Resonance in the human medial gastrocnemius muscle during cyclic ankle bending exercise

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The muscle-tendon unit (MTU) consists of muscle fibers and tendinous tissue that connect to muscle fibers in series. Owing to the viscoelasticity of tendinous tissue, length change of muscle fiber is not identical to that of the MTU in some cases (14). This suggests that, because the maximal force by muscle fibers is dependent on their length and velocity (11, 13), the viscoelasticity of tendinous tissues affects the maximal force-producing ability of muscle fibers. In addition, the storage and release of the elastic energy of tendinous tissues has been recognized as an important mechanism for efficient motions in humans and animals (4, 10, 12, 20). For instance, it has been shown that, during locomotion of animals and humans, muscle fibers of the leg do not change in length and tendinous tissue behaves like a spring, which causes energetical economy (10, 20).

Muscle models with viscoelastic elements imply that periodic movements such as locomotion could be considered forced oscillation (e.g., periodically shaking one end of a spring with mass on the other end) and that the behavior of the MTU is highly dependent on the frequency of the movement. There are several implications of this notion. First of all, resonance could occur in the MTU. Resonance can be defined as the large amplitude of the oscillation of a system caused by an external driving force at the natural frequency of the system. In the context of the MTU, it would be expected that periodic motion with the same range of motion can be performed with much smaller amplitude of length and velocity of muscle fibers at the natural frequency of the motion, which is favorable in terms of force-velocity relationship. Second, there would be phase shift between the length changes in fascicles and those in the MTU. At frequency much lower than natural frequency, the phase shift between the two would be almost the same, but they would be out of phase at much higher frequency. Third, the ratio of amplitude of fascicles to that of the MTU is also dependent on movement frequency. The ratio would be close to one at much lower frequency than resonance and maximized at natural frequency, as mentioned before. Much above the natural frequency, the ratio becomes smaller again. Finally, the relative phase at which high EMG activity appears could also change with respect to the joint angle as the movement frequency changes. The phase shift in length changes between the fibers and MTU causes the phase shift in the velocity changes between them. Therefore, owing to the force-velocity relationship, the phase where high EMG activity appears with respect to joint angles could change as the movement frequency changes. Overall, this frequency dependence of gain and phase could have significant effects in terms of energetics and/or motor control in periodic movement such as locomotion.

Several studies have discussed the possibility of resonance in the human MTU during periodic motions in both upper extremities (2, 8, 23) and lower extremities (3, 22). As for studies on upper extremities, a few studies measured the length changes in muscle fibers during movements (2, 8). However, the gain (the ratio of amplitude) and phase difference between the MTU length and fiber length, which characterize the viscoelastic property of the MTU, were not quantified. As for...
studies on lower extremity movements, the length change was estimated during ankle bending exercise by an inverse dynamics and muscle model (22). However, it should be noted that the estimation of length change in muscle fibers by using muscle models requires a lot of assumption and that the results could be sensitive to the parameters one chooses.

Therefore, the purpose of the present study was to investigate the relationship among the fascicle length, joint angle (MTU length), and EMG activity during cyclic movement at different frequencies. We focused on ankle bending exercise, in which subjects move up by plantar flexion and down by dorsiflexion in a standing position, for two reasons. First, as we will show in METHODS, it is possible to find the analytical relationship between the phase and gain as a function of movement frequency using a forced-oscillation model. The other reason is that our results could be extended to a study of locomotion such as walking. If the resonance is observed in the ankle bending exercise, it could also be possible that resonance affects the energetics of walking. Our hypothesis is that the relationship among the lengths change in muscle fibers and MTU and the pattern of the EMG signal is highly dependent on the frequency of the exercise.

METHODS

Subjects. Five healthy men (age 30.6 ± 7.7 yr, height 1.73 ± 0.6 m, body mass 66.4 ± 4.8 kg) participated in the present study. Informed consent was obtained from the subjects. The present study conformed to the Declaration of Helsinki and was approved by the ethical committee of the University of Tokyo.

Experimental protocol. After warm-up, the subjects performed repetitive one-legged ankle bending exercise at eight frequencies (from 1.33 to 3.67 Hz, every 0.33 Hz, Fig. 1A) in standing position on a force plate (9281B, Kistler). Subjects were instructed to keep their knees straight so that there is little effect from movement of the knee on the changes in MTU length. The order of frequencies was randomized, and rest between trials was set at 2–5 min. Each trial was set around 10–15 s. Data for ~7 s after the exercise reached a steady state were used for analysis.

Measurement and analysis. The longitudinal ultrasonic images of the medial gastrocnemius muscle (MG) were measured during the exercise by using real-time ultrasonic apparatus at 65 Hz (SSD-5500, Aloka). The fascicle length (L_{fas}) and fascicle angle (θ) were determined as the length from the superficial to the deep aponeurosis along the fascicle and the angle at which the fascicles arose from the deep aponeurosis, respectively (Fig. 1B). This analysis was performed by using the public-domain NIH Image program (developed at the U.S. National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/). To determine the contraction velocity of the fascicles, smoothing was performed by using a fourth-order zero-lag Butterworth filter with a cutoff frequency at 20 Hz. The positive velocity was defined as the shortening of the fascicles.

The angle changes of ankle and knee were calculated by using cinematographic data in the sagittal plane collected with a high-speed video camera at 200 Hz (MEMRECAM c2 Nac). The coordinates of anatomical landmarks were low-pass filtered at 4 Hz for the sets of the low frequency (1.33 Hz) and 10 Hz for the rest. The MTU length (the distance from the origin to insertion of the muscle) was calculated by substituting knee and ankle angles in the equations developed by Grieve et al. (11a). After the synchronization of cinematographic and force plate data, the resultant moment about the ankle (M_{ank}) was calculated by using inverse dynamics. The surface electromyography was recorded from MG at 1,000 Hz by using bipolar Ag-AgCl electrodes with a diameter of 5 mm. The intraelectrode distance was set at 20 mm. The EMG signals were amplified (1253A, NEC) with bandwidth of 5–1,000 Hz, full-wave rectified, and low-pass filtered (4th-order zero-lag Butterworth filter with a cutoff frequency of 20 Hz).

Averaging of the data. One cycle of the exercise was defined as the time interval from a maximum plantar flexed position of the ankle joint to the subsequent maximum plantar flexed position. To average over trials, the data were represented as a function of normalized time (0 to 100% cycle and the end points corresponded with the maximum plantar flexed positions) by spline interpolation. The average of five cycles was calculated for each frequency from each subject.

Calculation of work output. The force developed by the MG MTU is estimated by F = M_{ank}/MA, where MA is the moment arm obtained by differentiating Grieve’s equation (5). The mechanical power outputs produced by the MTU and the fascicles were calculated by multiplying force and shortening velocity of the MTU and the fascicles, respectively. Positive work by the MTU and fascicle during one cycle was calculated by integrating the corresponding positive power values.

Statistics. To determine statistically significant difference, Tukey’s multiple-comparison test was performed. The significance level was set at P < 0.05.

Forced-oscillation model. The MTU is modeled as the combination of three components (Fig. 1C), which consist of the contractile
component (CC), the linear series elastic component (stiffness: K), and the linear viscous component (viscous coefficient: C). A block of effective mass M is attached to the MTU. The contractile component length (L_{cc}) was calculated by L_{cc} = L_{tes} \times \cos \theta.

If the change of the CC length occurs sinusoidally at angular frequency \( \omega \), the equation of motion of the mass is

\[
\frac{d^2X}{dt^2} = -C \frac{dX}{dt} - K(X - A_{CC} \cos \omega t)
\]

(1)

where \( X \) is MTU length change, \( A_{CC} \cos \omega t \) is CC length change, and \( M \) is effective mass of the system. The steady-state solution to Eq. 1 is \( X = A_{MTU} \cos(\omega t - \phi) \), where \( A_{MTU} = A_{CC}/\sqrt{[1 - (\omega/a_{ao})^2] + (\omega C/K)^2} \) and \( a_{ao} = \sqrt{K/M} \) (called the natural frequency), where \( A_{CC} \) is amplitude of CC length change, and \( A_{MTU} \) is amplitude of MTU length change. Thus we obtain

\[
\frac{A_{MTU}}{A_{CC}} = \frac{1}{\sqrt{[1 - (\omega/a_{ao})^2] + (\omega C/K)^2}}
\]

(2)

This indicates that the relationship between frequency \( \omega \) and the amplitude of MTU length relative to that of CC length is expected to obey Eq. 2 and that the phase lag between the two is expected to obey Eq. 3. One can show that Eq. 2 has a peak at the damped natural frequency \( a_{ao} = \sqrt{\omega^2 - 2(C/2M)^2} \). The MTU and CC length changes were fitted by a sine curve, and then the amplitude ratio of the MTU length to the CC length was calculated. The ratio data were fitted by Eq. 2 as a function of \( \omega \) using a nonlinear least square method to determine \( a_{ao}, K, \) and \( C \) (Fig. 6, bottom). Theoretical values for the phase lag were determined using parameters above and imposed on the experimental data (Fig. 6, bottom).

The effective mass of the subject was determined by a following procedure (see also Ref. 9). The equation of motion for the center of gravity of a subject is

\[
m a^2 \frac{d^2x}{dt^2} = F - F_0
\]

(4)

where \( m \) is mass of a subject, \( x \) is the vertical displacement of the center of gravity, \( F \) is ground reaction force, and \( F_0 \) is ground reaction force at rest (= mg). On the other hand, the equation of motion for the MTU model is

\[
M \frac{d^2X}{dt^2} = F - F_0
\]

(5)

where \( F \) is force acting on mass (tendon force) and \( F_0 \) is force acting on mass at rest. We make three assumptions. 1) The displacement of the center of gravity is small. 2) The distance from the ankle joint to the center of pressure: the distance from the ankle joint to the end point of the Achilles tendon is constant during exercise, which is represented by \( a:b \), as in Fig. 1D, 3) The mass and moment of inertia of the foot segment are so small that the terms with inertia in the equation of motion are negligible. From assumptions 1 and 2, and geometrical relationship in the foot, we obtain \( b \times dx = a \times dX \). Therefore, \( ds/dt = (a/b)(dX/dt) \) and \( d^2x/dt^2 = (a/b)(d^2X/dt^2) \) hold. Furthermore, by using assumption 3 and the equation of rotational motion of the foot segment, we obtain \( fa = Fb \) and \( f_{oa} = F_{db} \). By substituting these into Eq. 4 to eliminate \( f \) and \( f_0 \), we can see

\[
m a^2 \frac{d^2x}{dt^2} = F - F_0
\]

(6)

Because \( f_0 = mg \) and \( f_{oa} = F_{db} \), we obtain \( ab = F_0/mg \) and substitute this into Eq. 6.

\[
\frac{F_0^2}{mg} \frac{d^2X}{dt^2} = F - F_0
\]

This equation should be equal to Eq. 5; we then obtain effective mass as \( F_0^2/mg^2 \). To find the explicit value of effective mass for each subject, \( F_0 \) was determined as the tendon force averaged over one cycle, and weight of each subject (mg) was measured by a force plate.

RESULTS

Primary observation. In the present study, resonance is observed as the maximized ratio of the amplitude of the MTU length to that of the fascicles at an intermediate frequency (the damped frequency of the exercise) of the exercise. This is clearly shown in the figures (Figs. 2 and 3 at 2.67 Hz and Fig. 4, top).

At every frequency of the exercise, changes in MTU length corresponded with changes in the ankle joint angle. When the ankle was plantar flexed, the whole muscle was shortened, and vice versa (Figs. 2 and 3).

At low frequency (1.33 Hz), the lengths of the fascicles and MTU varied almost in phase (Fig. 2, Fig. 3, and Fig. 4, bottom). However, the phase lag between the two increased nonlinearly as the frequency increased, and it reached almost out of phase at 3.33 Hz (Fig. 2, Fig. 3, and Fig. 4, bottom). We also observed a nonlinear relationship in the amplitude ratio of the MTU to the fibers (Fig. 4, top). It was almost equal to one at lowest frequency. It became maximized at intermediate frequency (2.67 Hz in the example from a subject shown in Fig. 2 and 3 Hz for the averaged data shown in Fig. 4, top), which is considered resonance. At higher frequencies, the ratio decreased again. The small amplitude of the length changes in the fascicles around the damped natural frequency also affected the amplitude of the velocity of the fascicles. The amplitude of the fascicle velocity was quite small with respect to that of the MTU velocity as a result of the small amplitude of the fascicles (Figs. 2 and 3).

Figure 5 shows the positive work by the fascicles and MTU and ratio of the work by the fascicles to that by the MTU. The ratio was minimized at 2.67 Hz. There was significant difference between 1.33 and 2.33−3.33 Hz, 1.67 and 2.33−3.00 Hz, 2.00 and 2.67 Hz, and 2.67 and 3.67 Hz. Figure 6 shows a result of the regression of the data of the amplitude ratio by use of the forced-oscillation model. The amplitude of the MTU relative to the CC was maximized at 160 cycles/min, which is the manifestation of resonance. The averaged natural frequency, damped natural frequency, stiffness of the series elastic element, and viscous coefficient for five subjects were \( 2.84 \pm 0.18 \) Hz, \( 2.81 \pm 0.17 \) Hz, \( 165.7 \pm 20.0 \) N/mm, and \( 1.98 \pm 0.76 \) N·mm\(^{-1}\)·s, respectively. Note that the difference between the natural and damped natural frequencies was small because of a relatively small viscous coefficient. The mean stiffness of the series elastic element is of the same order as stiffness in the literature (17, 21).

The patterns of the EMG activities dramatically changed with exercise frequency (Figs. 2, 3, and 7). At low frequency, high EMG activity appeared during the plantar flexion phase. However, at high frequency, it appeared during the dorsiflexion phase. Figure 7 shows the ratio of integrated EMG during plantarflexion phase to that during dorsiflexion phase. There was significant difference between 1.33 Hz and 2.00−3.67 Hz.
1.67 Hz and 2.33–3.67 Hz, 2.00 Hz and 2.33–3.67 Hz, and 2.67 Hz and 3.33–3.67 Hz.

**DISCUSSION**

In the present study, we quantified the length change in the fascicle length and determined the gain (amplitude ratio) and phase difference between the fascicles and MTU during cyclic ankle bending exercise at different frequencies. These results were well explained by the forced-oscillation model. Therefore, the major finding of the present study was that the viscoelasticity of the MTU has a significant effect on the behavior of the muscle fibers in a frequency-dependent manner.

**Resonance in MTU.** To maintain periodic movements like walking, net work done by muscle fibers in one cycle must be positive to compensate energy loss by dissipation such as viscosity (7, 15). Around the natural frequency of the ankle bending exercise, the shortening phase of the fibers corresponds with a high force-production phase, which results in large positive power production. The lengthening phase corresponds with a low force-produced phase, which results in small negative power production (Fig. 2, 2.67 Hz). Therefore, the net positive work sufficient to maintain the movement can be obtained with small amplitude of velocity of fibers at the natural frequency. As a result of this, the muscle fibers become quasi-isometric, which is advantageous in terms of the force-velocity relationship.

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Fig. 2. Behavior of the MTU during 1 cycle from 1 subject. Ankle angle changes are shown on the top of each block. Length changes in muscle fibers (thick solid line), MTU length (dashed line), and EMG activity (thin solid line) are shown on the second graph from the top of each block. Note that length changes are represented by the change from mean value during 1 cycle. Contraction velocity of muscle fibers relative to that of MTU is shown in the third graph and tendon force is shown at the bottom. Each block corresponds to the data at 1.33, 2.00, 2.67, and 3.33 Hz from the left on the top, respectively.
It has been shown that the stretch and recoil of tendinous tissues supplies mechanical work and reduces the work by muscle fibers during locomotion (10, 20). These studies showed that muscle fibers become quasi-isometric when the muscle is active. In our study, the consistent result was obtained around the damped natural frequency (Figs. 3 and 4). However, at the frequencies far from the resonance, this is not the case at all. For instance, at 3.33 Hz, the muscle fibers and MTU vary almost out of phase with the similar amplitudes (Fig. 3), and the fibers perform large work to maintain exercise (Fig. 5), leading to unfavorable situation to the muscle fibers. Our study clearly demonstrates that the operation of the muscle fibers is “optimized” owing to the resonance effect in the exercise.

A few studies examined the changes in the length of the muscle fibers during voluntary elbow flexion-extension movement (2, 8). They could not observe resonance or large phase shift at frequencies up to 5 Hz, whereas we observed resonance around 3 Hz. In their protocol, the subjects performed elbow flexion and extension without load, i.e., only the forearm was the load for the movement. In the present study, on the other hand, the whole body must be lifted up and down by only the ankle joint. Therefore, the effective mass of the movement was much larger in ankle bending exercise than the elbow flexion-extension movement, which resulted in much lower natural frequency in the voluntary ankle bending exercise than in the voluntary elbow flexion-extension movement.

Fig. 3. Behavior of the MTU during 1 cycle from the average over all the subjects. The same sets of data as Fig. 2 are shown as the average over all the subjects.
There have been several studies focusing on ankle bending exercise in a context of forced oscillation. We summarize the similarities and differences to the present study.

Shibayama et al. (22) estimated the length change of muscle fibers using an inverse dynamics and muscle model. They showed that the phase shift between the fibers and MTU changed abruptly from 0 to 180° at the natural frequency. However, our data indicate a gradual increase of the phase shift as the frequency increases rather than an abrupt one. The reason for the difference can be attributed to whether a muscle model has a viscous element. It can be shown that, in forced oscillation with a viscous element, the phase shift is predicted to change gradually as frequency changes, whereas, in one without it, there is discontinuity of the phase shift at the natural frequency of the system. Therefore, the gradual change in the phase shift observed in our experimental data indicates the existence of a viscous element in the MTU, which was taken into account in the model in the present study.

Nagano et al. (19) performed a computer simulation using the Hill-type muscle model to generate cyclic heel raise exercise at frequencies ranging from 1.11 to 3.33 Hz. They found that the ratio of the positive mechanical work by the series elastic component to that by the MTU increases as the movement frequency increases. As for the CC, the ratio of positive work to that by the MTU decreases as the movement frequency increases. In contrast to this result, our results show that work output by the CC is minimized at intermediate frequency (2.67 Hz). Taking account of the fact that the frequency at which the work by the fascicles is minimized corresponded to around the natural frequency of the movement (Fig. 7), it is indicated that in the musculoskeletal model by Nagano et al. the movement frequency they investigated is below the natural frequency of the movement and that, therefore, the natural frequency of the movement for our subjects is lower than that for the musculoskeletal model.

Bach et al. (3) determined the viscoelastic properties of calf muscle tendon unit from the signal of ground reaction force by the damped-oscillation method (6). The averaged natural frequency was 3.33 Hz, which is similar in value to our study. They also determined the gain and phase between the signals from the ground reaction force and EMG in the plantar flexor during oscillation about the ankle joint. The gain and phase determined from the data were matched well with those predicted by the damped-oscillation method. The advantage of the present study to theirs is that we directly measured the length change of the fascicles. Furthermore, it should be noted that the elastic coefficient we determined directly reflects the stiffness of tendinous tissue, whereas that determined by Cavagna (6) and Bach et al. is a somewhat “phenomenological” one, which has only indirect connection with the stiffness of tendinous tissue.

![Fig. 4. Gain (amplitude ratio) and phase of the length changes. Top: ratio of amplitude of length change of MTU to that of fascicles. Bottom: phase shift between MTU length and fascicle length change. Results of the average over 5 subjects are shown.](image)

![Fig. 5. Positive work by MTU and fascicle. Top: positive work during 1 cycle by the MTU (●) and fascicle (■) is represented as a function of frequency. The average of the 5 subjects is represented. Bottom: ratio of the positive work by fascicles to that by the MTU in 1 cycle is represented as a function of frequency. The average of the 5 subjects is represented. *Significant difference (P < 0.05).](image)
Loram et al. (16) found that the fascicle length changes out of phase with the MTU length during quasi-static body sway (below 1 Hz) of the body during quiet standing, whereas, in the present study, out-of-phase behavior does not appear until above 3 Hz. This difference suggests that the natural frequency of quiet standing is much lower than that of the ankle bending exercise. In quiet standing, torque by gravity increases as the body deviates from upright, and this torque cancels some of the restorative force, which may result in much lower effective stiffness and natural frequency. Another factor could be the difference in nature of the two movements (rotational motion vs. linear motion).

Implication for motor control. We discuss possible issues related to motor control on the effect of the frequency dependence of the gain and phase between the fascicles and MTU. First, we claim that the dependence of the pattern of the EMG signal on the movement frequency is caused by the phase difference between the fascicles and MTU. At low frequency, the high EMG activity appeared in the plantar flexion phase of the exercise, whereas at high frequency it appeared in the dorsiflexion phase. This may seem very surprising because the MG muscle is plantar flexor. However, this paradox is solved by the fact that high EMG activity corresponded with the shortening phase of the muscle fibers (Figs. 2 and 3). Because of the force-velocity relationship (13), it is reasonable to assume that higher EMG activity would be needed for the same amount of force in shortening contraction than lengthening contraction. This gives one a qualitative explanation about why higher EMG activity appears in the shortening phase of the fibers. Furthermore, by the phase difference between the fibers and MTU, there exists the frequency dependence of the patterns of EMG with respect to the changes in the MTU length.

This suggests that great care should be required to interpret EMG signals with respect to the movement of MTU (joint angle) under certain circumstances.

Second, the dependence of the amplitude and phase shift between the MTU and fascicle on the movement frequency could cause difficulty in certain situations for afferent signals from muscle spindles to be interpreted properly for precise motor control. For instance, at the natural frequency, the signals from muscle spindle might be interpreted as if the amplitude of the movement were much smaller than what it actually is, because the amplitude of the fascicles is much smaller than that of the MTU. Similarly, at the high frequency of the exercise where the length changes of the fascicles and MTU are out of phase, the central nervous system might be perceived as if the joint were moving out of phase with the way it really is moving.

We may expand the message from the present study to other cyclic movements such as walking and running, although the determination of natural frequency of those movements would be much more difficult than that of the ankle bending exercise. It has been reported that there is a concave relationship between the oxygen consumption and walking velocity (18), which is similar to our result on the relationship between the work by muscle fibers and movement frequency (Fig. 5). This agreement implies that the resonant effect due to the viscoelasticity of tendinous tissue may be one of the main reasons for the existence of the energetically optimal speed in walking.

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Fig. 6. Example of nonlinear regression from 1 subject. One example of result on nonlinear regression (see METHODS) is shown. Top: data on amplitude of MTU relative to that of CC. Bottom: data on phase lag. The theoretical line was determined by using parameters from the amplitude data.

Fig. 7. Ratio of integrated EMG (iEMG) activity during plantar flexion (PF) phase to that during dorsiflexion (DF) phase was plotted as a function of frequency. The average of the 5 subjects is represented. *Significant difference (P < 0.05).
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