Time Course of Changes in Muscle and Tendon Properties During Strength Training and Detraining

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Abstract

Kubo, K, Ikebukuro, T, Yata, H, Tsunoda, N, and Kanehisa, H. Time course of changes in muscle and tendon properties during strength training and detraining. *J Strength Cond Res* 24(2): 322–331, 2010—The purpose of this study was to investigate the time course of changes in mechanical and morphological properties of muscle and tendon during isometric training and detraining. Eight subjects completed 3 months of isometric knee extension training and detraining for another 3 months. At beginning and on every 1 month of training and detraining periods, muscle strength, neural activation level, muscle and tendon cross-sectional areas (CSA), and tendon stiffness were measured. Training increased muscle strength and neural activation level by 29.6 and 7.3% after 2 months and by 40.5 and 8.9% after 3 months (all p's < 0.05). Muscle CSA and tendon stiffness did not change until 2 months of training period, and afterward, the increases in muscle CSA and tendon stiffness reached statistical significance at the end of training period (both p's < 0.05). During detraining period, muscle strength and neural activation level did not change, although muscle CSA and tendon stiffness decreased to pre-training level at 1 and 2 months of detraining, respectively. These results suggest that the adaptations of tendon properties and muscle morphology to resistance training are slower than those of muscle function and inversely that the adaptations of former to detraining are faster than those of latter.

Key Words knee extensor, tendon stiffness, cross-sectional area, activation level

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Introduction

In general, an increase in muscle strength during the early phase of resistance training is mostly due to the intervention of neural factors; thereafter, the onset of muscle hypertrophy was found at the latter stage of training period (e.g., (12)). For example, Moritani and deVries (29) reported that muscle strength increased after short periods (2 weeks) of resistance training without muscle hypertrophy. Instead, many previous studies showed that muscle hypertrophy was found after 8–12 weeks of resistance training (6,19,31). Recently, several reports have used ultrasonography to investigate the effects of resistance training on the mechanical properties of human tendon in vivo (5,16,18,24,33). According to these findings, the stiffness of human tendons and muscle strength and mass increased significantly after "12–16 weeks" of resistance training (37–65%). However, the short-term exercise program (6–8 weeks) resulted in a little increase (19%; (19)) and unchanged (26) in tendon stiffness. Therefore, it is likely that the adaptation of tendon to the resistance training is relatively slower compared with muscle tissues.

In addition, previous studies have demonstrated that reductions in muscle strength, muscle size, and neural drive to the muscle are caused by detraining subsequent to resistance training (15,31). However, there have been no reports so far regarding the effect of detraining on tendon properties in humans. A number of studies have documented that the microgravity environment encountered during spaceflight or simulated by using models of weightlessness induces alterations in skeletal muscle function and size (17,32). These are also accompanied by changes in the mechanical properties of connective tissues, that is, tendon and ligament, induced by immobilization from animal studies (2,39). With regard to the effect of immobilization on the human tendons, Kubo et al. (17) and Reeves et al. (32) showed that the stiffness of human tendon decreased after bed rest. These findings indicate that unloading induces a reduction of tendon stiffness as an inverse effect of resistance training. However, no studies have investigated the time course of changes in the mechanical properties of

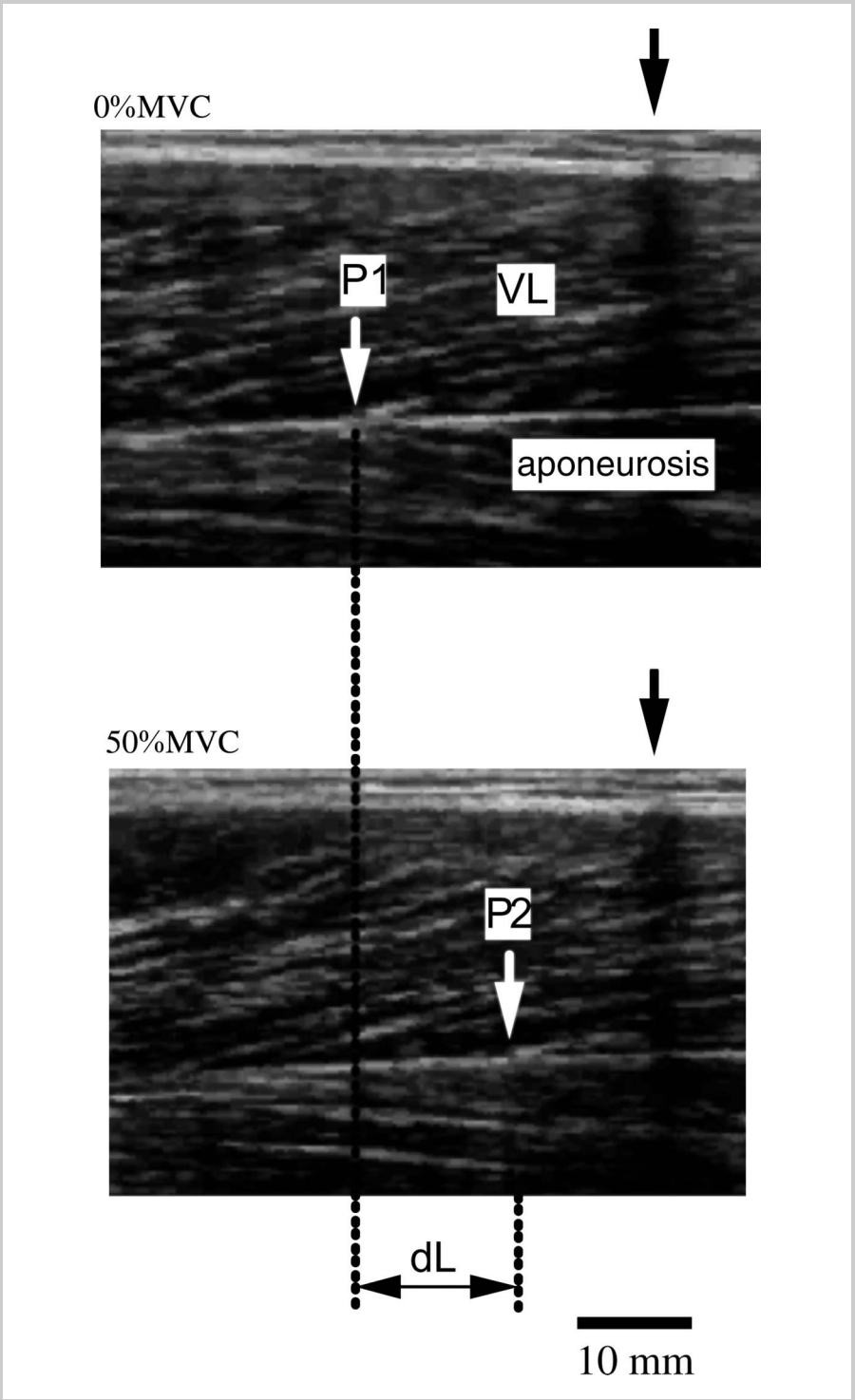

Figure 1. Ultrasonic images of longitudinal sections of the vastus lateralis (VL) muscle during isometric contraction. The black arrows point to the shadow generated by an echo-absorptive marker attached with adhesive on the skin. The crosspoint (P) was determined from the echoes of the deep aponeurosis and fascicles. The P moved proximally during isometric torque development from rest (P1) to 50% MVC (P2). The distance traveled by P (L) was defined as the length change of the tendon and aponeurosis during contraction.

human tendon and muscle during the resistance training and detraining in vivo.

Recent studies indicated that the tendon properties affect the performances during stretch-shortening cycle exercises (7,20,23,35). Therefore, information on the time course of changes in muscle and tendon properties during training and detraining is essential for improvement of performances in athletic field. Furthermore, if there is an imbalanced period of adaptations in muscle and tendon, the exercise-related musculoskeletal injuries would be caused during the resistance training and detraining. The purpose of this study was to investigate the time course of changes in mechanical and morphological properties of human muscle and tendon during isometric training and detraining in vivo. The tendon has generally been thought a structure with a slower metabolism compared with the muscle (8). Therefore, we hypothesized that the adaptation of tendon to training and detraining would be slower than that of muscle.

Methods

Experimental Approach to the Problem

To determine the time course of changes in mechanical and morphological properties of muscle and tendon during training and detraining, we examined these variables on every month of training (3 months) and detraining (3 months) periods. According to our previous studies (e.g., (18)), we adopted isometric training in which the stiffness of tendon structures increased considerably after training. Furthermore, we used the knee extension training (single-joint exercise) to

accurately assess the effect of resistance training on the tendon properties because multi-joint exercise (e.g., squat training) taken in the previous studies was difficult to specify the muscles mainly acting to perform the task.

Subjects

Fourteen healthy men volunteered to be subjects for this investigation. The subjects were randomly assigned to a training group ($n = 8$; age: 22.0 ± 0.8 years; height: 171.2 ± 6.7 cm; weight: 62.6 ± 9.3 kg; mean ± *SD*) and a control group ($n = 6$; age: 22.9 ± 1.5 years; height: 174.7 ± 1.7 cm; body mass: 69.4 ± 9.6 kg). The subjects were physically active but had not performed in any organized program of regular exercise for at least 1 year before testing. The subjects were fully informed of the procedures to be used and the purpose of this study. Written informed consent was obtained from all subjects. This study was approved by the Ethics Committee for Human Experiments, Department of Life Science (Sports Sciences), University of Tokyo.

Procedures

Experimental Design. In the weeks preceding the training period, the subjects were asked to visit the laboratory to become familiar with all testing procedures (see below). The subjects of training group were tested on every month of training (3 months) and detraining (3 months) periods (7 times). The subjects of control group were tested before and after 3 months of training and, subsequently, after 3 months of detraining (3 times).

Training and Detraining. Subjects performed unilateral knee extension exercise in seated position. They trained 4 times per week for 3 months and detrained for the following 3 months. The training protocol involved isometric knee extensions at 70% of maximal voluntary isometric strength (MVC). Each subject was seated on a test bench of a dynamometer (Vine, Tokyo, Japan) and fixed with the knee joint angles of 90° flexed. The training protocol involved 10 contractions of 15-second duration with a 30-second rest between each. The measurement of MVC was made every 1 month to adjust the training load. After the training period (3 months), the subjects entered a period of detraining (3 months). They were instructed to return to their usual lifestyle and level of physical activity during this period.

Muscle Strength and Neural Activation Level. Maximal voluntary isometric strength of the knee extensor muscles was determined by means of specially designed dynamometers (Applied Office, Tokyo, Japan). The subject sat in an adjustable chair with support for the back and the hip joint flexed at an angle of 80° (full extension = 0°) to standardize the measurements and localize the action to the appropriate muscle group. The ankle was firmly attached to the lever arm of the dynamometer with a strap and fixed with the knee joint flexed at an angle of 90°. The center of rotation of the dynamometer was visually aligned with the center of rotation of the knee joint.

Table 1. Measured variables of muscle, mean (*SD*).*†‡

	Training group ($n = 8$)							Control group ($n = 6$)		
	Pre	1 mo	2 mo	Post	De-1 mo	De-2 mo	De-3 mo	Pre	Post	De-3 mo
Maximum voluntary contraction (N·m)	226 (48)	238 (67)	289 (59)**	315 (62)***	303 (40)***	294 (49)***	290 (58)***	249 (64)	252 (53)	250 (59)
Activation level (%)	91.1 (5.6)	91.8 (7.9)	97.3 (2.5)*	98.8 (1.5)**	98.8 (0.7)**	98.7 (1.1)**	98.5 (1.3)*	92.7 (3.1)	94.3 (3.9)	93.5 (3.7)
mEMG (mV)	0.22 (0.06)	0.23 (0.05)	0.27 (0.06)*	0.29 (0.08)**	0.32 (0.12)*	0.27 (0.07)*	0.29 (0.08)*	0.24 (0.05)	0.25 (0.08)	0.23 (0.07)
Coactivation level (%)	12.1 (5.3)	10.7 (4.2)	12.7 (4.6)	13.1 (3.7)	12.1 (5.2)	13.3 (6.1)	12.5 (2.8)	13.4 (5.6)	12.9 (5.1)	13.1 (4.8)
Cross-sectional area (cm^2)	60.2 (7.1)	60.7 (7.4)	62.3 (8.1)	63.5 (7.9)*	60.9 (7.6)###	60.2 (7.1)##	60.6 (7.3)##			
Muscle thickness (mm)								39.6 (6.5)	39.4 (6.1)	39.8 (6.7)

Significantly different from pre ($p < 0.05$; **$p < 0.01$; ***$p < 0.001$).
†Significantly different from post (##$p < 0.01$; ###$p < 0.001$).
‡Pre = before training; 1 mo = after 1 month of training; 2 mo = after 2 months of training; post = after 3 months of training; De-1 mo = after 1 month of detraining; De-2 mo = after 2 months of detraining; De-3 mo = after 3 months of detraining; mEMG = mean of integrated electromyography.

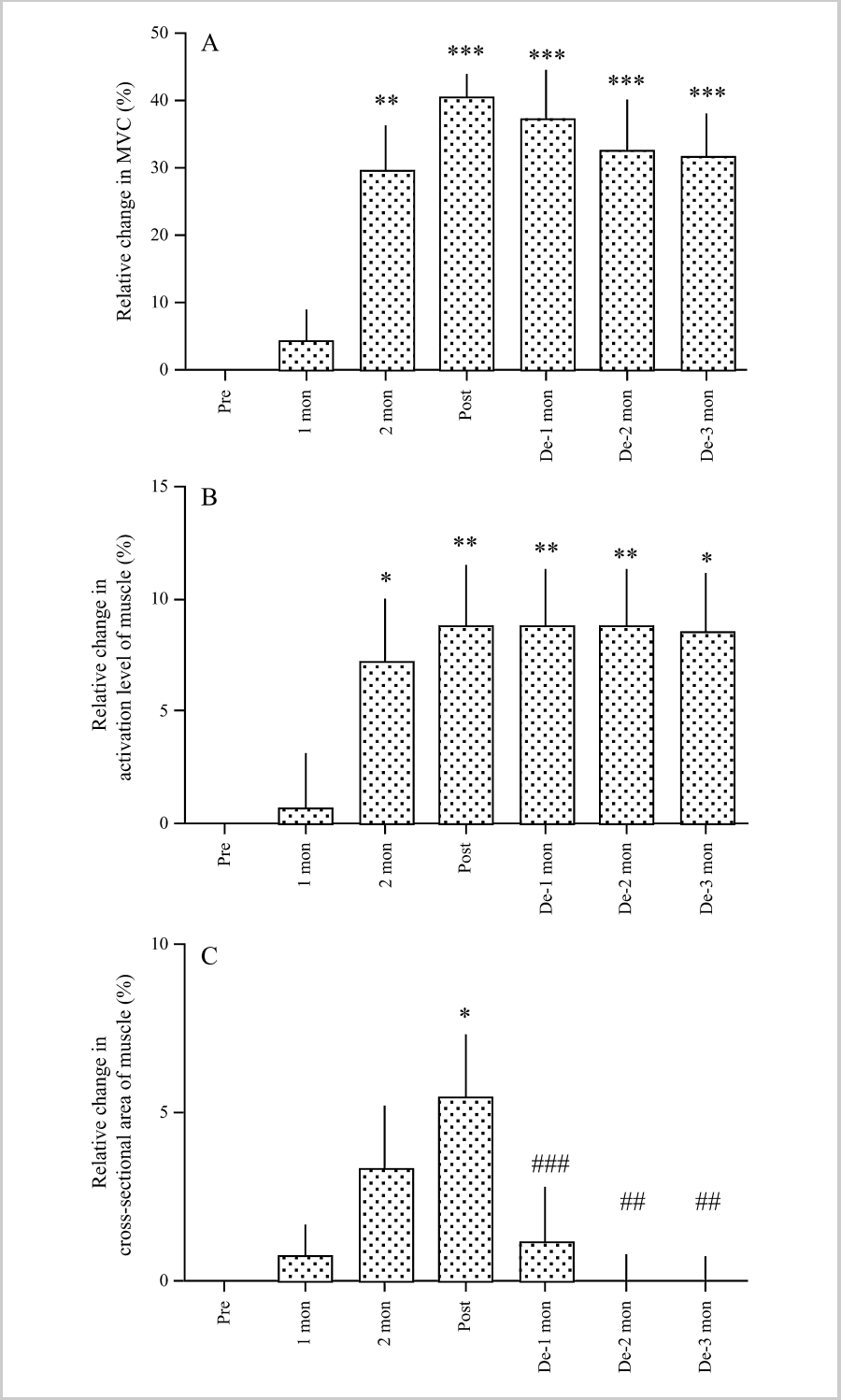

Figure 2. The relative changes in MVC (A), neural activation level (B), and cross-sectional area (CSA) (C) of muscle during the training and detraining periods for the training group. Data are expressed as mean ± *SEM*. Pre = before training; 1 mon = after 1 month of training; 2 mon = after 2 months of training; post = after 3 months of training; De-1 mon = after 1 month of detraining; De-2 mon = after 2 months of detraining; De-3 mon = after 3 months of detraining. *Significantly different from pre ($*p < 0.05$; $**p < 0.01$; $***p < 0.001$). #Significantly different from post ($\#\#p < 0.01$; $\#\#\#p < 0.001$).

When the voluntary torque peaked, evoked twitch contractions were imposed by supramaximal electrical stimulations. The stimulating electrodes were placed on the skin over the femoral nerve at the inguinal region (cathode) and the mid belly of the quadriceps muscle (anode). Rectangular pulses (triple stimuli with a 500-μs duration for one stimulus and an interstimulus interval of 10 milliseconds) were delivered using a high-voltage stimulator. The difference between peak twitch torque and MVC (twitch torque) was measured. Shortly (within 1–2 seconds) after MVC, the same stimulation was given to the muscle at rest (control twitch torque). The measured values shown below are the mean of 2 trials. The neural activation level (%) of the knee extensor muscles was calculated as: (1 − [twitch torque during MVC/control twitch torque]) × 100 as previously reported (e.g., (24)). Intraclass correlation coefficient (ICC) and mean coefficient of variation (CV) of the 2 measurements were 0.86 and 2.1%.

Mechanical Properties of Tendon. Subjects exerted isometric knee extension torque from zero (relax) to MVC within 5 seconds. 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) was used to obtain a longitudinal ultrasonic image of the vastus lateralis muscle (VL) at the level of 50% of the thigh length, that is, distance between the greater trochanter and the lateral epicondyle of the femur. The ultrasonic images were recorded on a videotape at 30 Hz and synchronized with recordings

of a clock timer (VTG-55; FOR.A, Tokyo, Japan) for subsequent analyses. The tester visually confirmed the echoes from the aponeurosis and VL fascicles (Figure 1). The point at which one fascicle was attached to the aponeurosis was visualized on the ultrasonic image. A marker (black shadow in Figure 1) that was placed between the skin and the probe and the crosspoint that was identified between the superficial aponeurosis and fascicle did not show any evidence of shifting during the measurements. Hence, the displacement of this point is considered to indicate the lengthening (L) of the deep aponeurosis and the distal tendon (e.g., (20)). In all the measurements, we measured at the same position according to the longitudinal length (at the level of 50% of the thigh length) and the distance from the boundary between VL and rectus femoris (RF) muscle. In addition, we tried to identify exactly the same point as collating with the previous ultrasonographic images.

The displacements of tendon and aponeurosis will be attributed to both angular rotation and contractile tension because any angular joint rotation occurs in the direction of knee extension during an "isometric" contraction (e.g., (21)). Thus, angular joint rotation needs to be accounted for to avoid an overestimation of tendon displacement during an isometric contraction. To monitor joint angular rotation, an electrical goniometer (Penny & Giles; Biomechanics Ltd., Gwent, United Kingdom) was placed on the lateral aspect of knee joint. To correct the measurements taken for the tendon elongation, additional measurements were taken under passive conditions. The displacement of this point caused by rotating the knee and ankle from 90 to 70° was digitized in sonographs taken. Thus, for each subject, the displacement of this point obtained from the ultrasound images could be corrected for that attributed to joint rotation alone. In the present study, only values corrected for angular rotation are reported. The measured values shown below are the mean of 2 trials.

The knee joint torque (TQ) measured by the dynamometer was converted to muscle force (Fm) by the following equation:

$$\mathrm{Fm} = k \cdot \mathrm{TQ} \cdot \mathrm{MA}^{-1},$$

where k is the relative contribution of VL to force production during knee extension, expressed as the percentage of its physiological cross-sectional area (CSA) to that of the quadriceps femoris muscle, 22% (30), and MA is the moment arm length of the quadriceps femoris muscle at the knee joint flexed at an angle of 90°, which was estimated from the thigh length of each subject as described by Visser et al. (38). In the present study, the Fm and L values above 50% MVC were fitted to a linear regression equation, the slope of which was adopted as an index of the stiffness (e.g., (20)). Intraclass

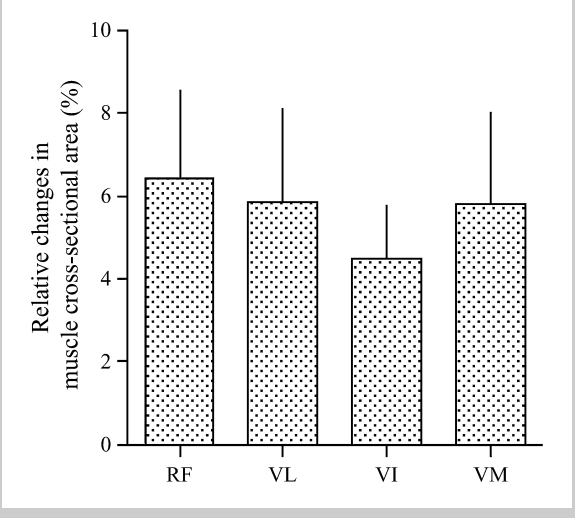

Figure 3. The relative changes in muscle cross-sectional areas (CSAs) of rectus femoris (RF), vastus lateralis (VL), vastus intermedius (VI), and vastus medialis (VM) muscles at 3 months of training.

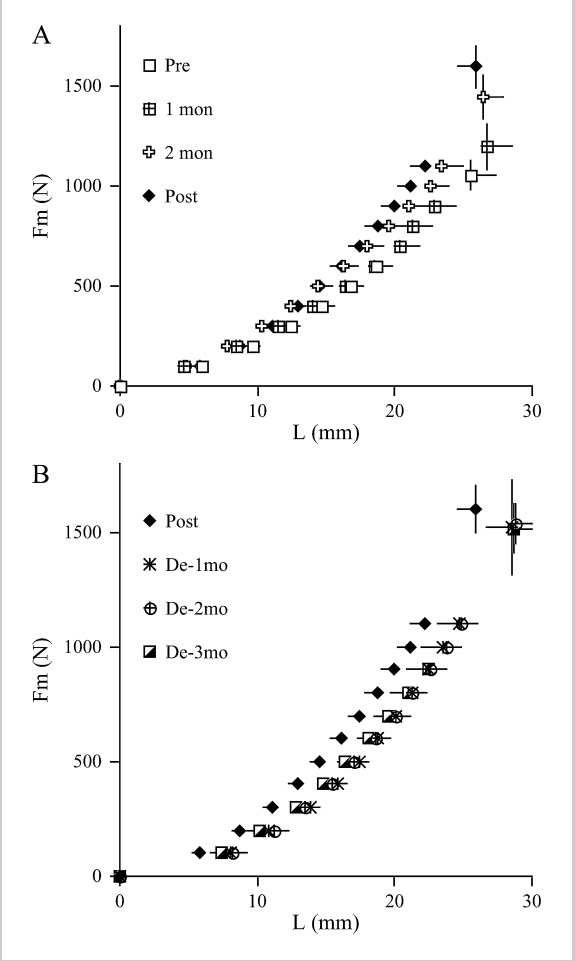

Figure 4. The estimated muscle force (Fm) and tendon elongation (L) relation during training (A) and detraining (B). Data are expressed as mean ± *SEM*. Pre = before training; 1 mon = after 1 month of training; 2 mon = after 2 months of training; post = after 3 months of training; De-1 mon = after 1 month of detraining; De-2 mon = after 2 months of detraining; De-3 mon = after 3 months of detraining.

correlation coefficient and mean CV of the 2 measurements were 0.91 and 6.7%.

Electromyographic Activity. The electromyographic (EMG) activity was recorded during the measurement of the maximal voluntary isometric strength and tendon properties. Bipolar surface electrodes (5 mm in diameter) were placed over the bellies of VL, RF, vastus medialis (VM), and biceps femoris (BF) muscles with a constant interelectrode distance of 25 mm. Reference electrodes were placed on the lateral tibial condyle. The positions of the electrodes were marked on the skin by small ink dots. These dots ensured the same electrode positioning in each test during the experimental period. The electrodes were connected to a preamplifier and differential amplifier with a bandwidth of 5–500 Hz (model 1253A; NEC Medical Systems, Tokyo, Japan). The EMG signals were transmitted to a computer at a sampling rate of 1 kHz. The EMG was full-wave rectified and integrated for a 1.0-second period of steady force output for the measurement of MVC to give integrated EMG. In addition, the mean of integrated electromyography in the knee extensors (VL, RF, VM) was defined as mEMG. To investigate the antagonist muscle activity of the BF (coactivation level), the integrated EMG of the BF was measured during knee extension contraction. To determine the maximal activation of the BF, a maximal knee flexion isometric contraction was performed at the same angle (90° of knee joint). We normalized the integrated EMG value of BF with respect to the integrated EMG value of BF at the same angle when acting as agonist at maximal effort.

Cross-Sectional Area of Muscle and Tendon. Measurements of muscle and tendon CSA were carried out by magnetic resonance imaging (MRI, Resona, 0.5 Tesla System; GE, Tokyo, Japan). T1-wighted, spin echo, axial plane imaging was performed with the following variables: repetition time (TR) 450 milliseconds, echo time (TE) 20 milliseconds, matrix 256 × 172, field of view 300 mm, slice thickness 10 mm, and interslice gap 0 mm. Each subject lay supine in the body coil with the legs fully extended and relaxed. To make the marks visible on the image, the oil-filled capsules were adhered to the skin at 30, 50, and 70% of the femur length, which is proximal from the greater trochanter to the edge of the lateral condyle. The muscles investigated were as follows: RF, VL, vastus intermedius (VI) muscle, and VM. From the axial image, outlines of each muscle were traced and the traced images were transferred to a computer for CSA calculation using a public domain National Institutes of Health image software package. The average of the muscle CSA at the 3 positions (30, 50, and 70% of the femur length) was calculated. In addition, the measurement of patella tendon CSA was taken at the 3 positions: 10, 20, and 30 mm below the patella for the patella tendon. The average of CSA at 3 positions was calculated as the representative of tendon CSA. The reliability (ICC and mean CV) of this method has been reported previously (18,19).

For the control group ($n = 6$), the muscle thickness for knee extensors was measured with an ultrasonic apparatus at

Table 2. Measured variables of tendon, mean (*SD*).*†‡

	Training group ($n = 8$)							Control group ($n = 6$)		
	Pre	1 mo	2 mo	Post	De-1 mo	De-2 mo	De-3 mo	Pre	Post	De-3 mo
Maximal tendon elongation (mm)	25.5 (5.3)	26.7 (5.2)	26.5 (4.1)	25.9 (3.6)	28.6 (5.4)#	28.8 (4.3)##	28.7 (5.4)#	25.4 (6.6)	26.8 (7.2)	25.9 (7.0)
Tendon stiffness (N/mm)	69.2 (19.4)	67.8 (29.1)	77.4 (18.7)	104.4 (37.2)*	93.2 (32.0)*#	85.4 (29.1)#	76.3 (20.7)#	78.6 (16.8)	82.3 (10.3)	81.8 (15.9)
Cross-sectional area of patella tendon (mm^2)	80.1 (18.7)	79.8 (19.2)	81.5 (17.7)	80.9 (20.0)	81.1 (18.4)	79.7 (20.3)	80.5 (19.6)			
Tendon thickness (mm)								3.5 (0.3)	3.4 (0.2)	3.4 (0.3)

*Significantly different from pre ($*p < 0.05$).
†Significantly different from post ($\#p < 0.05$; $\#\#p < 0.01$).
‡Pre = before training; 1 mo = after 1 month of training; 2 mo = after 2 months of training; post = after 3 months of training; De-1 mo = after 1 month of detraining; De-2 mo = after 2 months of detraining; De-3 mo = after 3 months of detraining.

the anterior surface 50% of the femur length. The muscles involved in the measurement of muscle thickness were RF and VI. The subjects remained in a supine position with legs straight and the muscles relaxed. In addition, the thickness of patella tendon was measured at 50% of tendon length. Intraclass correlation coefficient and mean CV of the 2 measurements were 0.98 and 1.8% for muscle thickness and 0.92 and 3.8% for tendon thickness, respectively. Unfortunately, we could not use MRI to measure muscle and tendon CSAs for control group because of scheduling limitations. This point was discussed later.

Statistical Analyses

Values are reported as mean ± *SD* unless otherwise stated. One-way analysis of variance (ANOVA) with repeated measures was used to detect significant differences in the measured variables. In the event of significant values of F in the ANOVA, Tukey's post hoc test of critical difference was used to identify significant differences among means. The level of significance was set at $p \leq 0.05$. Because of the small sample size of the training group, effect size (ES) was calculated for relevant variables. Power calculations (statistical power) were performed using G*Power computer software. Statistical power of >0.8 was obtained in the main significant changes, for example, MVC, stiffness.

Results

Maximal voluntary isometric strength increased by 29.6% after 2 months ($p < 0.01$, ES = 1.18) and by 40.5% after 3 months ($p < 0.001$, ES = 1.62) (Table 1 and Figure 2). Similarly, the activation level (using interpolated twitch technique) and mEMG increased by 7.3 and 27.4% after 2 months (both $p < 0.05$, ES = 1.55 and 0.83) and by 8.9 and 35.0% after 3 months (both p's < 0.01, ES = 2.20 and 1.00) (Table 1 and Figure 2). However, MVC, activation level, and mEMG did not change over the course of detraining for 3 months. No change in the coactivation level was found during training and detraining periods. The CSA of whole quadriceps femoris muscle increased by 5.5% after 3 months of training ($p = 0.015$, ES = 0.47) (Table 1 and Figure 2). There were no significant differences in the relative increase in the muscle CSA among RF, VL, VI, and VM (Figure 3). After 1 month of detraining, the CSA of muscle decreased to pre-training level (Table 1 and Figure 2). In the control group, no changes in the measured variables of muscles were found over the course of the experimental period (Table 1).

The average Fm-L relationships at each time point during training and detraining are shown in Figure 4. Although the maximal elongation of tendon remained unchanged during 3 months of training, the stiffness of tendon increased significantly by 54.0% after 3 months of training ($p = 0.013$, ES = 1.25) (Table 2 and Figure 5). During the detraining period, the maximal elongation values of tendon were significantly

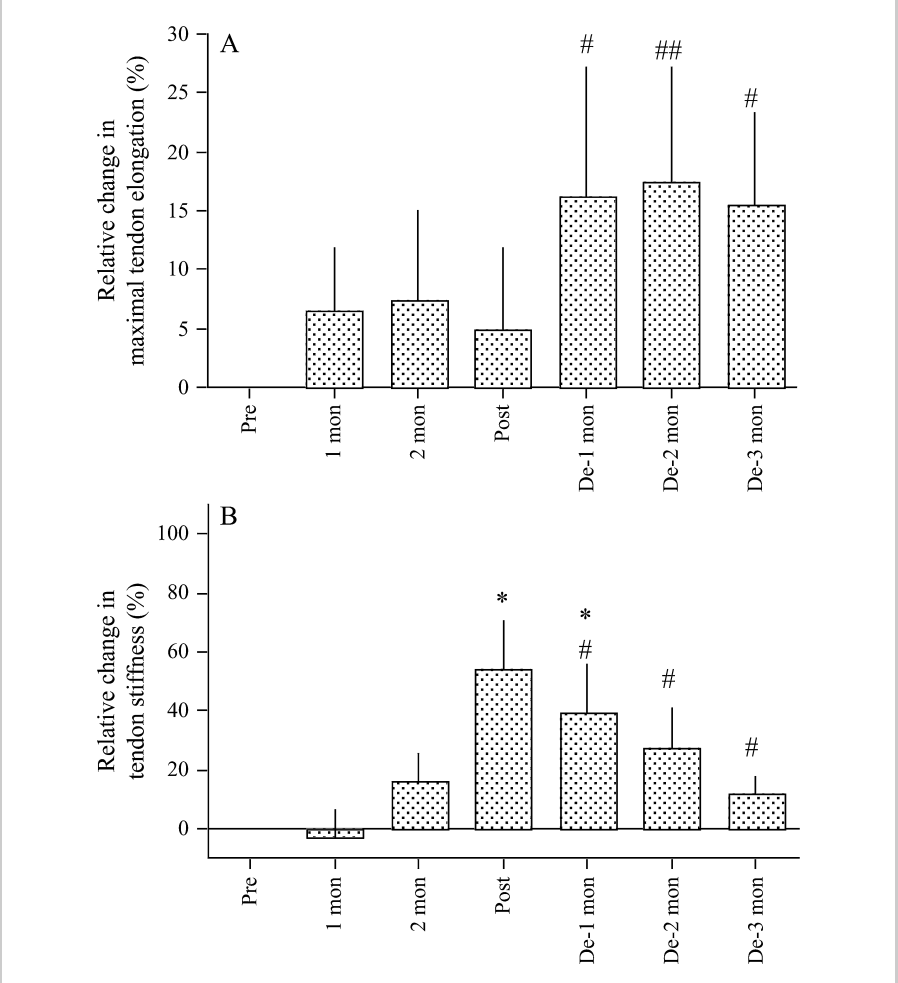

Figure 5. The relative changes in the maximal elongation (A) and stiffness (B) of tendon during the training and detraining periods for the training group. Data are expressed as mean ± *SEM*. Pre = before training; 1 mon = after 1 month of training; 2 mon = after 2 months of training; post = after 3 months of training; De-1 mon = after 1 month of detraining; De-2 mon = after 2 months of detraining; De-3 mon = after 3 months of detraining. *Significantly different from pre (*$p < 0.05$). #Significantly different from pre (#$p < 0.05$, ##$p < 0.01$).

greater compared with the post-training level ($p = 0.003$–0.021, ES = 0.60–0.74) (Table 2 and Figure 5). The tendon stiffness decreased to pre-training level after 2 months of detraining (Table 2 and Figure 5). Furthermore, no significant change in the CSA of patella tendons was found during training and detraining periods (Table 2). In the control group, no changes in the measured variables of tendon were found over the course of the experimental period (Table 2).

Discussion

The main findings of this study were that (a) the adaptations of tendon properties and muscle CSA to the resistance training are slower than those of muscle strength and neural activation and inversely that (b) the adaptations of the former to detraining are faster than those of the latter. To our knowledge, this is the first study to demonstrate the time course of changes in mechanical and morphological properties of human muscle and tendon during training and detraining in vivo.

Some previous studies showed that the stiffness of human tendon increased after 12–16 weeks of resistance training (5,16,18,24,33). On the other hand, relatively short-term exercise program (6–8 weeks) resulted in a little increase in tendon stiffness (19%; (19)) and unchanged in stress-strain curve and stiffness of tendon (26,37). Considering these previous findings, we hypothesized that 8 weeks of resistance training would be insufficient to increase the tendon stiffness. As expected, the stiffness of tendon structures did not change until 2 months of training period, and afterward, the increase (54%) in the tendon stiffness reached statistical significance at the end of training period (3 months). On the other hand, MVC, the activation level, and mEMG already increased significantly after "2 months" of training (Table 1). It is generally accepted that the tendon property is a structure with a slower metabolism compared with the muscle function (8). Recently, Miller et al. (27) showed that the magnitude of maximal change of the rate of collagen synthesis was less in the tendon (~1.7-fold) than muscle (2.8-fold). Therefore, we may say that the process of training-induced changes of muscle functions (muscle strength, neural activation) and tendon properties (tendon stiffness) were different, and thus the adaptation of tendon properties to resistance training would be slower than that of muscle functions. Notably, there is an imbalance between the muscle functions and tendon property adaptations after 1–2 months from the start of training.

During the training period, no significant changes in the maximal elongation of tendon were found despite large increases in muscle strength. This result agreed with the previous studies (5,16,18,24,37). However, the maximal tendon elongation determined at every phase of detraining period was significantly greater that that at 3 months of training (post training). Especially, the maximal elongation of tendon at "1 month of detraining" was already greater than at post-training. At the beginning of the study, it was expected that the adaptation of tendon properties to detraining would be slower than that of muscle. Indeed, de Boer et al. (10) reported that the rate of decline in the tendon stiffness during the latter of 23 days of bed rest was greater than that during the first half of the bed rest period. However, this hypothesis was denied in the present study. Our previous study also showed that the tendon elongation at a given force level increased significantly after only 3 weeks of bed rest (17), although "bed rest" condition was different from "detraining" condition strictly. As far as we know, no studies using animal and human have ever tried to examine the effect of "detraining" on the tendon properties. In addition to the increment of maximal tendon elongation, the tendon stiffness already returned to the pre-training level at 2 months of detraining, although the muscle strength and activation level remained unchanged during the detraining period. Taking the present results into account together with our previous finding (17), the elongation of tendon would increase immediately when the mechanical stress to the tendon during daily life and resistance training was removed. The mechanisms that resulted in the increase in tendon elongation during detraining are unknown. However, the changes in the internal structures of the tendon and aponeurosis might be involved. Furthermore, the variability of the mechanical quality of the tendons originates from differences in the cross-link pattern or structure of the collagen fibers (9). Regardless, further investigations using animals are needed to clarify this point.

Recently, Andersen et al. (4) reported that the detraining subsequent to resistance training increased maximal unloaded movement speed and power in untrained subjects. Furthermore, they stated that a phenotypic shift toward faster muscle myosin heavy chain isoforms in response to detraining explains this result. In the present study, we demonstrated that the detraining unchanged muscle strength and activation level with the increase of tendon elongation. Theoretically, because both the muscle strength and tendon elongation increased during detraining, the stored elastic energy during stretch-shortening cycle exercises would increase and thus enhance these performances. Our previous studies showed that the tendon stiffness was negatively correlated to the performance during stretch-shortening cycle exercises (20,23). Accordingly, the increase in tendon elongation during the detraining period might be assumed to be an advantage to perform effectively stretch-shortening cycle exercise. Hortobagyi et al. (14) showed that no significant changes in the heights of 3 types of vertical jumping (squat, countermovement, and drop jumps) were found after 2 weeks of detraining. However, a close look at the data of Hortobagyi et al. (14) will reveal that the jumping height of countermovement and drop jumps tended to increase after the detraining, although squat jump decreased. Namely, it is likely that the jumping abilities with countermovement increase after the 2 weeks of detraining. In the future, it is necessary to investigate the effect of the detraining

subsequent to resistance training on the performances during various exercises in relation to the possible changes in the muscle and tendon properties.

Tendon CSA did not change during the training and detraining periods (Table 2), which is in agreement with the previous studies (18,21,24,33). However, more recent studies have demonstrated tendon hypertrophy after heavy resistance training (5,16). As an explainable reason for the difference in the results for tendon hypertrophy after training, the intensity and mode of training, state of subjects, and the performance of MRI might be involved. According to the cross-sectional studies in vivo (25,34), however, the CSA of the Achilles tendon of runners has been shown to be greater than those in untrained subjects. Therefore, it is likely that the tendon hypertrophy may be caused by the longer term of resistance training.

Other interesting finding of this study was that MVC, neural activation level, and mEMG remained preserved during 3 months of detraining. This indicated that the training regimen in the present study induced long-lasting neural adaptations. As far as we know, no studies have ever tried to investigate the changes in muscle strength, neural activation level, and CSA at every month during training and detraining. Some previous researchers also reported that the muscle strength decreased but not to the pre-training level after the detraining (6,13,15). In contrast, the muscle CSA already returned to the pre-training level at 1 month of detraining. Andersen et al. (3) reported that the quadriceps CSA decreased to pre-training level after 3 months of detraining. In addition, Allen (1) showed that the CSA of fast twitch (FT) and slow twitch (ST) fibers decreased by 23 and 9% after 6 weeks of detraining. The present results agreed with the previous findings quoted above.

Unfortunately, we could not use MRI to measure muscle and tendon CSAs for control group because of scheduling limitations. Some previous studies showed that there were significant correlation relationships between the muscle thickness by ultrasonography and muscle CSA or volume by MRI (e.g., (28)). In addition, Finni et al. (11) reported that the tendon thickness by ultrasonography was significantly correlated with the tendon CSA by MRI. In the present study, for the training group, there was a significant correlation between the relative increases of muscle CSA (by MRI) and muscle thickness (by ultrasonography) ($r = 0.837$, $p < 0.01$; not showing these data). Therefore, we considered that this point did not affect the main results of this study.

In the present study, we used the isometric knee extension training (single-joint exercise) with submaximal contraction (70% of MVC) that did not use as a real program. In the field of competitive sports, however, the compound joint exercises (jumping, sprinting, etc.) with higher force production were performed to improve the performance of each event. Therefore, we must investigate the effects of these protocols on the measured variables. Furthermore, Staron et al. (36) reported that "retraining" for short periods elicited a rapid return to the trained state (this phenomenon has been termed "muscle memory"). In the future, it is necessary to investigate the effects of "retraining" on the time course of changes in muscle and tendon properties.

Practical Applications

We investigated the time course of changes in mechanical and morphological properties of muscle and tendon during isometric training and detraining. The present results indicated that the time course of changes in the mechanical and morphological properties of muscle and tendon during training and detraining periods were different from each other. Concretely, the adaptations of tendon properties and muscle morphology (muscle CSA) to the resistance training are slower than those of muscle function (strength and neural activation), and inversely, the adaptations of the former (tendon properties and muscle CSA) to the detraining are faster than those of the latter (muscle strength and neural activation). These results indicated that the time course of changes in both muscle and tendon should be given more attention during resistance training (for increasing performances) and rehabilitation program (for preventing injuries).

According to recent findings (7,20,23,35), the performance during stretch-shortening cycle exercise (e.g., sprinting, jumping) was influenced by the tendon properties and muscle functions. Therefore, to enhance the performances in athletic field, the present results would contribute to plan the training schedule during a long period, that is, periodization. On the other hand, our recent study showed that maximal strain of Achilles tendon of 30-year group was already lower than that of the 20-year group, although there were no differences in the muscle strength and activation level between 20- and 30-year groups (22). Furthermore, we suggested that the differences in age-related changes of muscle and tendon would play a role in the etiology and frequency of Achilles tendon ruptures in men in their thirties. Accordingly, the present results would be useful to prevent injuries due to an imbalance of adaptations in muscle and tendon during the resistance training and detraining.

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