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RESEARCH ARTICLE

Balance control under different passive contributions of the ankle extensors: quiet standing on inclined surfaces

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Abstract Human bipedal stance is often modeled as a single inverted pendulum that pivots at the ankle joints in the sagittal plane. Because the center of body mass is usually maintained in front of the ankle joints, ankle extensor torque is continuously required to prevent the body from falling. During quiet standing, both *passive* and *active* mechanisms contribute to generate the ankle extensor torque counteracting gravity. This study aimed to investigate the *active* stabilization mechanism in more detail. Eight healthy subjects were requested to stand quietly on three different surfaces of 1) *toes-up*, 2) *level*, and 3) *toes-down*. Surface electromyogram (EMG) was recorded from the medial head of the gastrocnemius (MG), soleus (SOL), and tibialis anterior muscles. Inclination angle of the body was simultaneously measured. As a result, we found that EMG activities of MG and SOL were lowest during the toes-up standing and highest during the toes-down, indicating that increased (decreased) passive contribution required less (more) extensor torque generated by active muscle contraction. Frequency domain analysis also revealed that sway-related modulation of the ankle extensor activity (0.12–4.03 Hz) was unchanged among the three foot inclinations. On the other hand, isometric contraction strength of these muscles increased as the slope declined (toes-up < level < toes-down). These results support the idea that by regulating the isometric contraction strength, the CNS maintains a constant level of muscle tone and resultant ankle stiffness irrespective of the passive contribution. Such control scheme would be crucial when we consider the low bandwidth of the intermittent controller.

Keywords Posture · Quiet standing · Inverted pendulum · Ankle extensors · EMG

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Introduction

Human bipedal stance is often modeled as a single inverted pendulum that pivots at the ankle joints in the sagittal plane (Jeka et al. 1998; Winter et al. 1998, 2001; Peterka 2002; Masani et al. 2003, 2006, 2007; Gage et al. 2004). Because the center of body mass (CoM) is usually maintained a few centimeters in front of the ankle joints during quiet standing (Smith 1957; Gatev et al. 1999), gravity continuously acts on the pendulum to produce a forward toppling torque. At the same time, the ankle extensor muscles coupled to the pendulum by the series elastic element pull the pendulum in the rearward direction to keep the CoM within the base of support. The dynamic equation of the inverted pendulum model is as follows:

$$I\ddot{\theta} = mgh\theta - T_a \quad (1)$$

where I is the moment of inertia of the body, θ is the sway angle, m is the body mass, g is the acceleration of gravity, h is the distance of the CoM from the ankle joints, and T_a is the ankle extensor torque.

The ankle extensor torque needed to counteract the gravitational toppling torque (T_a) can be evoked *passively* and *actively* (Morasso and Sanguineti 2002). The passive torque component results from intrinsic mechanical properties (i.e., stiffness and/or viscosity) of muscle, aponeurosis, tendon and joint structure, and acts without time delay. On the other hand, the active torque component is generated via muscle contractile elements that are regulated by neural commands. These neural commands can be further broken down into a tonic, time-invariant component and a phasic, sway-related component (Bottaro et al. 2005). The tonic component of the neural commands enhances the muscle tone to set the stiffness coefficient of the ankle joints (i.e., intrinsic ankle stiffness) (Winter et al. 1998, 2001). Although intrinsic ankle stiffness gives partial compensation for the effect of gravity, it is not comparable to load stiffness (mgh per unit angle) on its own [91% mgh; Loram and Lakie (2002) 65% mgh; Casadio et al. (2005)]. Therefore, sway-related modulation of the ankle extensor activity is required to prevent the body from falling.

Although such complementary relationship between the passive and active stabilization mechanisms has been proposed, the nature of the active one has not been fully understood. The present study was aimed to investigate the active stabilization mechanism of sway in more detail. In order to achieve this end, we required the participants to stand on three different surfaces of (1) *toes-up*, (2) *level*, *and* (3) *toes-down* to change the passive contribution of the ankle extensors. By comparing the activation patterns of the ankle extensor muscles under different passive contributions, we will provide further insight into the active stabilization mechanism of sway during quiet standing.

Materials and methods

Subjects

Eight healthy male subjects participated voluntarily in this study. Their age, height, and body mass were 25.1 ± 2.0 years, 169.8 ± 3.1 cm, and 71.5 ± 7.5 kg (mean ± SD), respectively. They had no history of neurological disorders. The experimental procedures used in this study were in accordance with the Declaration of Helsinki and were approved by the ethics standards of the committee on Human Experimentation at the Graduate School of Arts and Sciences, The University of Tokyo. All subjects gave their informed consent to participate in the study after receiving a detailed explanation of the purpose, potential benefits, and risks involved.

Experimental protocol and measurements

The barefoot subjects were requested to keep a quiet stance for 30 s on the three different surfaces of (1) toes-up, (2) level, and (3) toes-down with eyes open, hands at their sides, and feet kept parallel 15 cm apart between centers of the heels (Fig. 1). The slope of toes-up and toes-down was ±10°, respectively. In order to keep the inclination angle of the body at the same level among the conditions, we gave instructions to the subjects in the course of the experiment. Five trials were conducted for each slope condition. Surface electromyogram (EMG) was recorded using bipolar Ag–AgCl electrodes (Blue Sensor, Medicotest A/S, Denmark) with a diameter of 5 mm. Following the careful abrasion of the skin, the electrode pairs were placed longitudinally over the right medial head of the gastrocnemius (MG), soleus (SOL), and tibialis anterior (TA) muscles with an interelectrode distance of 20 mm. The ground electrode was placed on the medial malleolus. The EMG signals were amplified (model 1253A, NEC Medical Systems, Japan) with band-pass filtering between 5 Hz and 1 kHz. The horizontal position of a lumbar point of about L3 was measured with a charge-coupled device laser displacement sensor (resolution 1 μm, LK-2500, Keyence, Japan), then converted to the body angle. All electric signals were stored with a sample frequency of 1 kHz on the hard disk of a personal computer using a 16-bit A/D converter (PowerLab/16SP, ADInstruments, Australia).

Data analysis

For the time series of the full-wave rectified EMGs and the body angle, auto- and cross-spectral analysis was performed (Signal Processing Toolbox, MATLAB, The

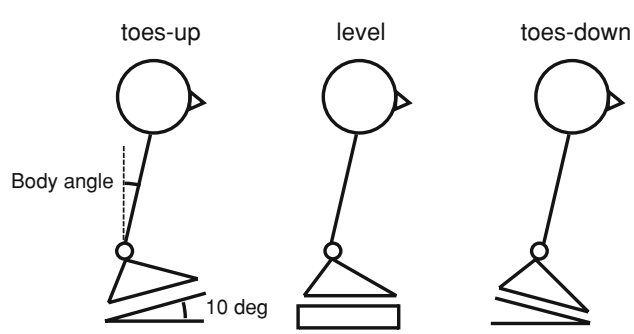

Fig. 1 Schematic diagrams of the experimental set-up and definition of the body angle

Mathworks, USA). The data for a single trial were divided into three subsets with a length of 8,192 data points each (with bias removed). A 13-bit fast-Fourier transform algorithm was applied to generate a Fourier spectrum for each subset after being passed through a Hamming-window. Then, auto-power spectral density function (PSD) for the rectified EMGs and cross-power spectral density function (CSD) between the rectified EMGs and the body angle were calculated. Both PSDs and CSDs were averaged over three subsets, and smoothed by a Bartlett-window. Coherency spectrum $\left(\mathrm{Coh}^2(f)\right)$ for two time series (x and y) was given as follows:

$$\mathrm{Coh}^2(f) = \frac{\left|S_{xy}(f)\right|^2}{S_x(f)S_y(f)} \tag{2}$$

where $S_{xy}(f)$ is smoothed CSD between x and y, $S_x(f)$ and $S_y(f)$ are smoothed PSD of x and y, respectively. If the coherence value is 1, it means that two signals are perfectly phase locked at the frequency, while if the coherence value is 0, it means that two signals at the frequency are perfectly randomly modulated each other.

Statistics

To test the difference among the slope conditions, a one-way ANOVA with repeated measures was used. The Tukey–Kramer test was used for post hoc analysis. $P < 0.05$ was used as a level of significance.

Results

Quantitative analysis of the body angle and the EMG activities

Figure 2a shows representative examples of the 30-s time series of the body angle for each slope condition. The mean body angle was 3.25° ± 0.70° in the toes-up condition, 3.25°± 0.66° in the level, and 3.33° ± 0.77° in the toes-down as the group averaged values (mean ± SD). There was no significant difference in the mean body angle among the conditions ($P = 0.883$). This confirms that the static toppling torque (mghθ) was the same among all conditions.

Figure 2b–d illustrate representative examples of the 30-s time series of the rectified EMGs (MG, SOL, and TA) for each slope condition. To the eye, MG and SOL show lowest activity in the toes-up condition and highest activity in the toes-down. Meanwhile, TA is about silent in all slope conditions.

Figure 3 shows group mean values of the root mean square (RMS) of the raw (non-rectified) EMGs for each slope condition. MG and SOL show monotonically increased activity with a declining slope (toes-up < level < toes-down) (MG; $P = 0.001$, SOL; $P = 0.009$). On the other hand, there was no significant difference in the activation level of TA among the slope conditions ($P = 0.427$). Because the activation level of TA was close to noise floor (0.004 mV) in all conditions, it was not analyzed further.

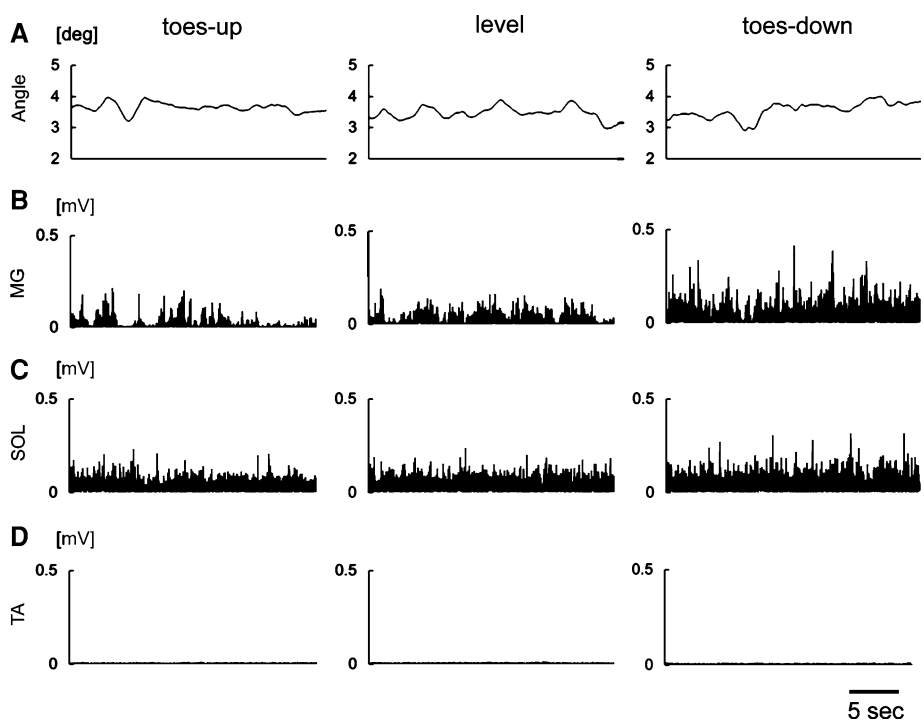

Fig. 2 Representative examples of the 30-s time series for each slope condition. **a** Body angle, **b** rectified EMG of MG, **c** rectified EMG of SOL, **d** rectified EMG of TA

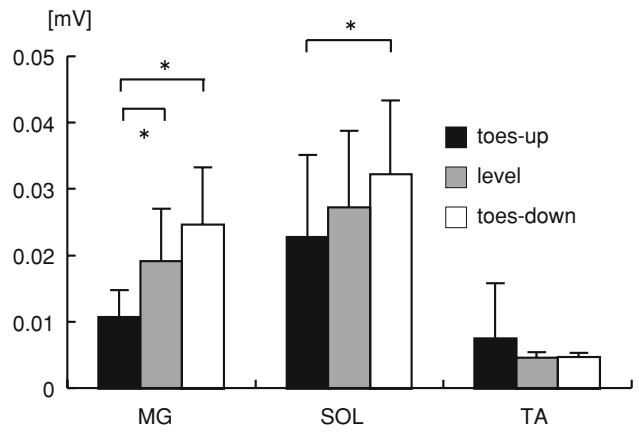

Fig. 3 Group mean values of root mean squares (RMS) of raw EMGs for each muscle and each slope condition. *Asterisks* indicates the significant difference between conditions $P < 0.05$. *Error bars* represent 1 SD

Frequency domain analysis

The most important observation of the present experiment is that MG is only intermittently activated in the toes-up condition, whereas it shows continuous activity (with slower modulation) in the toes-down condition (Fig. 2b). In order to examine this in a more systematic manner, auto-spectral analysis was performed on the rectified EMGs of MG and SOL. Figure 4 illustrates representative examples of the PSDs for two subjects. Two marked frequency components are observed for both muscles; one is at very low frequencies below 1 Hz (although SOL of subject 7 shows rather flat spectra, most of the remainder show marked frequency component at there) and the other is around 9 Hz.

In order to examine the functional significance of each frequency component of the ankle extensor activities, we performed cross-spectral analysis between the rectified EMGs (MG and SOL) and the body angle. Figure 5 illustrates the coherency spectra for each slope condition. The figure shows that, during the standing trials, interaction between the ankle extensor activities and the body sway occurs in the frequencies below 3–4 Hz. At very low frequencies (<1 Hz), there is a region that shows relatively high coherence. Also, relatively low, but non-negligible coherence is observed in the frequency region up to 3–4 Hz (this is because the ankle extensor activities are irregular and only partly synchronized with the body sway in there; Loram et al. 2005). On the other hand, there is approximately constant low coherence above 4–5 Hz, indicating that the frequency component above 4–5 Hz is independent of body sway. During the submaximal isometric contraction, the rhythmic position or force fluctuation of limbs or fingers due to the motor-unit synchronization is observed at a frequency around 8–12 Hz, which is commonly referred as physiological tremor (McAuley and Marsden 2000). Because the ankle extensors maintain isometric contraction to enhance the muscle tone during quiet standing (Winter et al. 1998, 2001), it is reasonable to assume that the ankle extensors show recurring activities similar to the physiological tremor. It has been also pointed out that tremor amplitude increases with the contraction strength up to 60% MVC (Löscher and Gallasch 1993). Therefore, the amplitude of the frequency component around 9 Hz can be regarded as indicative of isometric contraction strength of the ankle extensors.

Based on the above, we defined EMG activity occurring at 0.12–4.03 Hz as the low frequency component (LF).

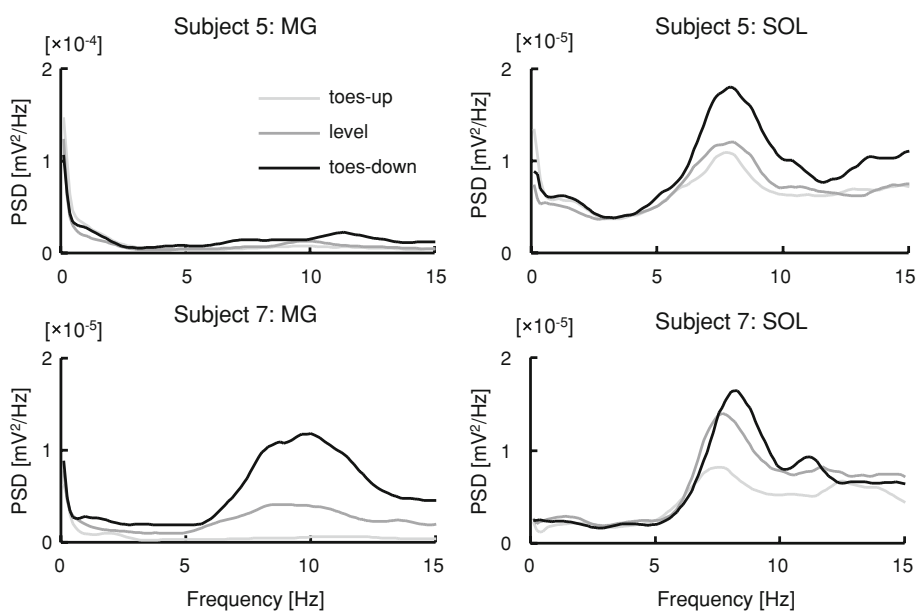

Fig. 4 Representative examples of auto-power spectral density function (PSD) for the rectified EMGs (*left panel* MG, *right panel* SOL) calculated from two subjects. The spectra are the ensemble averages from five trials for each condition

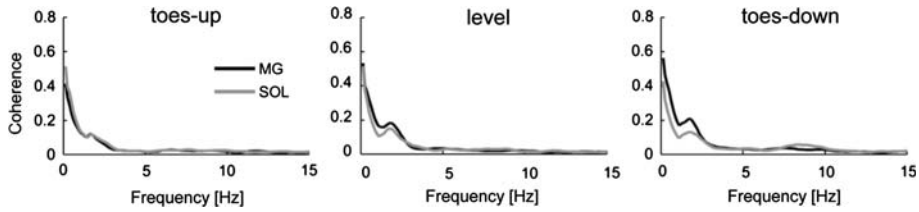

Fig. 5 The coherency spectra between the rectified EMGs and body angle (*solid line* MG, *faded line* SOL) for each slope condition. The *lines* are the ensemble averages of eight subjects

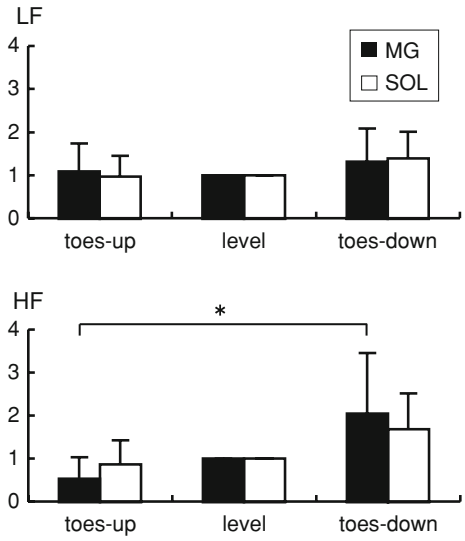

Fig. 6 The energy of the LF and HF. *Asterisks* indicates the significant difference between conditions $P < 0.05$. *Error bars* represent 1 SD

Then, we defined that occurring at 7.08–10.99 Hz as the high frequency component (HF). This was because we wanted to have the same 4 Hz band as the LF around the peak power frequency (the peak power frequency in the level condition was observed at 9.39 ± 0.86 Hz for MG, and 8.92 ± 1.42 Hz for SOL; mean ± SD). Finally, we calculated the energy of each component by integrating the PSD in these regions, and normalized the energy for each condition relative to that for the level condition (Fig. 6). We found that there was no significant difference in the LF among the conditions for either muscle (MG; $P = 0.546$, SOL; $P = 0.275$). Given that sway-related modulation of the ankle extensor activity (i.e., LF) compensates for the residual component of the stiffness-derived torque in the overall torque requirement (Morasso and Sanguineti 2002; Loram and Lakie 2002), these results indicate that intrinsic ankle stiffness relevant to quiet standing was unchanged in all slope conditions. On the other hand, the HF of MG showed significant increase with a declining slope (toes-up < level < toes-down) ($P = 0.018$). Although it failed to reach significance, the HF of SOL also increased as the slope declined ($P = 0.083$). These results indicate that isometric contraction strength of the ankle extensors increased as the slope declined.

Discussion

Complementary relationship between the passive and active stabilization mechanisms

In the present experiment, we at first demonstrated that EMG activities of MG and SOL were lowest during the toes-up standing and highest during the toes-down (Fig. 3). This result indicates that increased (decreased) passive extensor torque due to the foot inclinations required less (more) extensor torque generated by active muscle contraction.

Mezzarane and Kohn (2007) previously carried out an experiment similar to that of the present study, and reported that SOL EMG increased in the toes-down condition, while did not change in the toes-up when compared with the level condition. This contradicts our results. However, the inconsistency is assumed to be attributable to higher forward lean in the toes-up condition in the prior study (5.03° ± 0.95° in the toes-up condition, 4.08° ± 1.27° in the level, and 3.45° ± 0.98° in the toes-down, mean ± SD). Fitzpatrick et al. (1992) reported that the integral EMG of SOL has a linear relationship with ankle angle and ankle torque during quiet standing. This explains why SOL EMG did not decrease in the toes-up condition in the study of Mezzarane and Kohn (2007). On the other hand, the mean body angle was the same among the slope conditions in the present experiment. Therefore, the EMGs monotonically increased as the slope declined (toes-up < level < toes-down).

Possible influence of the shift in the tension/length relationship of the ankle extensor muscles

For the interpretation of the present results, we must take into account the possibility that the observed change in the EMGs (Fig. 3) might be affected by the shift in the tension/length relationship of the ankle extensor muscles due to the foot inclinations. Concerning this, Kawakami et al. (1998, 2000) previously demonstrated that, in the passive transition of the ankle joint from 15° of plantar flexion to 15° of dorsiflexion (with the knee fully extended), MG and SOL operated between the top of the ascending limb and the middle of the descending limb of the bell-shaped tension/length relationship. In the present experiment, the ankle

joints were approximately 7° plantar flexed during the toes-down standing, and about 13° dorsiflexed during the toes-up. Given that the ankle extensors are under quasi-passive condition during quiet standing (~10% MVC), the sarcomeric lengths of these muscles were thought to be limited to the descending limb of the tension/length relationship during the standing trials. This indicates that MG and SOL are relatively disadvantageous for force development in the toes-up condition, and relatively advantageous in the toes-down when compared with the level condition. In other words, more (less) EMG activity was required to develop same amount of force in the toes-up (toes-down) condition. Hence, if the shift in the tension/length relationship of the muscles were the main cause of the observed change in the EMGs, the EMGs should have been increased (decreased) in the toes-up (toes-down) condition. However, the reverse situation was true. Therefore, we are confident that the shift in the tension/length relationship of the ankle extensor muscles was not the main cause of the present results.

Two frequency components in the ankle extensor activity

Cross-spectral analysis revealed that there is a relatively high coherence between the ankle extensor activities and body sway at very low frequencies (<1 Hz), and relatively low (but non-negligible) coherence is still observed in the frequency region up to 3–4 Hz. This indicates that the LF (0.12–4.03 Hz) corresponds to sway-related modulation of the ankle extensor activity. The upper frequency of ~3–4 Hz is almost comparable with time scale of the active neural modulation of the ankle extensor activities during quiet standing as shown in the previous studies. For example, Loram et al. (2005) revealed that the interaction between the CoM angle and the ankle extensors (muscle lengths and EMGs) occurred in the frequency bandwidth 0–3 Hz.

We also found a marked frequency component around 9 Hz. It is well known that when healthy subject maintains low intensity, sustained contraction of limb or finger muscles, rhythmic position or force fluctuation occur at the frequency around 8–12 Hz (i.e., physiological tremor) (McAuley and Marsden 2000). Because the ankle extensors maintain sustained contraction to enhance the ankle stiffness during quiet standing (Winter et al. 1998, 2001), it is reasonable to assume that the ankle extensors show recurring activity similar to the physiological tremor. The present result is consistent with the reports by Mori (1973, 1975) that motor units in SOL synchronized at an interval of about 0.1 s during quiet standing. More recently, our research group (Masani et al. 2001; Kouzaki and Fukunaga 2008) has examined surface EMG of the ankle extensors during quiet standing, and demonstrated that the motor-unit synchronization occurs at the entire muscle level.

Balance control under different passive contributions

In the present experiment, we found no change in the LF (i.e., sway-related modulation of the EMG activity) among the three foot inclinations (Fig. 6, top). Given that sway-related modulation of the ankle extensor activity compensates for the residual component of the stiffness-derived torque in the total ankle torque (Morasso and Sanguineti 2002; Loram and Lakie 2002), the present result indicates that intrinsic ankle stiffness relevant to quiet standing was unchanged among the three foot inclinations. On the other hand, the HF increased with a declining slope (toes-up < level < toes-down) (Fig. 6, bottom), indicating that isometric contraction strength of the ankle extensors increased as the passive contribution decreased (toes-up > level > toes-down). Above-mentioned findings support the idea that by regulating the isometric contraction strength of the ankle extensors, the CNS maintains a constant level of muscle tone and resultant ankle stiffness during quiet standing. And thus, the burden on the intermittent controller was kept constant irrespective of the passive contributions.

Such control scheme not only reduces the burden quantitatively, but is more crucial when we consider the limitations of the bandwidth of the intermittent controller (Collins and DeLuca 1993; Lakie et al. 2003; Bottaro et al. 2005; Loram et al. 2006, 2007). Loram et al. (2006, 2007) have shown that the unstable time constant of the CoM (τ) is a function of the intrinsic ankle stiffness:

$$\tau = \sqrt{\frac{I}{mgh(1-c)}} \tag{3}$$

where I is the moment of the inertia, m is the body mass, g is the acceleration of gravity, h is the height of the CoM, and c is the intrinsic ankle stiffness normalized to load stiffness. Eq. 3 indicates that the unstable time constant increases as the ankle stiffness increases. Concerning this, Lakie et al. (2003) reported that manually balancing a human proportioned inverted pendulum via spring of different stiffness became difficult as the stiffness of the spring decreases. For example, springs that have normalized stiffness <50% load stiffness were impossible for most subjects. More recently, Loram et al. (2006) required the subjects to balance a real inverted pendulum with different moments of inertia, and found the task became impossibly difficult as the time constant decreased below 0.5 s. Loram et al. (2006) attributed the main reason for the increased difficulty to the intrinsically limited, low bandwidth of the intermittent controller (i.e., 2–3 unidirectional adjustments per second). Judging from the present results and the previous reports, it

is suggested that the CNS enhances the intrinsic ankle stiffness to a certain level in order not to require a higher frequency response of the intermittent controller.

Different appearance of the EMG activities among the synergists

It is of interest that activation pattern during quiet standing differ among the ankle extensor synergists; i.e., phasic appearance of MG and tonic appearance of SOL (Fig. 2b, c). It is possible that such a different appearance was attributable to the difference in the motoneuron excitability due to the difference in the muscle fiber composition; i.e., MG has 50–70% type-II fibers, whereas SOL has 80–100% type-I fibers (Johnson et al. 1973). Another possibility for the difference in the activation pattern between the ankle extensor synergists was pointed out by Nozaki et al. (2004). They suggested that the difference in the anatomical features between MG and SOL (i.e., MG is a biarticular muscle, while SOL is a monoarticular muscle) could be a cause for the difference in the activation pattern. Although the present study cannot confirm the cause for the difference in the activation pattern between MG and SOL, our results suggest that the role in balance control during quiet standing differs among ankle extensor synergists.

Conclusion

In the present study, we found that EMG activities of MG and SOL were lowest during the toes-up standing and highest during the toes-down indicating that increased (decreased) passive contribution required less (more) extensor torque generated by active muscle contraction. Frequency domain analysis also revealed that sway-related modulation of the ankle extensor activity (0.12–4.03 Hz) was unchanged among the three foot inclinations. On the other hand, isometric contraction strength of these muscles increased as the slope declined (toes-up < level < toes-down). These results indicate that the CNS maintains a constant level of muscle tone and resultant ankle stiffness irrespective of the passive contributions. Such control scheme would be crucial when we consider the low bandwidth of the intermittent controller.

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References

Bottaro A, Casadio M, Morasso PG, Sanguineti V (2005) Body sway during quiet standing: is it the residual chattering of an intermittent stabilization process? Hum Mov Sci 24:588–615

Casadio M, Morasso PG, Sanguineti V (2005) Direct measurement of ankle stiffness during quiet standing: implications for control modeling and clinical application. Gait Posture 21:410–423

Collins JJ, DeLuca CJ (1993) Open-loop and close-loop control of posture: a random-walk analysis of enter-of-pressure trajectories. Exp Brain Res 95:308–318

Fitzpatrick RC, Taylor JL, McCloskey DI (1992) Ankle stiffness of standing humans in response to imperceptive perturbation: reflex and task-dependent components. J Physiol 454:533–547

Gage WH, Winter DA, Frank JS, Adkin AL (2004) Kinematic and kinetic validity of the inverted pendulum model in quiet standing. Gait Posture 19:124–132

Gatev P, Thomas S, Kepple T, Hallett M (1999) Feedforward ankle strategy of balance during quiet stance in adults. J Physiol 514:915–928

Jeka JJ, Oie KS, Schöner GS, Dijkstra TMH, Henson E (1998) Position and velocity coupling of postural sway to somatosensory drive. J Neurophysiol 79:1661–1674

Johnson MA, Polgar J, Weightman D, Appleton D (1973) Data on the distribution of fiber types in thirty-six human muscles an autopsy study. J Neurol Sci 18:111–129

Kawakami Y, Ichinose Y, Fukunaga T (1998) Architectural and functional features of human triceps surae muscles during contraction. J Appl Physiol 85:398–404

Kawakami Y, Kumagai K, Huijing PA, Hijikata T, Fukunaga T (2000) The length–force characteristics of human gastrocnemius and soleus muscles in vivo. In: Herzog W (ed) Skeletal muscle mechanics: from mechanisms to function. Wiley, London, pp 321–341

Kouzaki M, Fukunaga T (2008) Frequency features of mechanomyographic signals of human soleus muscle during quiet standing. J Neurosci Methods 173:241–248

Lakie M, Caplan N, Loram ID (2003) Human balancing of an inverted pendulum with a compliant linkage: neural control by anticipatory intermittent bias. J Physiol 551:357–370

Loram ID, 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

Loram ID, Maganaris CN, Lakie M (2005) Human postural sway results from frequent, ballistic bias impulses by soleus and gastrocnemius. J Physiol 564:295–311

Loram ID, Gawthrop PJ, Lakie M (2006) The frequency of human, manual adjustments in balancing an inverted pendulum is constrained by intrinsic physiological factors. J Physiol 577:417–432

Loram ID, Maganaris CN, Lakie M (2007) The passive, human calf muscles in relation to standing: the non-linear decrease from short range to long range stiffness. J Physiol 584:661–675

Löscher WN, Gallasch E (1993) Myo-electric signals from two extrinsic hand muscles and force tremor during isometric handgrip. Eur J Appl Physiol 67:99–105

Masani K, Nakazawa K, Kouzaki M (2001) Two frequency components in ankle extensor activity during human quiet standing. Soc Neurosci Abstr 305:2

Masani K, Popovic MR, 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

Masani K, Vette AH, Popovic MR (2006) Controlling balance during quiet standing: proportional and derivative controller generates preceding motor command to body sway position observed in experiments. Gait Posture 23:164–172

Masani K, Vette AH, Kouzaki M, Kanehisa H, Fukunaga T, Popovic MR (2007) Larger center of pressure minus center of gravity in the elderly induces larger body acceleration during quiet standing. Neurosci Lett 422:202–206

McAuley JH, Marsden CD (2000) Physiological and pathological tremor and rhythmic central motor control. Brain 123:1545–1567

Mezzarane RA, Kohn AF (2007) Control of upright stance over inclined surfaces. Exp Brain Res 180:377–388

Morasso PG, Sanguineti V (2002) Ankle muscle stiffness alone cannot stabilize balance during quiet standing. J Neurophysiol 88:2157–2162

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

Mori S (1975) Entrainment of motor-unit discharges as a neuronal mechanism of synchronization. J Neurophysiol 38:859–870

Nozaki D, Hirano T, Nakazawa K, Akai M (2004) Cosine tuning can predict different activity patterns among triceps surae muscles during human quiet standing. Soc Neurosci Abstr 306:5

Peterka RJ (2002) Sensorimotor integration in human postural control. J Neurophysiol 88:1097–1118

Smith JW (1957) The forces operating at the human ankle joint during standing. J Anat 91:545–564

Winter DA, Patla AE, Prince F, Ishac M, Gielo-Perczak K (1998) Stiffness control of balance in quiet standing. J Neurophysiol 80:1211–1221

Winter DA, Patla AE, Rietdyk S, Ishac MG (2001) Ankle muscle stiffness in the control of balance during quiet standing. J Neurophysiol 85:2630–2633