

Figure 6 Ensemble averaged power spectrum of CoP sway during quiet stance with open eyes (upper panels) and closed eyes (lower panels) before- (thin lines) and after-bed rest (thick lines). Note that the y-axis scales are different below (left, $8 \times 10^{-2} \text{ cm}^2$) and above (right, $8 \times 10^{-4} \text{ cm}^2$) 1 Hz for visual purposes.

increased because of bed rest in both groups, indicating that postural sway does not correspond primarily to muscle volume and its balance around the ankle joint. These findings led us to conclude that the muscle volume around the ankle has little influence on the maintenance of postural sway during bed rest. This conclusion is supported by the previous findings of Loram & Lakie (2002), who concluded that mechanical ankle stiffness relating to muscle volume was not sufficient to stabilize the human inverted pendulum.

For BR-Con, there was no change in the AEMG of the plantar flexors as an indicator of muscle activity level, despite the decrease in muscle volume, showing that the quantitative property of muscle activity did not compensate for the loss in volume of the contributing muscle group. Therefore, it seems natural that the mean velocity of CoP accompanied by torque for plantar flexion ought to decrease during quiet standing in the BR-Con group. These suggestions highlight the contradiction that the responses of postural sway are not equivalent to the synergistic relation between muscle volume and muscle activity level. The results obtained from the plantar flexor muscles in response to bed rest do not sufficiently explain the reason for this contradiction. Recent studies have pointed out that hip joint motion likely plays an important role in the efficient maintenance of human standing (Accornero *et al.* 1997, Aramaki *et al.* 2001). Aramaki *et al.* (2001) suggested that coordination between movement of the hip and the

ankle joints minimizes body sway. Therefore, the contradiction mentioned above may be explained by the possibility that other body parts besides that which we focused on, i.e. the ankle joint, were critically involved.

Effects of bed rest and strength training on postural sway

The mean velocity of the CoP as a regulatory balancing activity for maintaining an upright posture (Maki *et al.* 1990) during quiet standing significantly increased after bed rest in both the BR-Con and BR-Tr groups for both eye conditions (EO and EC). This result would imply that factors other than the loss of muscle volume influence postural instability by bed rest.

Changes in the distribution of muscle activity among synergistic muscles have been suggested as one of the factors that may influence the fluctuations in torque during low-level contractions (Kouzaki *et al.* 2002, 2004). In fact, our previous study demonstrated that increases in torque fluctuation for plantar flexors were related to changes in muscle activation across the plantar flexor synergists after bed rest with strength training (Shinohara *et al.* 2003), which succeeded in maintaining the muscle mass of the plantar flexion (Akima *et al.* 2003). However, no changes were found in the distribution of EMG activity across plantar flexor muscles during quiet standing after bed rest in both groups. In contrast to agonist muscles, TA activity as an

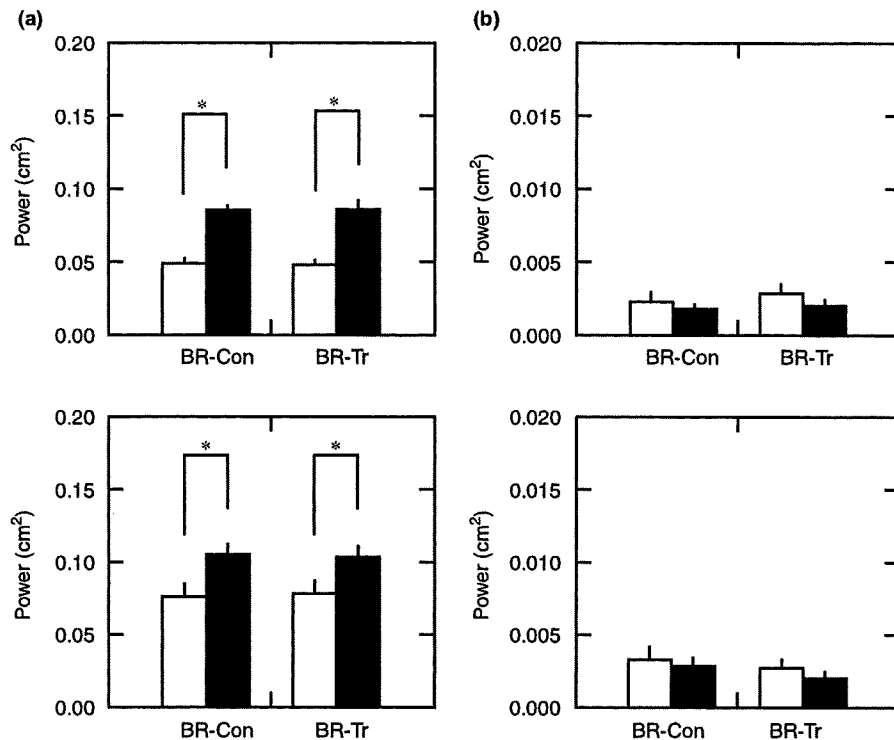


Figure 7 Low- (LF) and high-frequency (HF) components of CoP during quiet stance before and after bed rest. Group-averaged (\pm SE) low- (a) and high-frequency (b) components for power spectrum of CoP sway before (open bar) and after bed rest (filled bar) with both groups in EO (upper panel) and EC (bottom panel) conditions. * $P < 0.05$ was the significant difference between the before- and after-bed-rest values.

antagonist tended to increase because of bed rest in both groups. This is similar to the results of spaceflight (Roll *et al.* 1998). In contrast, the ratio of muscle volume in TA to that in the plantar flexors (SOL, MG and LG) increased only in BR-Tr, not in BR-Con. These results, therefore, imply that the decreased postural response resulting from bed rest is not related to the muscle volume and muscle activity around the ankle joint but to neural control mechanisms contributing to postural stabilization (Loram & Lakie 2002, Masani *et al.* 2003).

In the present study, structural posturographic parameters were computed using a sway density plot approach introduced by Baratto *et al.* (2002) to identify the feedforward control actions or motor commands for postural stability. MP extracted from SDC significantly decreased after bed rest, and MD significantly increased after bed rest. Furthermore, these changes could be observed in both the BR-Con and BR-Tr groups (Fig. 5). These findings were similar to those in previous studies that employed Parkinsonian patients (Baratto *et al.* 2002) and experimental pain (Corbeil *et al.* 2004). In contrast, the adaptation of MP and MD because of bed rest was quite different

from that for the osteoporotic patients (Baratto *et al.* 2002). The results obtained from the present study, therefore, suggest that the capacity of the postural control system to integrate sensory information and anticipate physiological internal delays to keep the vertical alignment of the body (Baratto *et al.* 2002) decrease because of bed rest, even though strength training for maintenance of muscle volume of the lower limbs was applied.

Postural control is detected by the vestibular, visual and somatosensory systems, and upright posture is stabilized by these feedback data (Nashner 1981). Mauritz & Dietz (1980) suggested that the vestibular loop is extremely important for stabilizing posture as demonstrated by the result that body sway at low frequencies increased when the blocking of peripheral afferents induced by leg ischemia was applied. Furthermore, the vestibular system is necessary in controlling equilibrium during quiet standing, as reported by Horak *et al.* (1990), who compared the postural responses of control subjects and patients with bilateral vestibular loss. It has been suggested that the vestibular roles in equilibrium are integrated with visual input during quiet standing (Bent *et al.* 2002), and the importance of

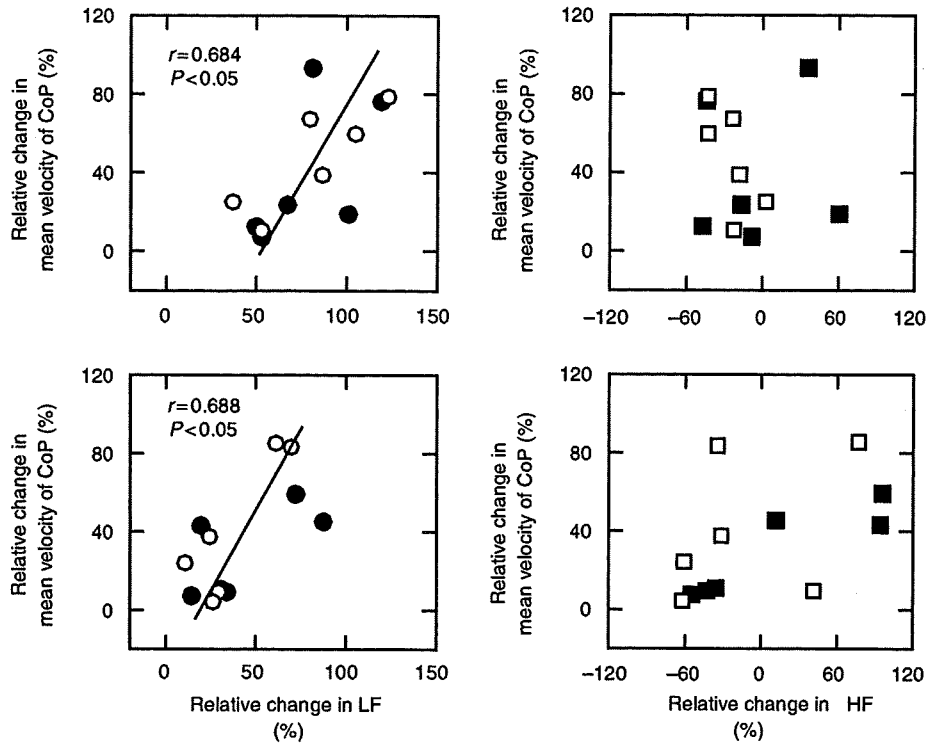


Figure 8 Relative changes in mean velocity of CoP as a function of relative changes in LF and HF components. Circles (left panels) and squares (right panels) indicate LF and HF respectively. Open and filled symbols represent individual values of BR-Tr and BR-Con respectively. The superimposed lines are the regression lines between each frequency component for CoP sway and the mean velocity of CoP including both subject groups. Upper and bottom panels indicate EO and EC conditions respectively.

	Eyes open		Eyes closed	
	Before	After	Before	After
BR-Con				
SOL	8.89 ± 2.27	10.71 ± 2.42	10.47 ± 2.33	10.59 ± 2.04
MG	3.70 ± 1.02	3.23 ± 0.81	4.75 ± 1.22	3.45 ± 0.83
LG	1.89 ± 0.57	2.48 ± 0.63	2.03 ± 0.57	2.50 ± 0.63
TA	0.39 ± 0.06	0.53 ± 0.09	0.47 ± 0.06	0.55 ± 0.08
BR-Tr				
SOL	10.46 ± 2.43	9.18 ± 0.88	11.09 ± 2.03	9.08 ± 0.88
MG	4.45 ± 1.01	5.37 ± 1.86	5.74 ± 1.20	6.02 ± 1.86
LG	2.98 ± 0.74	3.10 ± 0.88	3.43 ± 0.85	3.22 ± 0.92
TA	0.61 ± 0.12	1.14 ± 0.52	0.66 ± 0.12	1.18 ± 0.57

Data are mean ± SE for six subjects. AEMG normalized to that of maximal voluntary contraction (%MVC). BR-Con and BR-Tr indicate non-training group during bed rest and strength training group during bed rest respectively. SOL, soleus; MG, medial gastrocnemius; LG, lateral gastrocnemius; TA, tibialis anterior.

Table 2 Average electromyogram (AEMG) obtained from plantar flexor muscles during quiet standing before- and after- bed rest

visual information for postural stability has been emphasized (Diener *et al.* 1982). Several studies reported the significant contribution of pressure receptors in the plantar soles, which are known to transmit

information for postural control (Horak *et al.* 1990, Kavounoudias *et al.* 2001, Maurer *et al.* 2006). It has been suggested that the pressor information from the soles and plantar cutaneous sensitivity are of

importance for postural response via vestibular information (Magnusson *et al.* 1990, Kavounoudias *et al.* 2001). In the present study, the LF (≤ 1 Hz) of CoP sway in the EO and EC conditions was significantly increased after bed rest in both subject groups, and the relative change in LF by bed rest correlated significantly with that in the mean velocity of CoP (Fig. 8). Therefore, it is likely that a gravitational unloading by bed rest has an adverse affect on the postural sway because of the lack of ground reaction forces of the plantar soles and their spatial distribution. These findings suggest that strength training during bed rest cannot counteract the malfunction of the vestibular and visual systems with regard to postural stability. Another system related to body sway also assists stability and control. Namely, it has been reported that a somatosensory system including the proprioception functions of large diameter afferents contributes to the feedback mechanism to play a significant role in controlling quiet standing (Fitzpatrick & McCloskey 1994). In the present study, there was no significant change in the HF (from 1 to 10 Hz) of CoP sway because of bed rest in either group for either the EO or EC condition (Fig. 7b), and a lack of relative change in the mean velocity of CoP by bed rest was associated with the HF of CoP sway. Previous studies on neuromuscular adaptation in humans reported that inactivity, such as parabolic flight (Miyoshi *et al.* 2003) and long-term spaceflight (Lambertz *et al.* 2003), has little effect on the H-reflex amplitude. Namely, the somatosensory systems are considered to reflect changes in no influence of the gravity-related inactivity. In the present study, therefore, it is suggested that the somatosensory data, including proprioception information for maintaining stability, was not influenced by bed rest, and that the strength training employed in the present study had no effect on the somatosensory system. Taken together, these findings suggest the possibility that the postural ataxia caused by 20-day bed rest can be attributed mainly to the vestibular and visual systems for the maintenance of human body balance.

In conclusion, postural sway assessed by the mean velocity of CoP increased following bed rest even though the muscle volume of the contributing muscle group was maintained because of strength training. This suggests that the change in postural strategy because of 20-day unloading was induced by imbalance of the muscle volume around the ankle joint and postural control neural mechanisms. Furthermore, it is also suggested that strength training cannot counteract the postural ataxia associated with inactivity, and that the muscle volume around the ankle does not function as an important main factor in maintaining human equilibrium.

Conflict of interest

There are no conflicts of interest.

We are grateful to Drs Izumi Tabata (National Institute of Health and Nutrition), and Jun-ichi Ushiyama (Keio University) for their contributions to the study. This work was supported, in part, by Moritani Scholarship Foundation, Japan (to M. K.) and a grant from the Ground Research for Space Utilization awarded, promoted by the National Space Development Agency and Japan Space Forum (to T. F.).

References

- Accornero, N., Capozza, M., Rinalduzzi, S. & Manfredi, G.W. 1997. Clinical multisegmental posturography: age-related changes in stance control. *Electroenceph Clin Neurophysiol* 105, 213–219.
- Akima, H., Kawakami, Y., Kubo, K. *et al.* 2000a. Effect of short-duration spaceflight on thigh and leg muscle volume. *Med Sci Sports Exerc* 32, 1743–1747.
- Akima, H., Kubo, K., Kanehisa, H., Suzuki, Y., Gunji, A. & Fukunaga, T. 2000b. Leg-press resistance training during 20 days of 6 deg head-down-tilt bed rest prevents muscle deconditioning. *Eur J Appl Physiol* 82, 30–38.
- Akima, H., Kubo, K., Imai, M. *et al.* 2001. Inactivity and muscle: effect of resistance training during bed rest on muscle size in the lower limb. *Acta Physiol Scand* 172, 269–278.
- Akima, H., Ushiyama, J., Kubo, J. *et al.* 2003. Resistance training during unweighting maintains muscle size and function in human calf. *Med Sci Sports Exerc* 35, 655–662.
- Aramaki, Y., Nozaki, D., Masani, K., Sato, T., Nakazawa, K. & Yano, H. 2001. Reciprocal angular acceleration of the ankle and hip joints during quiet standing in humans. *Exp Brain Res* 136, 463–473.
- Baratto, L., Morasso, P.G., Re, C. & Spada, G. 2002. A new look at posturographic analysis in the clinical context: sway-velocity versus other parameterization techniques. *Motor Control* 6, 246–270.
- Bent, L.R., McFadyen, B.J. & Inglis, J.T. 2002. Visual-vestibular interactions in postural control during the execution of a dynamic task. *Exp Brain Res* 146, 490–500.
- Bloomfield, P. 2000. *Fourier Analysis of Time Series*. John Wiley and Sons Inc, Toronto, Canada.
- Convertino, V.A., Bisson, R., Bates, R., Goldwater, D. & Sandler, H. 1981. Effects of antiorthostatic bedrest on the cardiorespiratory responses to exercise. *Aviat Space Environ Med* 52, 251–255.
- Corbeil, P., Blouin, J.S. & Teasdale, N. 2004. Effects of intensity and locus of painful stimulation on postural stability. *Pain* 108, 43–50.
- Diener, H.C., Dichgans, J., Bruzek, W. & Selinka, H. 1982. Stabilization of human posture during induced oscillations of the body. *Exp Brain Res* 45, 126–132.
- Diener, H.C., Dichgans, J., Guschlbauer, B. & Bacher, M. 1986. Role of visual and static vestibular influences on dynamic posture control. *Hum Neurobiol* 5, 105–113.
- Edgerton, V.R. & Roy, R.R. 1996. Neuromuscular adaptations to actual and simulated spaceflight. In: M.J. Fregly &

- C.M. Blatteis (eds) *Environmental Physiology. Handbook of Physiology*, pp. 721–763. Oxford University Press, New York.
- Edgerton, V.R., Zhou, M.Y., Ohira, Y. et al. 1995. Human fiber size and enzymatic properties after 5 and 11 days of spaceflight. *J Appl Physiol* 78, 1733–1739.
- Fitzpatrick, R.D. & McCloskey, D. 1994. Proprioceptive, visual and vestibular thresholds for the perception of sway during standing in humans. *J Physiol* 478, 173–186.
- Fitzpatrick, R., Burke, D. & Gandevia, S.C. 1996. Loop gain of reflexes controlling human standing measured with the use of postural and vestibular disturbances. *J Neurophysiol* 76, 3994–4008.
- Freund, H.J. 1983. Motor unit and muscle activity in voluntary motor control. *Physiol Rev* 63, 387–436.
- Fukunaga, T., Miyatani, M., Tachi, M., Kouzaki, M., Kawakami, Y. & Kanehisa, H. 2001. Muscle volume is a major determinant of joint torque in humans. *Acta Physiol Scand* 172, 249–255.
- Gatev, P., Thomas, S., Kepple, T. & Hallett, M. 1999. Feed-forward ankle strategy of balance during quiet standing in adults. *J Physiol* 514, 915–928.
- Horak, F.B., Nashner, L.M. & Diener, H.C. 1990. Postural strategies associated with somatosensory and vestibular loss. *Exp Brain Res* 82, 167–77.
- Janssen, I., Heymsfield, S.B., Wang, Z. & Ross, R. 2000. Skeletal muscle mass and distribution in 468 men and women aged 18–88 yr. *J Appl Physiol* 89, 81–88.
- Kapteyn, T.S. & de Wit, G. 1972. Posturography as an auxiliary in vestibular investigation. *Acta Otolaryngol* 73, 104–111.
- Kavounoudias, A., Roll, R. & Roll, J.P. 2001. Foot sole and ankle muscle inputs contribute jointly to human erect posture regulation. *J Physiol* 532, 869–878.
- Kern, D.S., Semmler, J.G. & Enoka, R.M. 2001. Long-term activity in upper- and lower-limb muscles of humans. *J Appl Physiol* 91, 2224–2232.
- Kouzaki, M., Shinohara, M., Masani, K., Kanehisa, H. & Fukunaga, T. 2002. Alternate muscle activity observed between knee extensor synergists during low-level sustained contractions. *J Appl Physiol* 93, 675–684.
- Kouzaki, M., Shinohara, M., Masani, K. & Fukunaga, T. 2004. Force fluctuations are modulated by alternate muscle activity of knee extensor synergists during low-level sustained contraction. *J Appl Physiol* 97, 2121–2131.
- Lambertz, D., Goubel, F., Kaspranski, R. & Pérot, C. 2003. Influence of long-term spaceflight on neuromechanical properties of muscles in humans. *J Appl Physiol* 94, 490–498.
- LeBlanc, A., Schonfeld, E., Evans, H.J., Pienotok, C., Rowe, R. & Spector, E. 1992. Regional changes in muscle mass following 17 weeks of bed rest. *J Appl Physiol* 73, 2172–2178.
- Loram, I.D. & Lakie, M. 2002. Direct measurement of human ankle stiffness during quiet standing: the intrinsic mechanical stiffness is insufficient for stability. *J Physiol* 545, 1041–1053.
- Magnusson, M., Enbom, H., Johansson, R. & Pyykko, I. 1990. Significance of pressor input from the human feet in anterior–posterior postural control: the effect of hypothermia on vibration-induced body-sway. *Acta Otolaryngol* 110, 182–188.
- Maki, B.E., Holliday, P.J. & Fernie, G.R. 1990. Aging and postural control: a comparison of spontaneous- and induced-sway balance tests. *J Am Geriatr Soc* 38, 1–9.
- Masani, K., Popovic, M.R., Nakazawa, K., Kouzaki, M. & Nozaki, D. 2003. Importance of body sway velocity information in controlling ankle extensor activities during quiet stance. *J Neurophysiol* 90, 3774–3782.
- Maurer, C., Mergner, T. & Peterka, R.J. 2006. Multisensory control of human upright stance. *Exp Brain Res* 171, 231–250.
- Mauritz, K.H. & Dietz, V. 1980. Characteristics of postural instability induced by ischemic blocking of leg afferents. *Exp Brain Res* 38, 117–119.
- McCall, G.E., Goulet, C., Grindeland, R.E., Hodgson, J.A., Bigbee, A.J. & Edgerton, V.R. 1997. Bed rest suppresses bioassayable growth hormone release in response to muscle activity. *J Appl Physiol* 83, 2086–2090.
- McCall, G.E., Goulet, C., Roy, R.R. et al. 1999. Spaceflight suppresses exercise-induced release of bioassayable growth hormone. *J Appl Physiol* 87, 1207–1212.
- McCall, G.E., Grindeland, R.E., Roy, R.R. & Edgerton, V.R. 2000. Muscle afferent activity modulates bioassayable growth hormone in human plasma. *J Appl Physiol* 89, 1137–1141.
- Miyoshi, T., Nozaki, D., Sekiguchi, H. et al. 2003. Somatosensory graviception inhibits soleus H-reflex during erect posture in humans as revealed by parabolic flight experiment. *Exp Brain Res* 150, 109–113.
- Morasso, P.G. & Schieppati, M. 1999. Can muscle stiffness alone stabilize upright standing? *J Neurophysiol* 83, 1622–1626.
- Mori, S. 1973. Discharge patterns of soleus motor units with associated changes in force exerted by foot during quiet standing in man. *J Neurophysiol* 36, 458–471.
- Nakagawa, H., Ohashi, N., Watanabe, Y. & Mizukoshi, K. 1993. The contribution of proprioception to posture control in normal subjects. *Acta Otolaryngol* 504, 112–116.
- Nashner, L.M. 1981. Analysis of stance posture in humans. In: A.L. Towe & E.S. Luschei (eds) *Motor Coordination. Handbook of Behavioral Neurology*, pp. 527–565. Plenum Press, New York.
- Panzer, V.P., Bandinelli, S. & Hallett, M. 1995. Biomechanical assessment of quiet standing and changes associated with age. *Arch Phys Med Rehabil* 76, 151–157.
- Prieto, T.E., Myklebust, J.B., Hoffmann, R.G., Lovett, E. & Myklebust, M. 1996. Measures of postural steadiness: differences between healthy young and elderly adults. *IEEE Trans Biomed Eng* 43, 956–966.
- Roll, R., Gilhodes, J.C., Roll, J.P., Popov, K., Charade, O. & Gurfinkel, V. 1998. Proprioceptive information processing in weightlessness. *Exp Brain Res* 122, 393–402.
- Shinohara, M., Yoshitake, Y., Kouzaki, M., Fukuoka, H. & Fukunaga, T. 2003. Strength training counteracts motor performance losses during bed rest. *J Appl Physiol* 95, 1485–1492.
- Smith, J.W. 1957. The forces operating at the human ankle joint during standing. *J Anat* 91, 545–564.

Fascicle behavior of medial gastrocnemius muscle in extended and flexed knee positions

Taku Wakahara^{a,*}, Hiroaki Kanehisa^b, Yasuo Kawakami^c, Tetsuo Fukunaga^c

^aGraduate School of Human Sciences, Waseda University, 2-579-15 Mikajima, Tokorozawa, Saitama 359-1192, Japan

^bDepartment of Life Sciences (Sports Sciences), University of Tokyo, Meguro, Tokyo, Japan

^cFaculty of Sport Sciences, Waseda University, Mikajima, Tokorozawa, Saitama, Japan

Accepted 10 October 2006

Abstract

The present study tested the hypotheses that Achilles tendon forces during fast concentric actions do not differ between extended and flexed knee positions, and this phenomenon is attributable to the force–length characteristics and electromyograms (EMGs) of gastrocnemius muscle. Seven healthy men performed static and concentric plantarflexions at fully extended (K0) and 0.785 rad (45°) flexed (K45) knee positions with the maximal effort. In concentric actions, the angular velocities were set at 0.524 (slow) and 6.109 rad s⁻¹ (fast). Fascicle length of medial gastrocnemius (MG) was determined with ultrasonography. Surface EMGs of the MG were recorded during each action. Achilles tendon force was calculated from the torque and moment arm of the tendon. Peak tendon forces in fast concentric actions were similar in K0 and in K45, but those in static and slow concentric actions significantly ($P < 0.05$) differed between the two positions. When the tendon force peaked, the fascicle lengths in each action and fascicle velocities in both concentric actions were significantly ($P < 0.05$) greater in K0 than in K45. The EMGs were significantly ($P < 0.05$) higher in K0 than K45 during each action. The results suggest that (1) the difference in the tendon forces between the two positions can be explained by the force–length and –velocity characteristics and the EMGs of the MG, and (2) the contribution of the MG to the tendon force in flexed knee positions is greater in concentric actions than expected from the results in static actions.

© 2006 Elsevier Ltd. All rights reserved.

Keywords: Force–length characteristics; Force–velocity characteristics; Electromyogram

1. Introduction

Synergist muscles generally consist of mono- and bi (multi)-articular muscles. These muscles work differently in human movements (Gregoire et al., 1984; Duchateau et al., 1986). The action of the biarticular muscles is complicated, because the muscles are affected by rotation of both the joints that are crossed. Therefore, many attempts have been made to examine the neuro-muscular properties of biarticular muscles (Herzog and ter Keurs 1988; Herzog et al., 1990).

Gastrocnemius muscle is a biarticular muscle crossing knee and ankle joints. Previous studies have shown that the plantarflexion torque or Achilles tendon force exerted in

maximal static actions decreases with knee flexion (i.e., with shortening of the gastrocnemius muscle fibers) (Sale et al., 1982; Herzog et al., 1991; Arndt et al., 1998; Maganaris, 2003). From these results, the gastrocnemius has been assumed to work almost exclusively on the ascending limb of the force–length characteristics (Herzog et al., 1991; Maganaris, 2003). However, using cadaveric specimens, Cutts (1988) indicated that the sarcomere of human gastrocnemius operated entire range of force–length characteristics. In addition, Kawakami et al. (2000) showed that, while the sarcomere lengths of gastrocnemius were on the ascending, plateau and descending portion of the force–length characteristics in passive conditions, the lengths during maximal static actions were shifted to the ascending limb as a result of internal shortening of fibers. Therefore, the gastrocnemius muscle may not always be on the ascending limb except in the maximal static actions.

*Corresponding author. Tel.: +81 4 2947 6783; fax: +81 4 2947 7483.
E-mail address: waka1002@fuji.waseda.jp (T. Wakahara).

As a different phenomenon from that observed under static actions, however, the plantarflexion torque during high-velocity concentric actions has been reported to be similar between extended and flexed knee positions (Fugl-Meyer et al., 1979; Svantesson et al., 1991). Moreover, the maximal plantarflexion velocity against very low load was higher in the flexed compared to the extended knee position (Carpentier et al., 1996). The reason for the discrepancy between static and concentric conditions has not been clarified yet. Carpentier et al. (1996) speculated that the higher maximal velocity in the flexed knee position was not due to the neural activation, but due to the mechanical properties of the gastrocnemius, such as the force–length and –velocity characteristics. However, the mechanisms proposed by Carpentier et al. (1996) cannot explain the reduction in static torque with knee flexion (Herzog et al., 1991; Cresswell et al., 1995). It is important to resolve the above discrepancy in determining the neuro-muscular properties of gastrocnemius muscle in dynamic conditions.

If the gastrocnemius operates over the entire range of force–length characteristics as indicated by Cutts (1988), the discrepancy mentioned above can be explained as follows. In static conditions, because of the internal shortening of fibers (Kawakami et al., 2000), the sarcomere of the gastrocnemius may be on the ascending limb in both extended and flexed knee positions. Meanwhile, in concentric conditions (especially at high velocity), less internal shortening would occur than that of static actions, because the force exerted by the gastrocnemius should decrease with increasing shortening velocity of the fiber. Thus, it may be expected that the sarcomere of gastrocnemius would be on the descending limb in extended and on the near-plateau portion in flexed knee positions. This may result in the higher force generating potential with related to length in the flexed knee position than in the extended. On the other hand, the electromyograms (EMGs) of the gastrocnemius were shown to decrease with knee flexion in static (Cresswell et al., 1995) and concentric (Price et al., 2003) conditions. The decreased EMG may not be solely attributable to the muscle active insufficiency (i.e., the muscle fiber reaches a critical shortened length at which the fiber cannot exert force according to the force–length characteristics) (Arampatzis et al., 2006), but it suggests that the activation levels of the gastrocnemius decrease in the flexed knee positions. Hence, the interaction between the force-generating potential related to the length and the EMGs of the gastrocnemius may result in the similar plantarflexion torque between the extended-flexed knee positions during fast concentric actions.

In the present study, we measured the fascicle (fiber) lengths of medial gastrocnemius (MG) muscle during static and concentric actions. The purpose of the present study was to test the hypothesis that although Achilles tendon forces in static actions decrease with knee flexion, the tendon forces during fast concentric actions do not differ between extended and flexed knee positions, and the discrepancy between static and concentric actions can be

attributed to the interaction between the force–length characteristics and EMGs of the MG.

2. Methods

2.1. Subjects

Seven healthy men (age, 23.9 ± 3.1 yr; height, 170.5 ± 3.5 cm; and body mass, 63.8 ± 5.5 kg; mean \pm SD) participated as subjects. They were instructed about the aims and procedures of the study. Written informed consent was obtained from all subjects. This study was approved by the Human Research Ethics Committee in Faculty of Sport Sciences, Waseda University

2.2. Experimental setup

Subjects lay supine on a test bench of a dynamometer (CON-TREX, CMV AG, Switzerland). Two positions with the knee angles at fully extended (K0) and 0.785 rad (45°) flexed (K45) were taken to determine the plantarflexion torque (Fig. 1). The right thigh was secured to the bench in K0 and to a pad in K45 to reduce the knee joint rotation. The foot was firmly strapped to the footplate of the dynamometer. The subjects performed maximal static and concentric plantarflexions in the two positions in a randomized order. In static actions, the ankle was fixed at 0 rad (neutral position). In concentric actions, the range of motion of the ankle was between -0.175 rad (dorsiflexed) and 0.524 rad (plantarflexed). The subjects were completely relaxed at -0.175 rad and then asked to exert the maximal plantarflexion torque until the angle of ankle joint reached 0.524 rad. The angular velocity of the dynamometer was set at each of 0.524 rad s^{-1} (slow) and 6.109 rad s^{-1} (fast). To familiarize the subjects with the testing procedures, two or three trials were performed for each action with submaximal and maximal effort. Following a 2-min rest interval after completion the standardized warm-up and familiarization with the measurement procedure, the subjects were asked to perform two maximal trials for each action. The trials in which the greater peak torque was recorded were used for further analysis.

In fast concentric actions, the angular velocity of the ankle actually did not reach 6.109 rad s^{-1} because of the limited range of motion of the joint (0.698 rad). However, the time courses of angle and angular velocity of the ankle were almost the same between K0 and K45. Therefore, the task required for the subjects in the fast concentric actions would be equivalent for the two positions.

2.3. Torque and angle measurements

Plantarflexion torque was measured with the dynamometer. The ankle and knee angles were determined with two goniometers (ankle, SG110/A; knee, SG150; Biometrics, UK). The torque and angle signals were sampled at 1 kHz with a 16-bit A/D converter (PowerLab/16SP, ADInstruments, Australia) and transferred to a computer. The data were filtered with a

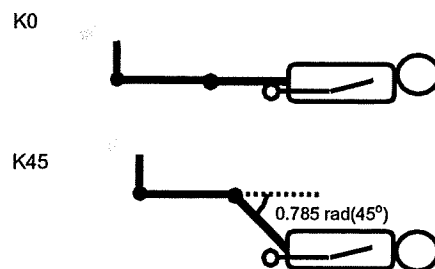


Fig. 1. Schematic illustration of the experimental setup. Subjects performed maximal voluntary plantarflexions in K0 (upper) and K45 (bottom).

Butterworth-type low-pass filter of fourth order. The cutoff frequency of the filter was 13 Hz, which was determined by residual analysis (Winter, 1990).

Achilles tendon force was calculated by dividing the torque by the moment arm of the tendon. The moment arm was calculated by differentiating the length change of gastrocnemius muscle-tendon complex with respect to the ankle angle (Grieve et al., 1978).

2.4. Ultrasonographic measurements

An ultrasonic apparatus (SSD-6500, Aloka, Japan) was used to visualize the MG fascicle (Fig. 2). A 10-MHz, linear-array probe (UST-5712, Aloka, Japan) was longitudinally placed to the belly of MG and secured to the skin. Ultrasound images were recorded on a videotape at 30 Hz in static and slow concentric actions. In fast concentric actions, the images were stored at 95 Hz in the computer memory of the apparatus. An electric signal was superimposed on the images to synchronize the images with the torque, joint angles and EMGs.

The ultrasound images were A/D converted (ADVC-500, Canopus, Japan) and stored on a computer. Fascicle lengths and pennation angles were measured using ImageJ software (National Institute of Health, USA). Measurements were performed two times for the same images and mean values were used for further analysis. The coefficients of variation in the two measurements were <6.8% for fascicle length and <8.5% for pennation angle. The intraclass correlation coefficients were >0.99 for both fascicle length and pennation angle. In fast concentric actions, the data obtained with the ultrasonography were interpolated every 10 ms with a cubic spline.

2.5. EMG recordings

Surface EMGs were recorded from the MG, lateral gastrocnemius (LG), soleus (SOL) and tibialis anterior (TA) muscles using bipolar Ag/AgCl electrodes (Blue Sensor, Ambu A/S, Denmark, sensor area: 13.2 mm²) with an inter-electrode distance of 20 mm. The EMG signals were amplified with a telemeter system (WEB-5000, NIHON KOHDEN, Japan; time constant: 0.03 s, hi-cut filter: off) and stored on the computer after A/D conversion at 1 kHz of sampling frequency (PowerLab/16SP, ADInstruments, Australia). The EMG data were full-wave rectified and averaged during a 0.5-s period in static actions and over the entire movement in concentric actions.

2.6. Statistics

Values are presented as means \pm SDs. Paired *t*-test was used to test the significance of the differences between K0 and K45. Statistical significance was set at $P < 0.05$.

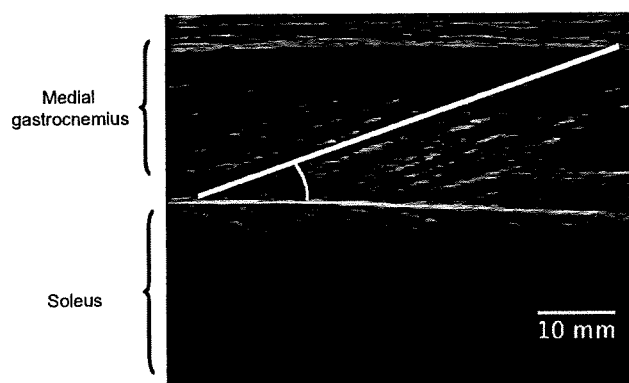


Fig. 2. An example of ultrasound image taken during static action. Fascicle lengths and pennation angles of MG were measured as shown in the image.

3. Results

Fig. 3 shows typical examples of the time courses of the ankle angle, Achilles tendon force, fascicle length, pennation angle, fascicle velocity and EMG of MG in each concentric action. The fascicle lengths were longer and the pennation angles were smaller in K0 than in K45 over the range of motion. The fascicle velocities were higher in K0 than in K45. The EMGs were also greater in K0 than in K45.

The peak values of the tendon force were significantly greater in K0 than in K45 in static ($P < 0.01$) and slow concentric ($P < 0.05$) actions (Fig. 4). In fast concentric actions, the peak tendon forces were almost the same between the two positions.

When the tendon force peaked, the ankle angles were not significantly different between K0 and K45 in static and slow concentric actions (Table 1). In fast concentric actions, however, the ankle angles were significantly different ($P < 0.05$) between the two positions. At the corresponding time, the fascicle lengths were significantly longer ($P < 0.01$) and the pennation angles were significantly smaller ($P < 0.01$) in K0 than in K45. The fascicle velocities were significantly higher ($P < 0.05$) in K0 than in K45 in both concentric actions, although no significant differences were observed in the angular velocities of ankle between the two positions.

The EMGs of MG were significantly higher in K0 than K45 in static ($P < 0.05$) and concentric ($P < 0.01$) actions (Fig. 5). Similar tendencies were observed in the EMGs of LG, although the difference between the two positions in the slow concentric actions was not significant ($P = 0.07$). There were no significant differences in the EMGs of SOL and TA between the two positions.

4. Discussion

The Achilles tendon forces in fast concentric actions did not decrease by knee flexion, while the tendon forces in static and slow concentric actions decreased in the flexed knee position (Fig. 4). This supports the former part of the hypothesis and was consistent with the previous findings in static (Sale et al., 1982; Arndt et al., 1998) and dynamic (Fugl-Meyer et al., 1979; Svantesson et al., 1991) conditions. However, the discrepancy in the plantarflexion torque or Achilles tendon force between static and concentric conditions has not been elucidated. In the present study, we determined the fascicle length and EMGs of MG during static and concentric actions, and found the differences in the lengths and velocities of the fascicle and the EMGs between the extended-flexed knee positions (Table 1, Fig. 5).

The fascicle lengths were different between K0 and K45 when the tendon force peaked in each action (Table 1). In MG, the fascicle length is equivalent to the muscle fiber length (Kawakami et al., 2000). Hence, the differences in the fascicle length would correspond to the differences in

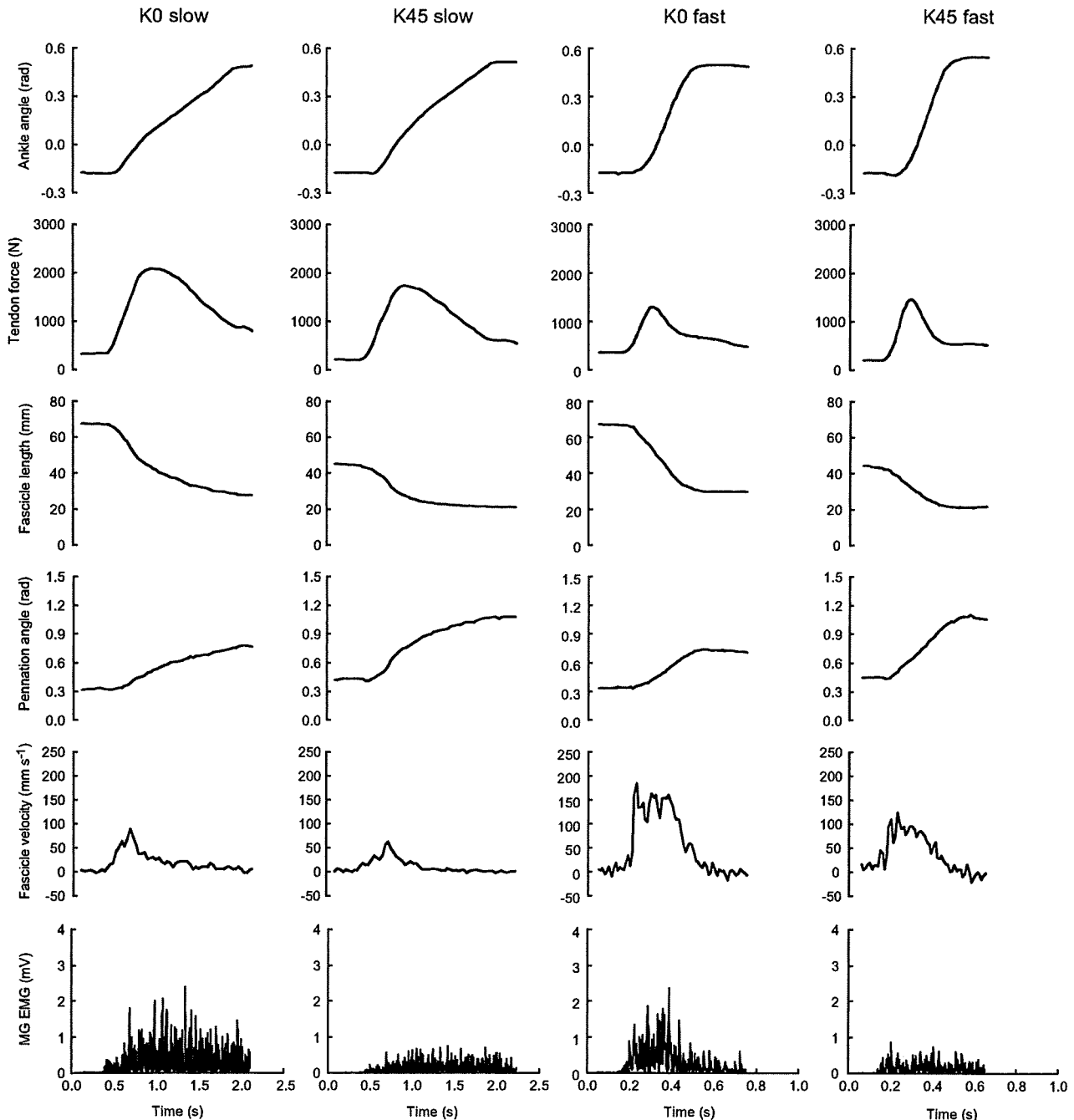


Fig. 3. Typical examples of the ankle joint angle, Achilles tendon force, fascicle length, pennation angle, fascicle velocity and EMG of MG during each of the concentric actions.

the length of sarcomeres, which are arranged in series within the fiber. Since sarcomere length is a major determinant of muscle force-generating potential (Gordon et al., 1966), we estimated the sarcomere lengths at peak force by dividing the fascicle lengths by the number of sarcomeres in series within MG fiber [17,600; Huijing (1985)], and superimposed it onto the force-length relationship of human sarcomere (Walker and Schrodt, 1974) (Fig. 6). In static actions, the sarcomere lengths in

both positions reached the ascending limb, and the sarcomere in K0 had greater force potential than in K45. Similarly, the force-generating potential of sarcomere in slow concentric actions was greater in K0 than K45. In fast concentric actions, however, the sarcomere in K45 had higher force potential than that in K0. Thus, the difference in fascicle lengths between the two positions could be a factor explaining the similar tendon forces during fast concentric action. However, while Fig. 6 represents the

active force–length relationship, it should be noted that the tendon force measured in the present study was the total force, including the passive force. The passive force was reported to be produced by muscles, skin and other connective tissues surrounding the joint (Gillette and Fell, 1996). In these tissues, the passive force of the gastrocnemius was indicated to be a small part of total force (Herzog et al., 1991). Therefore, we may say that the passive force of the gastrocnemius would have less influence on the magnitude of tendon force determined in the present study.

In both concentric actions, the fascicle velocities were higher in K0 than in K45 when the tendon force peaked (Table 1). The force-generating potential of a muscle decreases with increasing shortening velocity (Hill, 1938). Thus, the higher fascicle velocities in K0 would limit the force potential of MG during concentric actions. The different fascicle velocities despite of similar angular velocities of ankle may be explained by the tendon velocity (Zuurbier and Huijing, 1992) and/or angular effects (Gans and Gaunt, 1991; Zuurbier and Huijing, 1992), the latter of

which is to increase the muscle velocity along the line of action due to the change in pennation angle. To examine this assumption, we calculated the angular effects as follows:

$$AE = [(FL_2 \cdot \cos \alpha_2 - FL_1 \cdot \cos \alpha_1) - (FL_2 - FL_1)]/dt,$$

where AE is the angular effects, FL is the fascicle length, α is the pennation angle and subscripts 1 and 2 denotes right before and after the time of peak tendon force, respectively. As a result, the angular effects were not significantly different between the two positions in both concentric actions (Table 2). This implies that the differences in fascicle velocities might arise from the tendon velocities, not from the angular effects.

The MG EMGs were lower in K45 than in K0 (Fig. 5). This agrees with the earlier reports which examined the EMGs of MG under static (Cresswell et al., 1995; Miaki et al., 1999) and concentric (Carpentier et al., 1996, 1999; Price et al., 2003) conditions. In the case of surface EMG, the decrease in the MG EMG with knee flexion may be due to the impaired neuromuscular transmission or changes in electrode–muscle configuration (Cresswell et al., 1995). However, even when fine-wire electrodes were applied, the EMGs of MG were shown to decrease with knee flexion (Cresswell et al., 1995). Furthermore, using a needle electrode, Kennedy and Cresswell (2001) revealed that the activities of MG motor unit were inhibited in the flexed knee position. These findings suggest that the decline in the MG EMGs with knee flexion was not due to the change in electrode–muscle configuration but the impairment of neuromuscular transmission. The impairment has been considered to be induced by the active insufficiency (Kennedy and Cresswell 2001). However, Arampatzis et al. (2006) simultaneously determined the fascicle lengths and EMGs of MG while subjects performed the maximal static actions at various knee and ankle joint positions and showed that the EMGs decreased with knee flexion despite of almost the same fascicle lengths. This finding may imply that the decrease in the EMGs of MG with knee flexion cannot be solely explained by the active insufficiency. Therefore, the present result on EMG indicates that the activation level of MG decreased with knee flexion,

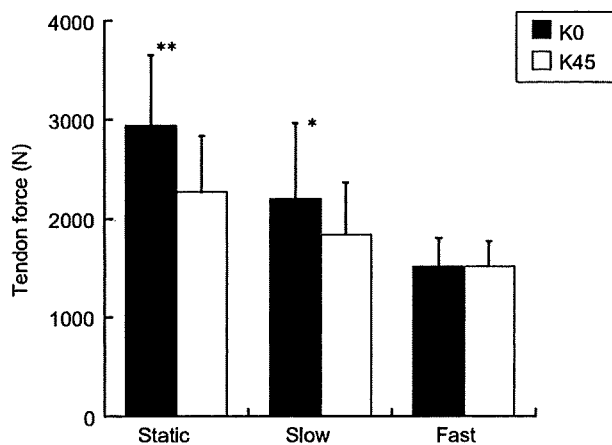


Fig. 4. Peak values of Achilles tendon force in each action. Means and SDs for seven subjects are presented for K0 (filled bars) and K45 (open bars). Significant differences between the extended and flexed knee positions are denoted by * ($P < 0.05$) and ** ($P < 0.01$).

Table 1
Measured variables when the tendon force reached its peak values

	Static		Slow concentric		Fast concentric	
	K0	K45	K0	K45	K0	K45
Ankle angle (rad)	0.101 ± 0.065	0.088 ± 0.048	0.076 ± 0.069	0.028 ± 0.070	-0.071 ± 0.029*	-0.101 ± 0.023
Knee angle (rad)	0.004 ± 0.068**	0.711 ± 0.065	-0.007 ± 0.049**	0.738 ± 0.036	-0.001 ± 0.021**	0.762 ± 0.029
Fascicle length (mm)	42 ± 7**	30 ± 5	51 ± 9**	36 ± 6	59 ± 8**	40 ± 6
Pennation angle (rad)	0.514 ± 0.077**	0.701 ± 0.123	0.447 ± 0.063**	0.574 ± 0.109	0.375 ± 0.046**	0.503 ± 0.087
Ankle velocity (rad s ⁻¹)	—	—	0.516 ± 0.090	0.556 ± 0.064	2.793 ± 0.520	2.574 ± 0.447
Fascicle velocity (mm s ⁻¹)	—	—	35 ± 9*	21 ± 4	117 ± 46*	51 ± 35

Values are means ± SDs. Significant differences between the extended and flexed knee positions are denoted by * ($P < 0.05$) and ** ($P < 0.01$).

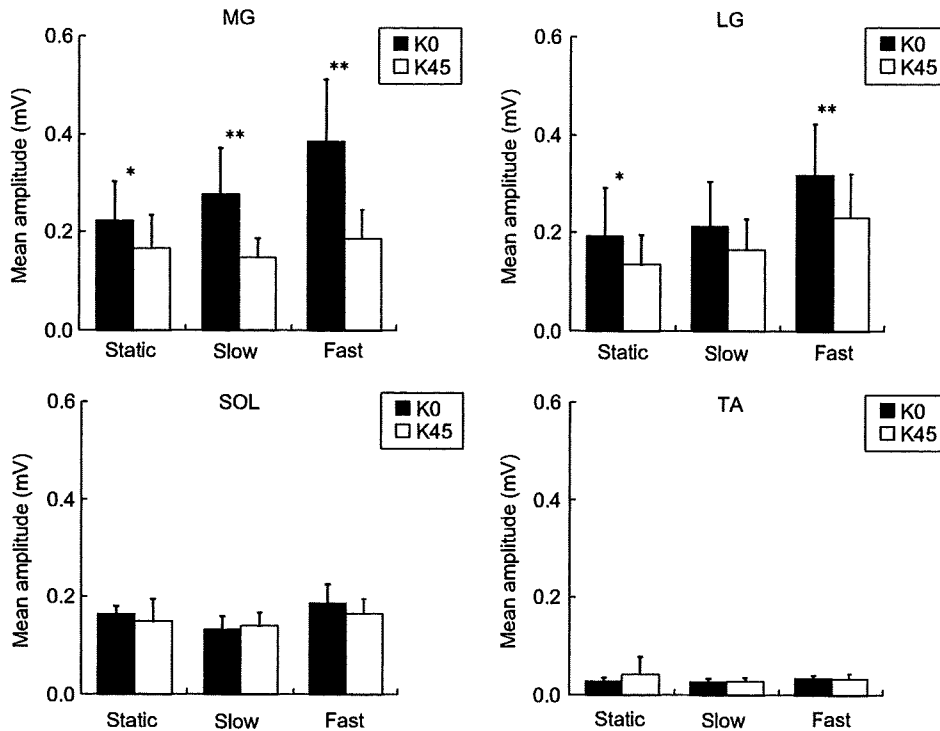


Fig. 5. EMG activities of MG, LG, SOL and TA during each action. Means and SDs for the subjects are presented for K0 (filled bars) and K45 (open bars). Significant differences between the extended and flexed knee positions are denoted by *($P < 0.05$) and **($P < 0.01$).

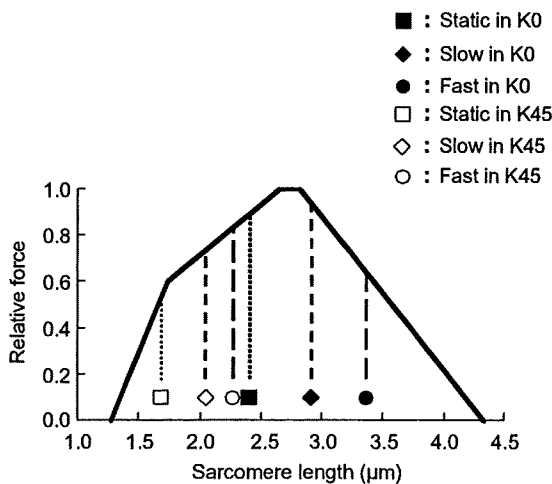


Fig. 6. Estimated sarcomere lengths of MG at peak tendon force and the force-length characteristics of human sarcomeres (Walker and Schrodt, 1974). The intersection points of the force-length relationship and vertical lines illustrate the force-generating potential of sarcomere at each length.

although the cause of the impairment of neuromuscular transmission is unclear.

Taken together, the difference in the tendon forces during static action could be attributed to the lower force potential due to the shorter fascicle length and the lower EMGs of MG in K45. Similarly, in slow concentric action,

Table 2
Angular effects due to pennation in concentric actions

	Slow concentric		Fast concentric	
	K0	K45	K0	K45
Angular effects (mm s^{-1})	3 ± 2	3 ± 2	10 ± 10	9 ± 7

Values are means \pm SDs.

the smaller peak tendon force in K45 would arise from the lower force potential of MG with the shorter fascicle length and the lower MG activation. However, the MG force potential in relation to fascicle velocity was higher in K45 than in K0. This may reduce the difference between the two positions in the tendon forces of slow concentric action (14.0%) compared to that of static action (22.3%). In fast concentric action, the MG force potential, based on the length and velocity of fascicle, was greater, but its EMGs were lower in K45. The interaction of the three factors could be a reason for the similar tendon forces in the fast concentric action. Consequently, although the latter part of the hypothesis of the present study, i.e., the discrepancy in the tendon forces between static and concentric actions could be attributed to the force-length characteristics and EMGs of MG, was partly supported, the fascicle velocity should also be involved to explain the discrepancy.

As mentioned above, the present results on the tendon forces were attributable to the differences in the fascicle length, fascicle velocities and EMGs of MG. However, LG, SOL and other plantarflexors also contribute to the tendon force and thus the influences of these muscles should be considered. Although LG fascicles have more sarcomeres in series than those of MG (Huijing 1985), the moment arm of LG at the knee is shorter than that of MG (Spoor et al., 1990). Accordingly, the influence of 0.785 rad of knee flexion on the sarcomere length of LG would be smaller as compared to that for MG. Furthermore, the physiological cross-sectional area of LG is about 40% of that of MG (Fukunaga et al., 1992). Therefore, the effects of the differences in LG fascicle length on the tendon force would be smaller than those in MG. On the other hand, the SOL and other plantarflexors cross only the ankle joint. When the tendon force peaked, the angles and velocities of ankle were not different between the two positions except for the ankle angles in fast concentric action (Table 1). However, the difference in the ankle angle of fast concentric action was only about 0.031 rad. Also, the SOL attaches to the common Achilles tendon with the gastrocnemius muscles. When the tendon forces were different in the two positions, the differences in the tendon elongation may affect the behavior of SOL fascicles. However, Kawakami et al. (1998) demonstrated that the fascicle lengths of SOL during maximal static actions were not influenced by the knee joint angles, although the plantarflexion torque decreased with knee flexion. The difference in the tendon force between the extended and flexed knee positions was smaller in the concentric actions than in the static actions (Fig. 4). Hence, it is natural to assume that the difference between the two positions in the tendon force during the concentric actions cannot be a factor changing the behavior of the SOL fascicles. In addition, there were no differences in the SOL EMGs between K0 and K45 (Fig. 5). These results suggest that the monoarticular plantarflexors contributed to the tendon force to a similar extent in the two positions. Consequently, the differences between K0 and K45 in tendon forces would primarily be due to the differences in fascicle length, fascicle velocities and EMGs of MG. However, the present study did not examine the behavior of SOL in K0 and K45. Further investigation will be needed to elucidate the behavior of SOL during dynamic conditions in the extended and flexed knee positions.

In the discussion of force–length relationship mentioned above, a constant value of 17,600 was used for all subjects as the serial sarcomere number of MG. However, the mean number of sarcomeres in human MG, which has been reported in previous studies, ranged from 15,333 to 18,500 [i.e., 15,333: Wickiewicz et al. (1983); 16,614: Huijing (unpublished but cited in Out et al., 1996); 17,614: Huijing (1985); 18,400: Woittiez et al. (1985); 18,500: Vossen and Huijing (unpublished but cited in Bobbert et al., 1986)]. Hence, it is possible that interindividual variability in the number of sarcomeres might affect

on the discussion based on the sarcomere length estimation. In the present study, the value reported by Huijing (1985) as the number of sarcomeres was applied to estimate sarcomere lengths, since it was obtained from a greater number of cadavers ($n = 8$) as compared to the other studies and was close to the intermediate in the range mentioned above. Furthermore, even when the other values reported as the number of sarcomeres were used, the relationship of the force generating potential between K0 and K45 was not altered in the static and concentric actions, except for the value of Wickiewicz et al. (1983) in slow concentric actions. Therefore, the interindividual variability in the number of sarcomeres would not have a great effect on the discussion based on the estimation of the sarcomere lengths.

In conclusion, we showed that the Achilles tendon forces in concentric actions did not always decrease with knee flexion. This could be attributed to the force–length and –velocity characteristics and the EMGs of MG. The present findings indicate that the gastrocnemius significantly contribute to the tendon force not only in the extended but also in the flexed knee positions in concentric conditions by maintaining the high force potential associated with the length and velocity of the fascicle.

References

- Arampatzis, A., Karamanidis, K., Stafilidis, S., Morey-Klapsing, G., Demonte, G., Bruggemann, G.P., 2006. Effect of different ankle- and knee-joint positions on gastrocnemius medialis fascicle length and EMG activity during isometric plantar flexion. *Journal of Biomechanics* 39, 1891–1902.
- Arndt, A.N., Komi, P.V., Bruggemann, G.P., Lukkariniemi, J., 1998. Individual muscle contributions to the in vivo Achilles tendon force. *Clinical Biomechanics* 13, 532–541.
- Bobbert, M.F., Huijing, P.A., van Ingen Schenau, G.J., 1986. A model of the human triceps surae muscle–tendon complex applied to jumping. *Journal of Biomechanics* 19, 887–898.
- Carpentier, A., Duchateau, J., Hainaut, K., 1996. Velocity-dependent muscle strategy during plantarflexion in humans. *Journal of Electromyography and Kinesiology* 6, 225–233.
- Carpentier, A., Duchateau, J., Hainaut, K., 1999. Load-dependent muscle strategy during plantarflexion in humans. *Journal of Electromyography and Kinesiology* 9, 1–11.
- Cresswell, A.G., Loscher, W.N., Thorstensson, A., 1995. Influence of gastrocnemius muscle length on triceps surae torque development and electromyographic activity in man. *Experimental Brain Research* 105, 283–290.
- Cutts, A., 1988. The range of sarcomere lengths in the muscles of the human lower limb. *Journal of Anatomy* 160, 79–88.
- Duchateau, J., Le Bozec, S., Hainaut, K., 1986. Contributions of slow and fast muscles of triceps surae to a cyclic movement. *European Journal of Applied Physiology and Occupational Physiology* 55, 476–481.
- Fugl-Meyer, A.R., Sjostrom, M., Wahlby, L., 1979. Human plantar flexion strength and structure. *Acta Physiologica Scandinavica* 107, 47–56.
- Fukunaga, T., Roy, R.R., Shellock, F.G., Hodgson, J.A., Day, M.K., Lee, P.L., Kwong-Fu, H., Edgerton, V.R., 1992. Physiological cross-sectional area of human leg muscles based on magnetic resonance imaging. *Journal of Orthopaedic Research* 10, 928–934.
- Gans, C., Gaunt, A.S., 1991. Muscle architecture in relation to function. *Journal of Biomechanics* 24, 53–65.

- Gillette, P.D., Fell, R.D., 1996. Passive tension in rat hindlimb during suspension unloading and recovery: muscle/joint contributions. *Journal of Applied Physiology* 81, 724–730.
- Gordon, A.M., Huxley, A.F., Julian, F.J., 1966. The variation in isometric tension with sarcomere length in vertebrate muscle fibres. *The Journal of Physiology* 184, 170–192.
- Gregoire, L., Veeger, H.E., Huijing, P.A., van Ingen Schenau, G.J., 1984. Role of mono- and biarticular muscles in explosive movements. *International Journal of Sports Medicine* 5, 301–305.
- Grieve, D.W., Pheasant, S., Cavanagh, P.R., 1978. Prediction of gastrocnemius length from knee and ankle joint posture. In: *Biomechanics VI-A* 405–412.
- Herzog, W., ter Keurs, H.E., 1988. Force-length relation of in vivo human rectus femoris muscles. *Pflugers Archiv* 411, 642–647.
- Herzog, W., Abrahamse, S.K., ter Keurs, H.E., 1990. Theoretical determination of force-length relations of intact human skeletal muscles using the cross-bridge model. *Pflugers Archiv* 416, 113–119.
- Herzog, W., Read, L.J., ter Keurs, H.E., 1991. Experimental determination of force-length relations of intact human gastrocnemius muscles. *Clinical Biomechanics* 6, 230–238.
- Hill, A.V., 1938. The heat of shortening and the dynamic constants of muscle. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 126, 136–195.
- Huijing, P.A., 1985. Architecture of the human gastrocnemius muscle and some functional consequences. *Acta Anatomica* 123, 101–107.
- Kawakami, Y., Ichinose, Y., Fukunaga, T., 1998. Architectural and functional features of human triceps surae muscles during contraction. *Journal of Applied Physiology* 85, 398–404.
- Kawakami, Y., Kumagai, K., Huijing, P.A., Hijikata, T., Fukunaga, T., 2000. The length-force characteristics of human gastrocnemius and soleus muscles in vivo. In: Herzog, W. (Ed.), *Skeletal Muscle Mechanics: Mechanisms to Function*. Wiley, New York, pp. 327–341.
- Kennedy, P.M., Cresswell, A.G., 2001. The effect of muscle length on motor-unit recruitment during isometric plantar flexion in humans. *Experimental Brain Research* 137, 58–64.
- Maganaris, C.N., 2003. Force-length characteristics of the in vivo human gastrocnemius muscle. *Clinical Anatomy* 16, 215–223.
- Miaki, H., Someya, F., Tachino, K., 1999. A comparison of electrical activity in the triceps surae at maximum isometric contraction with the knee and ankle at various angles. *European Journal of Applied Physiology and Occupational Physiology* 80, 185–191.
- Out, L., Vrijkotte, T.G., van Soest, A.J., Bobbert, M.F., 1996. Influence of the parameters of a human triceps surae muscle model on the isometric torque-angle relationship. *Journal of Biomechanical Engineering* 118, 17–25.
- Price, T.B., Kamen, G., Damon, B.M., Knight, C.A., Applegate, B., Gore, J.C., Eward, K., Signorile, J.F., 2003. Comparison of MRI with EMG to study muscle activity associated with dynamic plantar flexion. *Magnetic Resonance Imaging* 21, 853–861.
- Sale, D., Quinlan, J., Marsh, E., McComas, A.J., Belanger, A.Y., 1982. Influence of joint position on ankle plantarflexion in humans. *Journal of Applied Physiology* 52, 1636–1642.
- Spoor, C.W., van Leeuwen, J.L., Meskers, C.G., Titulaer, A.F., Huson, A., 1990. Estimation of instantaneous moment arms of lower-leg muscles. *Journal of Biomechanics* 23, 1247–1259.
- Svantesson, U., Ernstoff, B., Bergh, P., Grimby, G., 1991. Use of a Kin-Com dynamometer to study the stretch-shortening cycle during plantar flexion. *European Journal of Applied Physiology and Occupational Physiology* 62, 415–419.
- Walker, S.M., Schrodt, G.R., 1974. I segment lengths and thin filament periods in skeletal muscle fibers of the Rhesus monkey and the human. *Anatomical Record* 178, 63–81.
- Wickiewicz, T.L., Roy, R.R., Powell, P.L., Edgerton, V.R., 1983. Muscle architecture of the human lower limb. *Clinical Orthopaedics and Related Research* 179, 275–283.
- Winter, D.A., 1990. *Biomechanics and Motor Control of Human Movement*, second ed. Wiley, New York.
- Woittiez, R.D., Rozendal, R.H., Huijing, P.A., 1985. The functional significance of architecture of the human triceps surae muscle. In: *Biomechanics IX-A* 21–26.
- Zuurbier, C.J., Huijing, P.A., 1992. Influence of muscle geometry on shortening speed of fibre, aponeurosis and muscle. *Journal of Biomechanics* 25, 1017–1026.

Influences of tendon stiffness, joint stiffness, and electromyographic activity on jump performances using single joint

Keitaro Kubo · Masanori Morimoto ·
Teruaki Komuro · Naoya Tsunoda ·
Hiroaki Kanehisa · Tetsuo Fukunaga

Accepted: 20 October 2006 / Published online: 15 November 2006
© Springer-Verlag 2006

Abstract The present study aimed to examine the influences of tendon stiffness, joint stiffness, and electromyographic activity on jump performances consisting of a single-joint movement. Twenty-four men performed three kinds of unilateral maximal jump using only the ankle joint (squat jump: SJ; counter-movement jump: CMJ; drop jump: DJ) on the sledge apparatus. The relative differences in the jump height of CMJ and DJ compared to SJ were defined as pre-stretch augmentation. During jumping exercises, electromyographic activities (mEMG) were recorded from the plantar flexors. Ankle joint stiffness was calculated as the change in the joint torque divided by the change in ankle joint angle during the eccentric phase of DJ. Achilles tendon stiffness was measured using ultrasonography during isometric plantar flexion. No significant correlations were found between joint stiffness and pre-stretch augmentation in both CMJ and DJ. On the contrary, tendon stiffness was significantly correlated with pre-stretch augmentation in both CMJ ($r = -0.471$) and DJ ($r = -0.502$). The relative mEMG value of CMJ (to that of SJ) during the concentric phase was significantly correlated with pre-stretch

augmentation ($r = 0.481$), although this relationship was not found in DJ. These results suggested that (1) the greater jump height in CMJ could be explained by both the tendon elasticity and the increased activation level of muscle, (2) tendon elasticity played a more significant role in the enhancement of jump height during DJ, and (3) joint stiffness was not related to either pre-stretch augmentation or tendon stiffness.

Keywords Achilles tendon · EMG ·
Stretch-shortening cycle · Ultrasonography

Introduction

The stretch-shortening cycle is a commonly used muscle action in human movement. It is well known that if an activated muscle is stretched prior to shortening, its performance is enhanced during the concentric phase (Alexander and Bennet-Clark 1977; Bosco et al. 1982; Fukunaga et al. 2001; Kawakami et al. 2002; Kubo et al. 1999; Kubo 2005; Svantesson and Grimby 1995). The enhancement of performance during stretch-shortening cycle exercise may be attributed to the combined effects of utilization of elastic energy and stretch reflex potentiation of muscle activity (e.g., Bosco et al. 1982). In the former case, the tendons have been thought to act as a spring (Alexander and Bennet-Clark 1977; Fukunaga et al. 2001). Recent studies have investigated the relationship between tendon properties and jump performances in vivo (Kubo et al. 1999; Kubo 2005; Bojsen-Moller et al. 2005). Among them, Kubo et al. (1999) reported that the tendon stiffness in knee extensors was inversely correlated with the relative difference in jump height

K. Kubo (✉) · H. Kanehisa
Department of Life Science (Sports Sciences),
University of Tokyo, Komaba 3-8-1, Meguro-ku,
Tokyo 153-8902, Japan
e-mail: kubo@idaten.c.u-tokyo.ac.jp

M. Morimoto · T. Komuro · N. Tsunoda
Department of Physical Education, Kokushikan University,
Tokyo, Japan

T. Fukunaga
Department of Sports Sciences, Waseda University,
Tokorozawa, Saitama, Japan

between vertical jumps performed with and without countermovement, i.e., pre-stretch augmentation. However, the previous studies (Kubo et al. 1999; Kubo 2005; Bojsen-Moller et al. 2005) included some flaws. First, jump tests taken in the previous studies consisted of multi-joint movements, and so it was difficult to specify the muscles mainly acting to perform the task. Bobbert et al. (1996) pointed out that the performance difference observed between jumps performed with and without countermovement might be attributed to the differences in moment and work by the hip extensor muscles. In order to accurately assess the role of tendon elasticity during stretch-shortening cycle exercise, one needs to select a movement that minimizes the contribution of other muscles and number of working joints.

Second, the previous studies (Kubo et al. 1999; Kubo 2005; Bojsen-Moller et al. 2005) did not examine the effects of other factors except for tendon elasticity during stretch-shortening cycle exercises, e.g., the activation level of muscles. Kilani et al. (1989) indicated that the myoelectric responses accounted for up to 85% of the increase in jump height following a countermovement. Bobbert and Casius (2005) also suggested that the greater jump height with countermovement could be explained by the difference in the active state developed during preparatory countermovement. On the contrary, Svantesson and Grimby (1995) reported that electromyographic activities during stretch-shortening cycle exercise decreased or remained constant compared to those during pure concentric action, suggesting that myoelectrical potentiation did not contribute to the increased concentric torque in stretch-shortening cycle exercise. To clarify the reasons for pre-stretch augmentation, therefore, it is necessary to investigate the electromyographic activities of muscles as well as tendon elasticity during stretch-shortening cycle exercises.

Different methods have been used to study the mechanical properties of the lower leg and single joint (Arampatzis et al. 1999; Chelly and Denis 2001; Kuitunen et al. 2002a, b). Chelly and Denis (2001) found that leg stiffness (ratio of the change in the ground reaction force to the displacement of the center of mass) assessed during a hopping task was positively correlated with maximal sprint velocity. Similarly, Farley and Morgenroth (1999) and Kuitunen et al. (2002b) demonstrated that joint stiffness (ratio of the change in joint torque to joint angular displacement) increased with running speed and hopping height. Furthermore, Arampatzis et al (2001) reported that there was an optimum leg and ankle stiffness values to maximize mechanical power during drop jump.

Therefore, these findings led us to speculate that joint stiffness would be related to performance during stretch-shortening cycle exercise, but no direct evidence of this has been presented.

Although some previous studies through modeling and/or simulation approaches demonstrated that during jumping there was an interaction between the tendon and joint stiffness and the activation level of muscles (Bobbert 2001; Hof et al 2002), no report has so far been available regarding the influences of these variables on the jump performances which was tested experimentally in humans. Therefore, the purpose of this study was to examine the influences of tendon stiffness, joint stiffness, and electromyographic activity on pre-stretch augmentation during countermovement and drop jumps consisting of a single-joint movement. Our hypothesis was that pre-stretch augmentation would be correlated with tendon stiffness (negatively) and joint stiffness (positively), but not to the change in electromyographic activity.

Methods

Subjects

Twenty-four men (age 23 ± 4 year, height 170 ± 3 cm, body mass 64 ± 11 kg, mean \pm SD) volunteered to take part in the present study. The subjects in the study were either sedentary, or mildly to moderately active men, but none were involved in any type of resistance exercise program at the time of the study. The procedures, purpose, and risks associated with the study were explained to all the subjects before they gave their written informed consent to participate. This study was approved by the office of the Department of Sports Sciences, University of Tokyo, and complied with their requirements for human experimentation.

Jump performance

Three kinds of unilateral maximal jumps using only the ankle joint (squat jump: SJ; countermovement jump: CMJ; drop jump: DJ) were performed on the sledge apparatus (VR-4100, Cybex, USA) with an inclination of 17° from the horizontal position. The subjects lay on the sliding table of this apparatus. The table was designed to slide with minimal friction with a constant load through a steel cable connected to adjustable weights. The load used was 50% of the body mass for each subject. A force plate (Kistler, 9281B, Switzerland) was mounted firmly onto the footplate of this apparatus. A wooden block was attached to the force

plate and the subjects placed the ball of their right foot on the block with the knee fully extended. The vertical component of the ground reaction force (F_z) was recorded from the force platform. Three retroreflective landmarks were placed over the following anatomical landmarks on the right side of the subjects: the fifth metatarsophalangeal joint, the lateral malleolus, and the lateral epicondyle of the knee. During jumping, subjects were filmed from the right side in the sagittal plane with a digital high-speed video camera at a sampling frequency of 200 Hz (HSV-500C³, Nac, Japan).

Before the experiment the subjects were familiarized with the jumping actions. For all tests, they were instructed to jump to a maximal height. The test was repeated five times per subject, except trials in which ankle angle differed by more than $\pm 5^\circ$, with at least 3 min between trials. These angles were accurately controlled by the use of an electrogoniometer (Penny and Giles). For SJ, the subjects initially kept the ankle position maximally dorsiflexed, and supported the load at this position. Then, the subjects started ankle movement until the ankle was fully plantar flexed and the toe lifted away from the wooden block. For CMJ, the ankle was initially positioned at maximal plantar flexion. Then, subjects commenced to develop plantar flexion force until the foot came to a stop at maximal dorsiflexion (the same position as the initial position in SJ), and rebounded to start plantar flexion until the toe finally lifted away from the wooden block. For DJ, the subjects were dropped down from a height of 20 cm. After landing on the edge of the wooden block with the ball of the right foot, the ankle joint was dorsiflexed until the maximally dorsiflexed position. Then, the subjects started plantar flexion and took off. We excluded the trials in which knee joint was flexed slightly according to the images of high-speed video camera. In a preliminary study with five males among all the subjects, the optimal load for three jump tests and the drop height for DJ were investigated. In the concrete, we determined the effects of load level (30, 40, 50, 60 and 70% of body mass) and the drop height (10, 20, 30 and 40 cm) on jump heights of each task. As a result, the maximal jump heights of the jump tests were observed using the load of 50% of the body mass for each subject and the drop height of 20 cm. Accordingly, the load of 50% of the body mass for each subject and the drop height of 20 cm were identified.

Using a public domain National Institute of Health (NIH) image software package, the ankle joint angle and jump height were measured. Assuming that the displacement of the retroreflective landmark of the lateral malleolus was equal to that of the center of mass,

the jump height was defined as the maximum displacement of the retroreflective landmark of the lateral malleolus from the resting position (ankle joint angle was 90°). Three individual jump height recordings excluding the largest and smallest values were averaged. Electromyographic activity (EMG) was recorded during jump tests. Bipolar surface electrodes (5 mm in diameter) were placed over the bellies of the medial gastrocnemius (MG), lateral gastrocnemius (LG), soleus (SOL), and tibial anterior (TA) with a constant interelectrode distance of 25 mm. EMG signals were transmitted to a computer at a sampling rate of 1 kHz. The EMG was full-wave rectified and averaged for the duration of the contraction. The mean value of EMG activity from the plantar flexors (MG, LG, and SOL) was calculated from the eccentric and concentric phases, respectively, according to the ankle joint angle (mEMG). The difference between the heights of CMJ or DJ and SJ, expressed as the percentage of that in SJ, was proposed as an index of pre-stretch augmentation (Kubo et al. 1999). The mean coefficient of variation (CV) values of the three measurements were 5.2% for SJ, 4.6% for CMJ, and 7.1% for DJ.

Joint stiffness

Ankle joint torque (TQ) during DJ was estimated from the following equation (Kawakami et al. 2002; Kubo et al. 2000b):

$$TQ = F_z \cdot L_1 \cdot \cos(A_J - 90)$$

where F_z , L_1 , and A_J are the vertical component of the ground reaction force, the length from the estimated center of ankle joint to the ball of the foot (measured for each subject), and the ankle joint angle, respectively (see Fig. 3 of Kawakami et al. 2002). The precision and validity of this procedure have been confirmed by Kawakami et al. (2002) and Kubo et al. (2000a, b).

A typical relationship between ankle joint torque and angle during DJ is presented in Fig. 1. According to Kuitunen et al. (2002a), ankle joint stiffness was calculated as a change in joint torque divided by the change in the ankle joint angle during the eccentric phase. As mentioned above, three trial values for jumping heights were averaged. The mean CV value of the three measurements for joint stiffness was 8.2%.

Tendon stiffness

The experimental set-up has been described in detail previously (Kubo et al. 2005a). The subject was

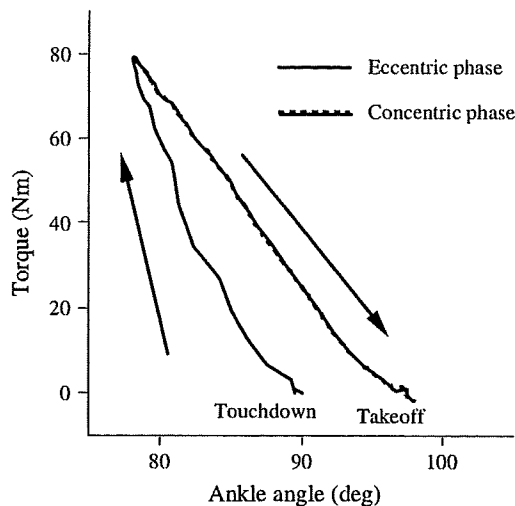


Fig. 1 Typical example of the ankle joint torque-angle relationship during the drop jump. Joint stiffness was calculated as an average value in the eccentric phase by dividing the change in joint torque by the corresponding change in joint angle

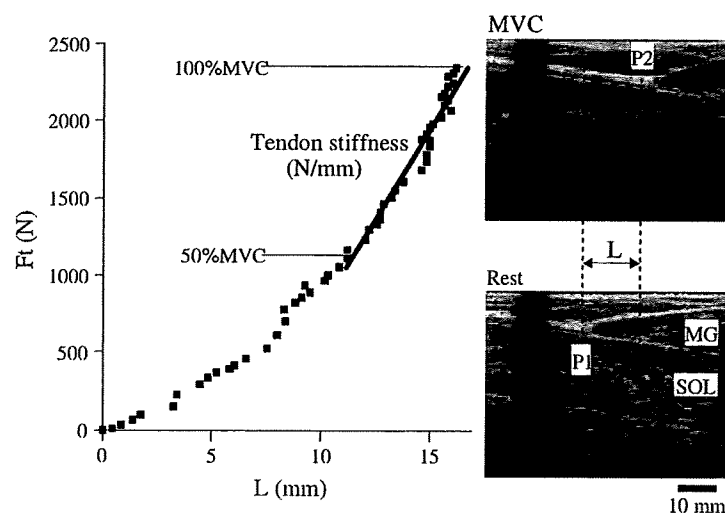
instructed to develop a gradually increasing force from a relaxed state to maximal voluntary contraction (MVC) within 5 s. The task was repeated two times per subject with at least 3 min between trials. The measured values shown below are the means of the two trials. An ultrasonic apparatus (SSD-2000, Aloka, Tokyo, Japan) with an electronic linear array probe (7.5-MHz wave frequency with 80 mm scanning length; UST 5047-5, Aloka, Tokyo, Japan) was used to obtain longitudinal ultrasonic images of the medial gastrocnemius muscle. The probe was longitudinally attached to the dermal surface with adhesive tape, which prevented the probe from sliding. To evaluate the

elongation of the Achilles tendon, the displacement of the distal myotendinous junction (L ; Fig. 2) of the medial gastrocnemius muscle in the transition from a resting state to MVC was measured (Kubo et al. 2005a; Muraoka et al. 2005). In the present study, the Achilles tendon was defined as the distance from the Achilles tendon insertion on the calcaneus to the distal myotendinous junction of the medial gastrocnemius muscle (Kubo et al. 2005a; Muraoka et al. 2005). Ultrasonic images were recorded on videotape at 30 Hz, and synchronized with force recordings using a clock timer for subsequent analyses.

Tendon displacement is attributed to both angular rotation and contractile tension, since any angular joint rotation occurs in the direction of ankle plantar flexion during an “isometric” contraction (Magnusson et al 2001; Muramatsu et al 2001). To monitor ankle joint angular rotation, an electrical goniometer (Penny and Giles) was placed on the lateral aspect of the ankle. To correct the measurements taken for the elongation of the Achilles tendon, additional measurements were made under passive conditions. Displacement of the myotendinous junction of the medial gastrocnemius muscle caused by rotating the ankle from 90° to 70° was digitized in sonographs taken as described above. Thus, for each subject, displacement of the myotendinous junction obtained from the ultrasound images could be corrected for that attributed to joint rotation alone (Magnusson et al 2001; Muramatsu et al 2001). In the present study, only values corrected for angular rotation are reported.

The measured torque (TQ) during isometric plantar flexion was converted to tendon force (Ft) by the following equation:

Fig. 2 Ultrasonic images of longitudinal sections of the Achilles tendon at rest and MVC (right panel). The distance traveled by P1 and P2 was defined as the elongation of the Achilles tendon during contraction. Typical example of the tendon force (Ft)–elongation (L) relationship (left panel). The slope of Ft– L relation between 50 and 100% MVC was calculated as the stiffness of the Achilles tendon



$$F_t = TQ \cdot MA^{-1}$$

where MA is the moment arm length of the triceps surae muscles at 90° of the ankle joint, which is estimated from the lower leg length of each subject (Kubo et al. 2005a). In the present study, the Ft and L values above 50% of MVC were fitted to a linear regression equation, the slope of which was adopted as stiffness (Fig. 2; Kubo et al. 1999). The mean CV value of the two measurements for tendon stiffness was 6.8%.

Statistics

Descriptive data included means ±SD. One-way analysis of variance (ANOVA) was used for comparison among the three jumping tests. If the F statistic of the analysis of variance was significant, differences between groups were assessed by the Scheffe test. To assess the relationships among measured parameters, Pearson product-moment correlation was computed. The level of significance was set at P < 0.05.

Results

Descriptive data on the measured variables during the three kinds of jump tests are summarized in Table 1. There was no significant difference in the ankle joint angle at the lowest position among SJ, CMJ, and DJ (P = 0.193). During the eccentric phase, the mEMG value in CMJ was significantly lower than that in DJ (P < 0.001). During the concentric phase, on the contrary, the mEMG value in CMJ was significantly higher than that in both SJ and DJ (both P < 0.001). The jump heights in both CMJ and DJ were significantly higher than that in SJ (P < 0.001), although there was no difference between CMJ and DJ (P = 0.150). There was no significant difference in the pre-stretch augmentation between CMJ and DJ (P = 0.213).

Joint stiffness and tendon stiffness were 3.84 ± 1.18 Nm/deg (2.02–6.19 Nm/deg) and 130.1 ± 30.6 N/mm (70.5–189.9 N/mm), respectively. Correlation coefficients

Table 2 Correlation coefficients between two kinds of stiffness and the jump heights

	vs. Joint stiffness	vs. Tendon stiffness
SJ height	0.229	0.423*
CMJ height	0.12	0.251
DJ height	0.082	0.186

*P < 0.05

for the relationships between the two kinds of stiffness and jump heights are summarized in Table 2. There were no significant correlations between joint stiffness and the three kinds of jump heights. Tendon stiffness was significantly correlated with SJ height but not CMJ and DJ heights. Furthermore, there was no significant correlation between tendon stiffness and joint stiffness (Fig. 3).

No significant correlations were found between joint stiffness and pre-stretch augmentation in both CMJ and DJ (both P > 0.05; Fig. 4). On the other hand, tendon stiffness was negatively correlated with pre-stretch augmentation in CMJ and DJ (both P < 0.05; Fig. 5). The relative mEMG value of CMJ (to its of SJ) during the concentric phase was positively correlated with pre-stretch augmentation (P < 0.05), although this relationship was not found in DJ (P > 0.05; Fig. 6).

Discussion

The present results showed that pre-stretch augmentation in both CMJ and DJ was significantly correlated with tendon stiffness (Fig. 5). We also previously reported that tendon stiffness in knee extensors was inversely correlated with the relative difference in jump height between vertical jumps performed with and without countermovement (Kubo et al. 1999; Kubo 2005). However, according to the correlation coefficient of r = -0.471 for CMJ and r = -0.502 for DJ between the two parameters, the tendon stiffness only accounted for 22–25% of the variance in the pre-stretch augmentation. The remaining might be accounted for by other

Table 1 Measured variables during SJ, CMJ, and DJ (mean ± SD)

	SJ	CMJ	DJ
Maximal dorsiflexion angle (deg)	68.1 ± 4.6	69.7 ± 5.0	71.1 ± 5.6
mEMG during eccentric phase (mV)	–	0.105 ± 0.046	0.242 ± 0.096**
mEMG during concentric phase (mV)	0.290 ± 0.072	0.377 ± 0.069*,***	0.314 ± 0.100
Jump height (cm)	20.7 ± 3.3	23.6 ± 3.9*	24.4 ± 4.8*
Pre-stretch augmentation (%)	–	14.2 ± 8.9	17.6 ± 12.6

SJ squat jump, CMJ countermovement jump, DJ drop jump

*Significantly different from SJ, **significantly different from CMJ, ***significantly different from DJ

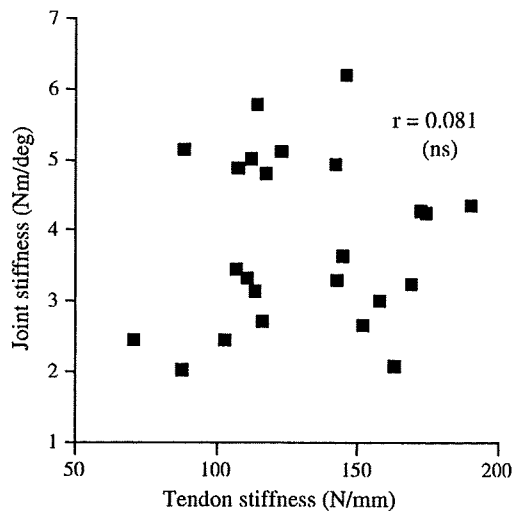


Fig. 3 Relationship between tendon stiffness and joint stiffness

factors such as potentiation of force-generating capacity within the contractile machinery and reutilization of elastic energy stored in cross-bridges (Cavagna et al. 1968; Edman et al. 1978). Furthermore, the effects of other muscles (i.e., hip extensors and plantar flexors) cannot be disregarded because this test consisted of multi-joint movement. In the present study, there was also a similar relationship between tendon stiffness and pre-stretch augmentation during a stretch-shortening cycle consisting of single joint exercise. In fact, previous studies demonstrated that the rapid shortening of tendon during the concentric phase of stretch-shortening cycle exercises played a role in lowering the velocity of muscle fibers (Kawakami et al. 2002; Kubo et al. 2000b). Furthermore, recent studies based on a similar methodology showed that the fast recoil of tendon was made possible by the muscle fibers that operated in a near-isometric region of the force-velocity relationship during walking and jumping (Finni et al. 2003; Fukunaga et al. 2001). These findings indicated that during a ballistic exercise with countermovement, the muscle fibers optimally worked at a lower shortening velocity. Taken together, these results suggested that the tendon elasticity plays a more significant role during stretch-shortening cycle exercises.

According to the report of Bobbert et al. (1996), the crucial contribution of countermovement seemed to be that it allowed the muscles to build up a high level of active state and force before the start of shortening. On the contrary, Svantesson and Grimby (1995) reported that the electromyographic activities during the stretch-shortening cycle exercise decreased or remained constant compared to those during pure concentric action, which implied that myoelectrical

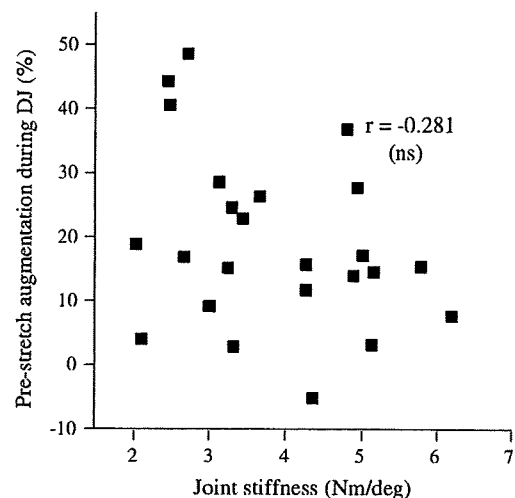
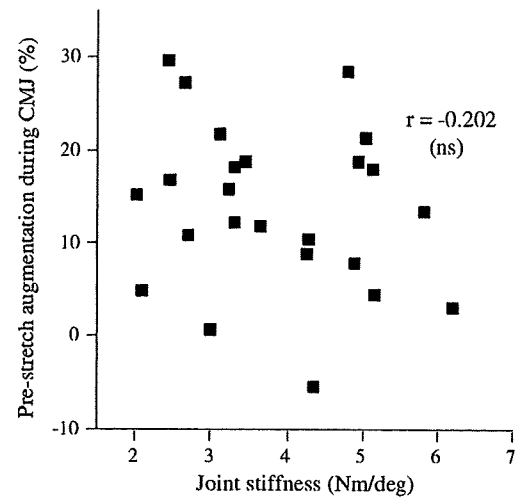


Fig. 4 Relationships between joint stiffness and pre-stretch augmentation during countermovement (CMJ; upper) and drop (DJ; lower) jumps

potentiation did not contribute to the increased performance during the stretch-shortening cycle exercise. In the present study, the mEMG value of the concentric phase in CMJ was significantly higher than that in SJ (Table 1). Furthermore, the relative increase in mEMG during CMJ compared to SJ was significantly correlated to pre-stretch augmentation during CMJ (Fig. 6a). Bosco et al. (1982) also reported that EMG activity during the concentric phase was higher in CMJ than SJ, and that the average force difference during the concentric phase between CMJ and SJ was correlated with the respective difference in EMG activity. Therefore, we may say that the increased jumping height during CMJ compared to SJ was attributed to the combined effects of the tendon elasticity and increase in the activation level of muscles.

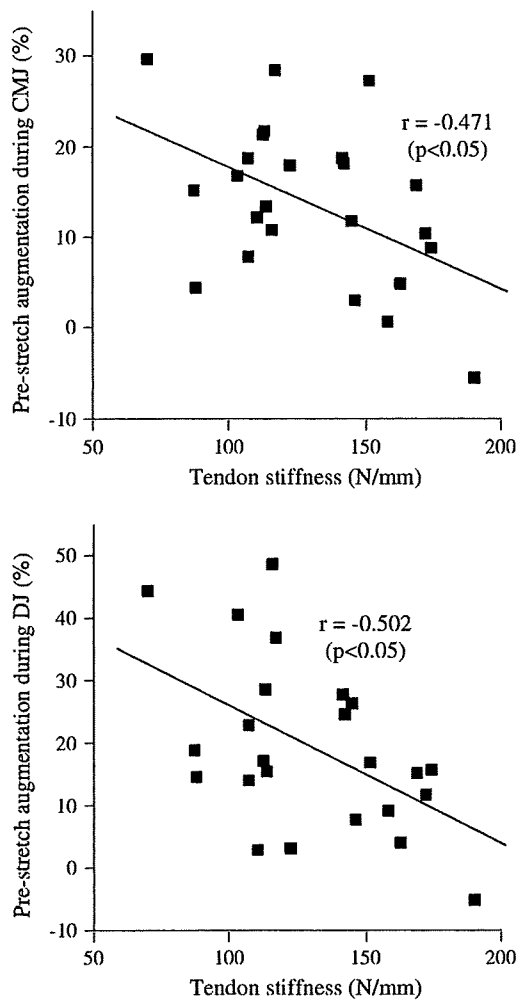


Fig. 5 Relationships between tendon stiffness and pre-stretch augmentation during countermovement (CMJ; upper) and drop (DJ; lower) jumps

In DJ, however, the mEMG value of the “concentric” phase was similar to that in SJ. On the other hand, the mEMG value during the “eccentric” phase was significantly higher in DJ than CMJ (Table 1). In addition, it is clear that the Achilles tendon force at the changing phase from dorsi- to plantar-flexion was higher in DJ than CMJ (Finni et al. 2003). Finni et al. (2003) observed that the shortening velocity of muscle fiber during the plantar-flexion phase was lower in DJ than CMJ. This will enable the working muscles to develop more tension in relation to their force–velocity properties. Considering these findings, it seems reasonable to suppose that tendon elasticity plays a more significant role in the enhancement of jumping height during DJ.

Some previous researchers reported a positive correlation between running velocity and leg and/or joint

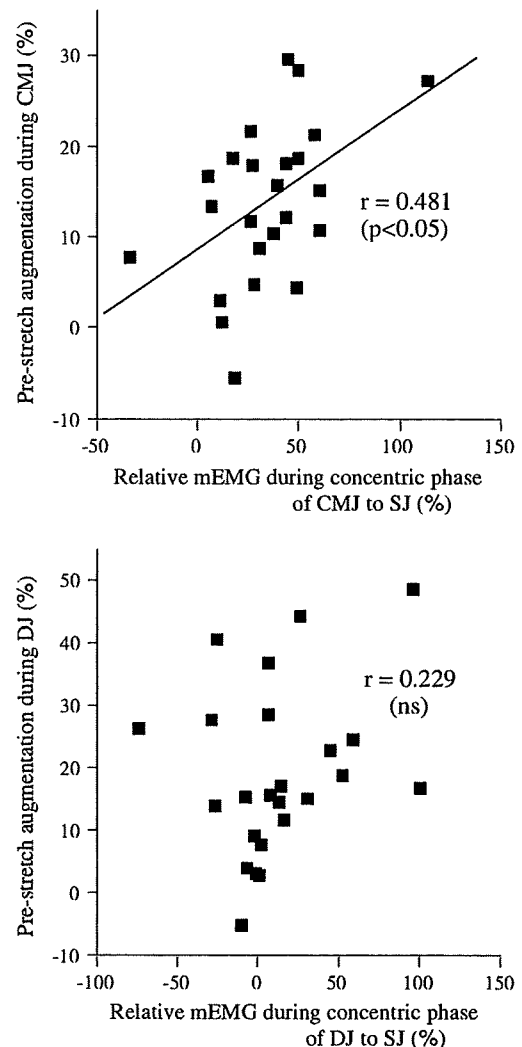


Fig. 6 Relationships between the relative mEMG value during the concentric phase to the squat jump and the pre-stretch augmentation during countermovement (CMJ; upper) and drop (DJ; lower) jumps

stiffness (Arampatzis et al. 1999; Chelly and Denis 2001; Kuitunen et al. 2002b). In addition, Heise and Martin (1998) showed a positive correlation between leg stiffness and running economy, thus concluding that less economical runners possessed a running style that was more compliant during ground contact. These previous findings led us to hypothesize that joint stiffness of the lower limbs is higher, which facilitates the transmission of exerted muscle force to bone, influencing performance during stretch-shortening cycle exercise. In the present study, however, joint stiffness was not related to either jump height (Table 2) or pre-stretch augmentation (Fig. 4). There are two reasons for this discrepancy. One is that we could not measure