of the plantarflexors in humans (Blanpied & Smidt 1992). Prestretch plantarflexion torque and active joint stiffness were higher at 6° of dorsiflexion compared with 6° and 18° of plantarflexion. However, stiffness measurements were not made at joint angles beyond optimum. The optimal angle for peak plantarflexion torque may be 20° of dorsiflexion or greater (Winegard *et al.* 1997) and since this is close to the anatomic limit of dorsiflexion motion, the ankle joint may not be ideal for looking at stiffness at angles beyond optimum. By contrast, the optimal angle for knee extension torque is between 60° and 90°, and torque measurements can be reliably made at greater knee flexion angles (Aagaard *et al.* 2000). Therefore, the purpose of this study was to examine the effect of knee flexion angle on active joint stiffness during maximum voluntary knee extension contractions. The term active muscle stiffness is used to refer to the stretch response during isometric knee extension contractions. Since active joint stiffness regulates the initial response to external perturbations it is important to understand factors affecting this response. It was hypothesized that stiffness would be decreased at joint angles beyond the optimal angle for torque production.

## Methods

Eighteen subjects (11 males, seven females) volunteered to participate (age  $29 \pm 7$  years, height  $174 \pm 10$  cm, weight  $76.3 \pm 15.7$  kg;  $\pm$ SD) with informed consent. Subjects performed maximum isometric knee extension contractions on an isokinetic dynamometer (Biodex System 2, Shirley, NY, USA) at 30°, 50°, 70°, 90°, and 110° of knee flexion. Subjects were seated upright (90° of trunk flexion). The distal portion of the dynamometer arm was strapped just proximal to the ankle joint and the axis of rotation was aligned with the lateral femoral condyle of the knee. In order to verify reproducible joint angles between subjects, 90° of knee flexion was defined as the angle at which the dynamometer arm was perfectly vertical, as determined by a carpenter's level. The slight knee extension that occurred at the onset of each isometric contraction due to compression of the padding on the dynamometer arm was not accounted for. Therefore, the actual knee flexion angles for the isometric contractions were somewhat less than the angles reported. It was felt that minimal further padding compression occurred during the stretch. It was also apparent that the dynamometer arm yielded approximately 1° at the onset of some



**Figure 1** Knee extension torque and knee flexion angle during isometric contractions and during imposed 5° stretches. (a) Two contractions at 70° are shown. Isometric contraction begins after the dynamometer reaches the target angle. Stretch is indicated by change in knee flexion angle during the contractions. The subject relaxed after the stretch and torque returned to zero. The two arrows on the x-axis indicate the time period highlighted in (b). (b) Isometric torque was averaged between the first and second vertical lines. The stretch-induced torque augmentation shows an initial increase followed by a plateau and then a continued increase. Active joint stiffness was calculated from the increase in torque relative to change in angle between the second and third vertical lines (50 ms).

high force contractions (Fig. 1a) but this was not thought to have affected the torque measurements.

During each contraction the dynamometer arm was set to move 5° in flexion thereby imposing a stretch on the activated quadriceps. Subjects were instructed to maintain each contraction for 3 s. The stretch was imposed 2 s into the contraction and subjects were instructed to maintain maximum effort during the stretch. The dynamometer velocity was set at  $2.62 \text{ rad s}^{-1}$  for the stretch (highest available velocity). Two contractions were performed at each angle with 7 s between contractions and 2 min between tests at the different angles. For each set of two contractions the leg was set at the test angle and recordings began with torque set to zero. Therefore, at each test angle baseline torque due to leg mass and passive muscle tension was not measured and the isometric torque at each angle represented the contractile force production.

Torque and angle data were acquired from the dynamometer using Myosoft software (Noraxon, Scottsdale, AZ, USA). Data were sampled at 1000 Hz. The average isometric torque for the 200 ms prior to stretch was recorded as the isometric knee extension value at each test angle. Active joint stiffness was computed from the angle and torque recordings (Fig. 1). Measurement resolution was 0.1° and 0.1 Nm. The beginning of the stretch was defined as the point at

which the position recording changed from baseline. The increase in torque during the first 50 ms of stretch was divided by the change in knee flexion angle to provide a measure of angular stiffness. This time frame was chosen to avoid any potential neural effects that would occur with a longer duration stretch (Sinkjaer *et al.* 1988, Blanpied & Smidt 1992, 1993). The first 50 ms of stretch occurred during the acceleration phase, with an average knee flexion velocity of  $0.52 \text{ rad s}^{-1}$  ( $1.5^\circ$  knee flexion in 50 ms; Fig. 1). The active joint stiffness values for the two trials at each knee flexion angle were averaged. The measured active stiffness represents the total stiffness due to both the active and passive components. In order to correct for the effects of leg mass and passive muscle tension, the torque response to passive flexion was measured from  $0^\circ$  to  $115^\circ$  at  $0.087 \text{ rad s}^{-1}$ . While this joint velocity was lower than the active stretch velocity, it was felt that complete muscle relaxation was more easily achieved during the slow stretch. Electrical silence in the vastus medialis, vastus lateralis and rectus femoris during the passive stretch was confirmed by use of surface electromyography. The passive torque changes ( $30^\circ$ – $35^\circ$ ,  $50^\circ$ – $55^\circ$ ,  $70^\circ$ – $75^\circ$ ,  $90^\circ$ – $95^\circ$  and  $110^\circ$ – $115^\circ$ ) were computed in  $\text{Nm rad}^{-1}$ . Although the active stiffness measurements were computed for  $1.5^\circ$  changes, it was felt that analysis of  $5^\circ$  during the passive trials would provide better measurement resolution than  $1.5^\circ$  intervals. These passive values were subtracted from the total stiffness values measured during the stretches imposed on the isometric contractions. For example, the combination of leg mass and torque due to passive hamstring tension decreased from  $30^\circ$  to  $35^\circ$  of knee flexion and represented a negative stiffness. From  $110^\circ$  to  $115^\circ$  the leg mass and torque due to passive quadriceps tension increased and was represented by a positive stiffness. This means of correction did not account for the inertial components of the response to the acceleration phase of the stretch during contraction. Prior to testing subjects, simulation trials were recorded to ensure that there was no torque response from the dynamometer during unloaded  $5^\circ$  rotations at the test velocity at each of the test angles.

The stiffness measurements for  $5^\circ$  increments in the passive trial represented the combined contributions of leg mass and passive muscle and joint tension. For example, passive tension close to full extension is due to the combined effects of hamstring stiffness and leg mass, while passive tension beyond  $90^\circ$  is due to the combined effects of leg mass and quadriceps stiffness. Since there is no leg mass effect at  $90^\circ$  of knee flexion, the gravitational effect of leg mass at  $70^\circ$  was equal and opposite of that at  $110^\circ$ . Therefore, the increase in passive tension from  $70^\circ$  to  $110^\circ$  reflects passive muscle tension with the leg mass component eliminated. This

increase in passive tension was quantified for each subject and expressed in  $\text{Nm rad}^{-1}$ . This passive stiffness measurement was made to compare active and passive joint stiffness measurements.

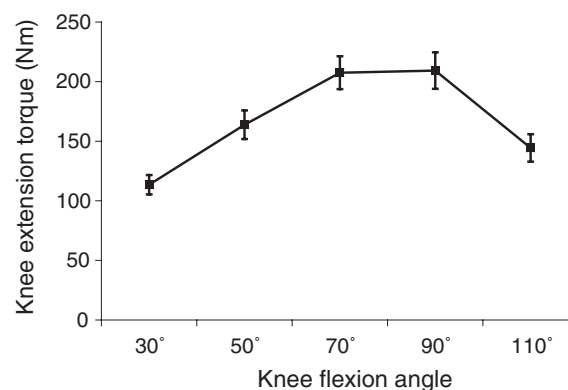
### Statistical analysis

Repeated measures analysis of variance was used to examine the effects of knee flexion angle on knee extension torque and active joint stiffness (total and active stiffness). All pairwise comparisons were performed with Bonferroni corrections. The significant ( $P < 0.05$ ) pairwise comparisons are reported where there was a significant main effect of knee flexion. Mean  $\pm$  SD is reported in the text and mean  $\pm$  SE is shown in the figures.

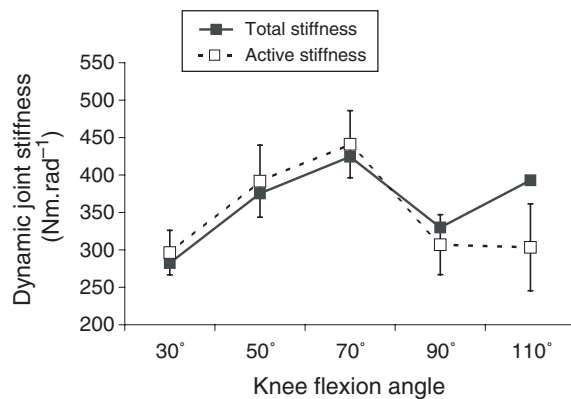
### Results

Knee extension torque at  $70^\circ$  and  $90^\circ$  was greater ( $P < 0.05$ ) than torque at  $30^\circ$ ,  $50^\circ$  and  $110^\circ$  (Fig. 2). Additionally, torque at  $50^\circ$  was greater than torque at  $30^\circ$  ( $P < 0.05$ ). Total active joint stiffness was higher ( $P < 0.05$ ) at  $70^\circ$  compared with  $30^\circ$  and  $90^\circ$  (Fig. 3). Following correction for the passive component, active stiffness at  $70^\circ$  was also higher ( $P < 0.05$ ) than stiffness at  $110^\circ$ , with no significant differences in stiffness between the other angles (Fig. 3).

Peak torque occurred at  $50^\circ$  in one subject,  $70^\circ$  in eight subjects and  $90^\circ$  in nine subjects. Peak stiffness occurred at  $30^\circ$  in one subject,  $50^\circ$  in six subjects,  $70^\circ$  in 10 subjects and  $90^\circ$  in one subject. Peak stiffness occurred at the same angle as peak torque in five subjects and at a knee flexion angle prior to the angle for peak torque in the other subjects.



**Figure 2** Knee extension torque (Nm) at each knee flexion angle (mean  $\pm$  SE). Torques at  $70^\circ$  and  $90^\circ$  were greater than torques at  $30^\circ$ ,  $50^\circ$ , and  $110^\circ$  ( $P < 0.01$ ). Torque at  $50^\circ$  was greater than torque at  $30^\circ$  ( $P < 0.01$ ).



**Figure 3** Total and active joint stiffness (corrected for the passive component) in  $\text{Nm rad}^{-1}$  at each knee flexion angle (mean  $\pm$  SE). Total stiffness at 70° was greater than stiffness at 30° and 90° ( $P < 0.05$ ). Active stiffness at 70° was greater than stiffness at 30°, 90° and 110° ( $P < 0.05$ ).

Passive joint stiffness was  $28.7 \pm 15.4 \text{ Nm rad}^{-1}$ , which was considerably less than active joint stiffness ( $296.4 \pm 125.8 \text{ Nm rad}^{-1}$  at 30°,  $391.7 \pm 204.1 \text{ Nm rad}^{-1}$  at 50°,  $441.1 \pm 189.9 \text{ Nm rad}^{-1}$  at 70°,  $306.9 \pm 170 \text{ Nm rad}^{-1}$  at 90°,  $303.4 \pm 246.1 \text{ Nm rad}^{-1}$  at 110°). Passive stiffness was unrelated to active stiffness at any angle (Pearson product-moment correlations  $r = 0.41$  to  $-0.06$ ,  $P = 0.09$  to  $P = 0.81$ ). Passive stiffness was related to isometric knee extension torque at 30°, 50° and 70° ( $r = 0.55$ – $0.70$ ,  $P < 0.05$ ) but not at 90° ( $r = 0.4$ ,  $P = 0.1$ ) and 110° ( $r = -0.02$ ,  $P = 0.9$ ). Passive stiffness was significantly correlated with the decrease in knee extension torque from 70° to 110° ( $r = 0.68$ ,  $P < 0.01$ ), indicating that subjects with a greater loss of torque from 70° to 110° had a greater increase in passive torque in this range.

## Discussion

These results clearly demonstrate an effect of knee flexion angle on active joint stiffness measured during voluntary knee extension contractions. Stiffness values at 70° were on average 49% higher than at 30°, 44% higher than at 90° and 45% higher than at 110°, but were not significantly different from stiffness values at 50° (13% difference). By comparison isometric knee extension torque at 70° was 82% higher than torque at 30°, 27% higher than at 50° and 44% higher than at 110°, but not significantly different from torque at 90° (<1% difference). Previous studies have demonstrated that ankle stiffness is a function of prestretch plantar-flexion torque (Blanpied & Smidt 1992, 1993). This data was based on stiffness measurements made at different contraction intensities at the same joint angle. In the present study, prestretch knee extension torque

was varied by changing knee flexion angle rather than contraction intensity. The resultant stiffness measurements appeared to be related to prestretch torque with respect to results at 70°, 30° and 110°. However, the results at 90° clearly did not fit this relationship. There was no difference in isometric torque between 70° and 90° while stiffness was 44% higher at 70°.

The angle–torque relationship is analogous to the length–tension relationship, but during knee extension, torque production is affected by changes in the patellar tendon moment arm at different joint angles. The patellar tendon moment arm is greatest between 30° and 60° of knee flexion, declining progressively at greater angles (Nisell 1985). Therefore, knee extension torque at 110° can be assumed to have been on the descending limb of the length–tension relationship, with torque production at 30° and 50° on the ascending limb and torque at 70° and 90° in a plateau region. Based on this estimate of the length–tension relationship it would be difficult to attribute decreased stiffness at 90° to changes in cross-bridge formation as a function of muscle length. If muscle length-induced changes in cross-bridge formation contributed to the difference in stiffness between 70° and 90°, a further decline in stiffness would have been expected at 110°. However, stiffness at 110° was only 1.2% lower than stiffness at 90°. Testing subjects in supine would have lengthened the rectus femoris and possibly shifted the angle–torque relationship to the left. This may have provided more than one angle on the descending limb of the angle–torque curve. However, subject stabilization during testing and maintenance of joint alignment with the dynamometer become issues in this position. Unfortunately increasing knee flexion beyond 115° was problematic with this dynamometer.

The difference between total stiffness and stiffness corrected for the passive component was most apparent at 110° of knee flexion. At this angle the torque contribution of leg mass is small but the contribution from passive quadriceps tension is large. Of note, total stiffness at 70° and 110° were not different. This emphasizes the importance of the passive component in the mechanical response to stretch of contracted muscles. At 70° of knee flexion the torque contribution from passive tension in the quadriceps (or hamstrings) was presumably minimal and the magnitude of the leg mass contribution was the same as at 110° (acting in an opposite direction). Therefore, it was not surprising that the corrected active joint stiffness measurement was only 3.9% lower than the total stiffness at 70° whereas this difference was 23% at 110°.

The computation of passive joint stiffness from the increase in passive torque from 70° to 110° provided a measure of passive joint stiffness with the leg mass contribution eliminated. Active stiffness was more than

10 times higher than passive stiffness. Although active and passive stiffness were unrelated it was apparent that passive joint stiffness was related to maximum isometric knee extension torque. The relationship between passive stiffness and the decline in isometric torque from 70° to 110° is functionally relevant. A greater decline in active torque represents a greater loss of torque on the descending limb of the length–tension relationship. The fact that a greater increase in passive stiffness occurs with greater losses in active torque production, indicates that the functional range of the joint may be linked to the passive stiffness of that joint. This relationship warrants further investigation.

In this study, it was not possible to determine which structures contributed to active joint stiffness. Similar *in vivo* measurements have been attributed to cross-bridge mechanics (Blanpied & Smidt 1992, 1993). However, it is possible that the tendon and aponeurosis absorb the lengthening imposed by the stretch. For example, in running turkeys (Roberts *et al.* 1996) and walking cats (Griffiths 1991) the tendon and aponeurosis absorb lengthening of the whole muscle-tendon unit, thereby allowing the muscle fibres to function isometrically, or actually shorten. Similarly, in humans during stretch-shortening cycle movements, the tendon and aponeurosis store energy during the loading (stretching) phase that is utilized during the propulsive (shortening) phase (Finni *et al.* 2000). Significant tendon and aponeurosis strain has been demonstrated during ramp isometric contractions of the plantarflexors (Magnusson *et al.* 2001). However, the slope of the stress/strain curve indicated minimal strain with increased stress close to maximum. Since the stretches in this study were imposed after 3 s of maximum isometric contraction, further tendon strain may not have occurred. This would imply that the contractile component was yielding to a rigid non-contractile component. Depending on muscle architecture and function it is possible for the non-contractile component (e.g. tendon) to yield to a rigid contractile component (e.g. muscle fibres) as has been demonstrated in the kangaroo gastrocnemius muscle (Morgan *et al.* 1978). It is also important to note that differential strains may be seen between the tendon and aponeurosis (Finni *et al.* 2003, Magnusson *et al.* 2003). Based on these observations (Morgan *et al.* 1978, Griffiths 1991, Roberts *et al.* 1996, Finni *et al.* 2003, Magnusson *et al.* 2003) it would be difficult to determine which structures absorb the slight lengthening imposed by the stretch in this study.

Active joint stiffness has been measured during voluntary contractions of the plantarflexors (Blanpied & Smidt 1992, 1993) and dorsiflexors (Sinkjaer *et al.* 1988) using similar techniques to those used here. The reported stiffness values are comparable with the values

reported here. At a stretch velocity of 0.87 rad s<sup>-1</sup> plantarflexor stiffness was approximately between 143 and 344 Nm rad<sup>-1</sup> for contractions ranging from 20 to 60% of maximum (Blanpied & Smidt 1992). Stiffness values of 143 Nm rad<sup>-1</sup> were reported for dorsiflexors at 80% maximum with the ankle in 10° of plantarflexion (Sinkjaer *et al.* 1988). The stiffness values in the present study ranged from a mean of 296 Nm rad<sup>-1</sup> at 30° to 441 Nm rad<sup>-1</sup> at 70°.

Stretch-induced torque augmentation has been investigated during voluntary quadriceps contractions using a stretch of larger amplitude and velocity than that used in this study (Webber & Kriellaars 1997). A 12° stretch at 60° of knee flexion at 100°/s resulted in an average increase in knee extension torque of 44%. Mean isometric torque at 60° was 319 Nm (Webber & Kriellaars 1997). This translates into a stiffness value of 670 Nm rad<sup>-1</sup> for a 12° stretch. In this study mean torque at 70° was 208 Nm. A 12° stretch resulting in a 44% increase in torque would give a stiffness value of 435 Nm rad<sup>-1</sup>. This is remarkably similar to the measured stiffness value of 441 Nm rad<sup>-1</sup> at 70°. It should be noted that stiffness values for smaller amplitude stretches would be higher than stiffness values for larger amplitude stretches (Rack & Westbury 1974). However, the higher angular velocity for the stretch used by Webber & Kriellaars (1997) would be expected to result in a greater augmentation in torque.

Despite the general agreement between the active joint stiffness values reported here and values either reported elsewhere (Sinkjaer *et al.* 1988, Blanpied & Smidt 1992, 1993), or extrapolated from similar work (Webber & Kriellaars 1997), there are methodological limitations to this study. The change in knee flexion angle during the stretch may have been overestimated due to further compression of the padding during the stretch. The measured angular deformation during the stretch varied slightly from trial to trial (95% confidence intervals 1.4°–1.7°). Of note, angular displacement in 50 ms was not affected by prestretch torque. The variance was probably due to variance in detecting the onset of the stretch from the angle recording rather than variance in the actual movement of the dynamometer. Importantly, the magnitude of the torque increase during 50 ms (not expressed relative to the angular displacement) showed the same statistical differences between angles as shown for total stiffness. This indicates that the variance in angular displacement did not affect comparison of stiffness between angles. A further limitation was that the separation of the active and passive components did not specifically account for inertial effects. Additionally, the stretch velocity was relatively low compared with previous studies (Sinkjaer *et al.* 1988, Blanpied & Smidt 1992, 1993, Webber & Kriellaars 1997). A higher stretch velocity was not

possible due to the limitations of the dynamometer. While these limitations may have affected measurement accuracy it was not felt that these factors affected the main findings in the study. There was a clear affect of knee flexion angle and a general agreement with stiffness values reported previously.

In conclusion, peak active joint stiffness occurred at, or prior to (shorter muscle length), the angle for optimal isometric knee extension torque. Lowest stiffness values were observed at knee flexion angles representing the shortest and longest muscle lengths.

## References

- Aagaard, P., Simonsen, E.B., Andersen, J.L., Magnusson, S.P., Bojsen-Moller, F. & Dyhre-Poulsen, P. 2000. Antagonist muscle coactivation during isokinetic knee extension. *Scand J Med Sci Sports* 10, 58–67.
- Blanpied, P. & Smidt, G.L. 1992. Human plantarflexor stiffness to multiple single-stretch trials. *J Biomech* 25, 29–39.
- Blanpied, P. & Smidt, G.L. 1993. The difference in stiffness of the active plantarflexors between young and elderly human females. *J Gerontol* 48, 58–63.
- Campbell, K.S. & Lakie, M. 1998. A cross-bridge mechanism can explain the thixotropic short-range elastic component of relaxed frog skeletal muscle. *J Physiol* 510, 941–962.
- Finni, T., Komi, P.V. & Lepola, V. 2000. In vivo human triceps surae and quadriceps femoris muscle function in a squat jump and counter movement jump. *Eur J Appl Physiol* 83, 416–426.
- Finni, T., Hodgson, J.A., Lai, A.M., Edgerton, V.R. & Sinha, S. 2003. Nonuniform strain of human soleus aponeurosis-tendon complex during submaximal voluntary contractions in vivo. *J Appl Physiol* 95, 829–837.
- Flitney, F. & Hirst, D. 1978. Cross-bridge detachment and sarcomere 'give' during stretch of active frog's muscle. *J Physiol* 276, 449–465.
- Gordon, A.M., Huxley, A.F. & Julian, F.J. 1966. The variation in isometric tension with sarcomere length in vertebrate muscle fibers. *J Physiol* 184, 170–192.
- Griffiths, R.I. 1991. Shortening of muscle fibres during stretch of the active cat medial gastrocnemius muscle: the role of tendon compliance. *J Physiol* 436, 219–236.
- Haugen, P. & Sten-Knudsen, O. 1981. The dependence of the short-range elasticity on sarcomere length in resting isolated frog muscle fibres. *Physiol Scand* 112, 113–120.
- Huxley, A.F. & Peachey, L.D. 1961. The maximum length for contraction in vertebrate striated muscle. *J Physiol* 156, 150–165.
- Magnusson, S.P., Aagaard, P., Rosager, S., Dyhre-Poulsen, P. & Kjaer, M. 2001. Load-displacement properties of the human triceps surae aponeurosis in vivo. *J Physiol* 53, 277–288.
- Magnusson, S.P., Hansen, P. & Aagaard, P. *et al.* 2003. Differential strain patterns of the human gastrocnemius aponeurosis and free tendon, in vivo. *Acta Physiol Scand* 177, 185–195.
- Malamud, J.G., Godt, R.E. & Nichols, T.R. 1996. Relationship between short-range stiffness and yielding in type-identified, chemically skinned muscle fibres from the cat triceps surae muscles. *J Neurophysiol* 74, 2280–2289.
- Morgan, D.L., Proske, U. & Warren, D. 1978. Measurements of muscle stiffness and the mechanism of elastic storage of energy in hopping kangaroos. *J Physiol* 282, 253–261.
- Nisell, R. 1985. Mechanics of the knee. A study of joint and muscle load with clinical applications. *Acta Orthop Scand* 216 (Suppl.) 1–42.
- Rack, P.M.H. & Westbury, D.R. 1974. The short range stiffness of active mammalian muscle its effect on mechanical properties. *J Physiol* 240, 331–350.
- Roberts, T.J., Marsh, R.L., Weyand, P.G. & Taylor, C.R. 1996. Muscular force in running turkeys: the economy of minimizing work. *Science* 275, 1113–1115.
- Sinkjaer, T., Toft, E., Andreassen, S. & Hornemann, B.C. 1988. Muscle stiffness in human ankle dorsiflexors: intrinsic and reflex components. *J Neurophysiol* 60, 1110–1121.
- Walmsley, B. & Proske, U. 1981. Comparison of stiffness of soleus and medial gastrocnemius muscles in cats. *J Neurophysiol* 46, 250–259.
- Webber, S. & Kriellaars, D. 1997. Neuromuscular factors contributing to in vivo eccentric moment generation. *J Appl Physiol* 83, 40–45.
- Whitehead, N.P., Gregory, J.E., Morgan, D.L. & Proske, U. 2001. Passive mechanical properties of the medial gastrocnemius muscle of the cat. *J Physiol* 536.3, 893–903.
- Winegard, K.J., Hicks, A.L. & Vandervoort, A.A. 1997. An evaluation of the length-tension relationship in elderly human plantarflexor muscles. *J Gerontol* 52A, B337–B343.