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What triggers the continuous muscle activity during upright standing?

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ABSTRACT

The ankle extensors play a dominant role in controlling the equilibrium during bipedal quiet standing. Their primary role is to resist the gravity toppling torque that pulls the body forward. The purpose of this study was to investigate whether the continuous muscle activity of the anti-gravity muscles during standing is triggered by the joint torque requirement for opposing the gravity toppling torque, rather than by the vertical load on the lower limbs. Healthy adults subjects stood on a force plate. The ankle torque, ankle angle, and electromyograms from the right lower leg muscles were measured. A ground-fixed support device was used to support the subject at his/her knees, without changing the posture from the free standing one. During the supported condition, which eliminates the ankle torque requirement while maintaining both the vertical load on the lower limbs and the natural upright standing posture, the plantarflexor activity was attenuated to the resting level. Also, this attenuated plantarflexor activity was found only in one side when the ipsilateral leg was supported. Our results suggest that the vertical load on the lower limb is not determinant for inducing the continuous muscle activity in the anti-gravity muscles, but that it depends on the required joint torque to oppose the gravity toppling torque.

1. Introduction

Human upright standing posture requires continuous muscle activity in several muscles of the body, especially of the legs. According to their postural function, i.e., the contribution to maintaining the upright standing posture against gravity, they are oftentimes referred to as the anti-gravity muscles. Because the continuous muscle activity in the anti-gravity muscles is a prerequisite for weight bearing in biped upright posture, understanding the activity's underlying mechanisms is critical for the management and rehabilitation of neuromuscular disorders and muscle atrophy associated with spinal cord injury [1] and exposure to microgravity [2], i.e., when the anti-gravity muscles are not used.

In animal studies, the brain stem has been suggested to be the center or origin of the continuous muscle activity in the ant-gravity muscles [3]. While the continuous muscle activity can be modulated via the cerebellum [4], it is still unclear where associated sensory inputs originate. Load receptors including cutaneous mechanoreceptors of the foot sole as well as joint proprioceptive sensors of the joint have been hypothesized to provide key sensory inputs. In addition, the effect of the vertical load on the motor unit excitability has been intensively investigated [5–11], but is not conclusive. It has, however, been established that cutaneous mechanoreceptor inputs induce postural responses [12–14], making a considerable contribution to postural balance [15–18]. Therefore, it has been hypothesized that sensory stimulation of the cutaneous mechanoreceptors is a prerequisite for the presence of continuous muscle activity [2,19,20]. Following this line of thought, mechanical stimulation of the feet has been proposed as a countermeasure to neuromotor degradation and muscle atrophy during space flights [21–23].

In any case, the vertical load that stimulates load receptors has been assumed to be the critical trigger for controlling the response and the level of continuous muscle activity. However, based on the dynamics of quiet standing, the level of continuous muscle activity should be determined according to the required ankle torque irrespective of the amount of the vertical load. As the feet do not move during quiet standing, the ankle joint has a critical role in maintaining the center of mass (COM) equilibrium. Due to the fact that the COM is in front of the ankle joint during the natural standing posture, a gravity-induced torque continuously accelerates the body forward from the vertical position. While the dorsiflexors are not activated in the natural standing posture [24,25], the plantarflexors continuously provide the corrective ankle extension torque required to resist the gravity toppling torque and to ensure that the COM remains close to the equilibrium position. As a consequence, we hypothesize that the critical trigger determining the continuous

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muscle activity must be the required torque in the standing posture based on the described dynamics of quiet standing. To test this hypothesis, the current study set out to investigate whether the continuous muscle activity of the anti-gravity muscles is triggered by the joint torque requirement for opposing the gravity toppling torque, rather than by the vertical load on the lower limbs.

2. Methods

We performed two experiments. In the first experiment (Experiment 1), we investigated the ankle muscle activity during standing when supported by a mechanical support device at the subject's shanks. In this condition, the gravity toppling torque was compensated by the support device while the subject's vestibular gravity sensation and cutaneous pressure receptor sensation (i.e., load on the feet sole) were kept approximately the same as for the natural standing condition. In case the continuous muscle activity in the ankle extensors disappears due to the lack of need to compensate the gravity toppling torque, the vestibular gravity sensation and cutaneous pressure receptor sensation prove to be non-fundamental in triggering the continuous muscle activity during standing. To explore the contribution of the torque requirement to the continuous muscle activity, we investigated the ankle muscle activity during standing when only the left leg was supported (Experiment 2). The data of Experiment 1 were obtained from the study underlying a previous publication [26].

2.1. Experiment 1

2.1.1. Subjects

Ten healthy adults (nine male and one female; age 21–39 years; height 174 ± 7.0 cm; weight 71.7 ± 11.2 kg) participated in this experiment. They had no medical history or signs of neurological disorders. All subjects gave their written informed consent to participate in the study after receiving a detailed explanation about the purposes, benefits, and risks associated with the participation in the study. The procedures used in this experiment were approved by the local ethics committee.

2.1.2. Measurements

The center of pressure (COP) and three orthogonal components of the ground reaction force were measured using a force platform (Accu Sway ACS-DUAL, Advanced Mechanical Technology Inc., USA) (Fig. 1A). The displacement of a middle point on the shank was measured by a charge-coupled laser displacement sensor (LK-2500, Keyence, Japan) (Fig. 1A). Surface electromyograms (EMGs) were recorded from the right soleus muscle (SOL), the medial (MG) and lateral (LG) heads of the gastrocnemius muscle, and the tibialis anterior muscle (TA). The EMGs were amplified and bandpass filtered between 20 and 500 Hz (Bangnoli 8 EMG System, Delsys, USA). All data were sampled at 1 kHz and stored on a personal computer for subsequent analysis. In this paper, we focus only on the anteroposterior body sway, since the ankle extensors contribute primarily to the stabilization of body sway in this direction.

The ankle angle was calculated using the laser displacement sensor data, under the assumption that the feet did not move on the force plate during standing. The exerted torque at the ankle joint was calculated using COP and the ground reaction forces.

2.1.3. Procedures

Three conditions were investigated: (1) a natural standing condition (free standing, FS), (2) a standing posture with keeping the average joint angles and foot sole pressures the same as respective averages during FS, while relieving the plantarflexors from the responsibility to generate the stabilizing torque (support standing, SS), and (3) sitting rest (RT). To realize SS, we adopted a unique experimental setup. As shown in Fig. 1B, the ground-fixed support device was used to externally counteract the toppling effect of gravity during standing, eliminating the requirement of joint torque exertion. During SS, the support device was positioned just below the subject's patellas of both legs. The device, whose surface had a rectangular shape (3 cm × 30 cm), was positioned as horizontally as possible to support the body from the front while minimizing the exertion of vertical support forces. However, in spite of the size and shape of the device, it only supported the subject at two points around the tibial tuberosities (one point per leg). The position of the support device was carefully selected as not to change the ankle angle in comparison to FS. Note that the subject did not intentionally lean forward but tried to keep the natural standing posture as much as possible. A uniaxial load cell (MLP-100-CO-C, Transducer Techniques, USA) was built into the support device to measure the force exerted on it. The torque due to this force component was also calculated (load cell, or LC torque).

In both tasks (FS and SS), the subject stood with bare feet and eyes closed, the arms hanging along the sides of the body, and the heels 15 cm apart. The subject did not change the position of the feet between the trials while he/she sat down on a chair in order to take a rest. One trial for each task was executed. The duration of each trial was 30 s. Prior to these trials, the EMGs were also recorded in a sitting posture for 30 s (RT condition).

The magnitude of muscle activity was evaluated using the root mean square (RMS) of each muscle's EMG. A one-way ANOVA with repeated-measures and a Bonferroni multiple comparisons test were used to compare the muscle activity among FS, SS, and RT for each muscle. The mean ankle angle was compared between FS and SS using a paired t-test. The mean ankle torque during FS and SS, and the ankle torque + LC torque (SS) were compared using a one-way ANOVA with repeated-measures and a Bonferroni multiple comparisons test. The load on the foot soles was evaluated using the vertical force component measured by the force plate, and was compared between FS and SS using a paired t-test. $p < 0.05$ was used as the level of statistical significance.

2.2. Experiment 2

2.2.1. Subjects

Eight healthy male adults (age 22–40 years; height 178.6 ± 5.2 cm; weight 80.9 ± 10.8 kg) participated in this experiment. They had no medical history or signs of neurological disorders. All subjects gave their written informed consent to participate in the study after receiving a detailed explanation about the purposes, benefits, and risks associated with the participation in the study. The procedures used in this experiment were approved by the local ethics committee.

2.2.2. Measurements and procedures

Surface EMGs were recorded from the left (LSOL) and right (RSOL) soleus muscles and the left (LTA) and right (RTA) tibialis anterior muscles. The EMGs were amplified and bandpass filtered between 20 and 500 Hz (Bangnoli 8 EMG System, Delsys, USA). All data were sampled at 1 kHz and stored on a personal computer for subsequent analysis. We compared the muscle activity among four conditions: (1) natural standing (FS), (2) left leg supported standing (LS), (3) both leg supported standing (BS), and (4) sitting rest (RT). In all conditions, the subject stood with bare feet and eyes closed, the arms hanging along the sides of the body, and the heels 15 cm apart. The subject did not change the position of the feet between the trials while he sat down on a chair in order to take a rest. One trial for each task was executed. The duration of each trial was 30 s. Prior to these trials, the resting EMG was also recorded in a sitting posture for 30 s (RT condition).

The magnitude of muscle activity was evaluated using the RMS of each muscle's EMG. A one-way ANOVA with repeated-measures and a Bonferroni multiple comparisons test were used to compare the muscle activity among FS, BS, LS, and RT for each muscle. $p < 0.05$ was used as the level of statistical significance.

3. Results

3.1. Experiment 1

Fig. 1C–E shows the recorded time series for a single subject. Fig. 1C shows the time series in FS: the ankle angle shows that the body fluctuates around 0.1 rad from the vertical; the ankle torque shows that the exerted ankle torque fluctuates around 30 N m; compared to RT (Fig. 1E), TA and LG do not show prominent muscle activity (similar to the resting condition), whereas SOL and MG show considerable activity (EMGs are shown as rectified EMGs). Fig. 1D shows the time series in SS: the ankle angle shows that the body was at approximately the same angle as during FS, whereas the fluctuation was very small; the ankle torque was close to zero, whereas the LC torque was about the same as the ankle torque in FS. Both torques in SS did not fluctuate much compared to the torque in FS; all muscles showed similarly low activity as during RT (Fig. 1E).

Fig. 2A–C shows the group averages of the ankle angle (A), ankle torque (B), and the load on the feet (C). The ankle angle was not significantly different between FS and SS ($p = 0.985$) (Fig. 2A). The ANOVA test indicated that the ankle torque was significantly different among the different calculated values ($p < 0.001$) (Fig. 2B). The post hoc test revealed that it was not significantly different between FS and the summation of the ankle torque and LC torque in SS, but that the SS ankle torque was significantly smaller than the FS torque and the summation of the ankle torque and LC torque in SS. The load on the feet during FS was significantly larger than during SS ($p < 0.001$) (Fig. 2C).

Fig. 3A–D shows the muscle activity of all muscles for each condition. For SOL, MG, and LG, the ANOVA tests revealed that the muscle activity was different among the conditions ($p < 0.001$, $p = 0.004$, $p < 0.001$, for SOL, MG, and LG, respectively). For SOL and LG, the post hoc tests revealed that the activity in FS was

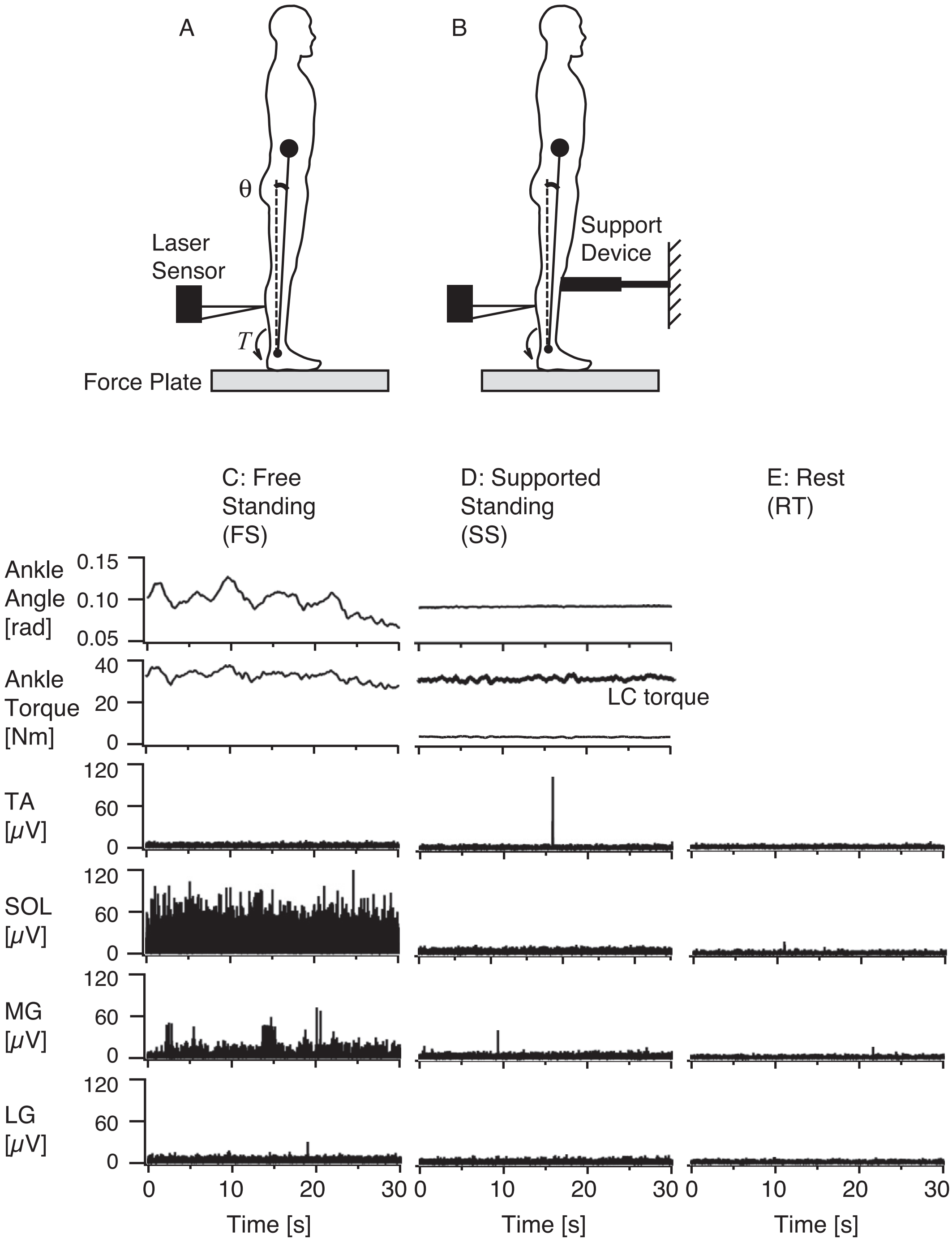

Fig. 1. Experimental setups (A and B), and example recordings for one subject (C, D, and E). A: Experimental setup for free standing (FS). The subject stood on a force plate, and a laser displacement sensor measured a point on the calf by which the ankle angle was calculated. B: The subject was supported by a support device from his/her front. The support device was ground-fixed and had a load cell built in. C, D, and E: From the top, the traces indicate the ankle angle, ankle torque, and EMGs of SOL, MG, LG, and TA for FS (C), SS (D), and RT (E). On the graphs of the ankle torque for SS, the thick line labeled 'LC torque' indicates the torque provided by the load cell.

significantly larger than in SS and RT, while there was no significant difference between SS and RT. For MG, the post hoc test did not show any statistically significant differences between each pair of conditions. For TA, no significant differences between the conditions were revealed by the ANOVA test ($p = 0.985$).

3.2. Experiment 2

Fig. 4A shows the muscle activities of RSOL and LSOL in each condition of FS, BS, LS, and RT. It clearly shows that both of RSOL and LSOL in BS had the same activity levels as in RT, and that in LS, RSOL kept the same activity level as in FS while LSOL was the same as in RT.

Fig. 4B (RSOL) and C (LSOL) shows the group averages of the activity of each muscle for each condition. The ANOVA test revealed that there was a significant difference among the conditions for both of RSOL and LSOL ($p < 0.0001$, for both). The post hoc test showed that the RSOL activity was not different between FS and LS, and that it was not different between BS and RT. Further, the LSOL activity in FS was different from all of BS, LS, and

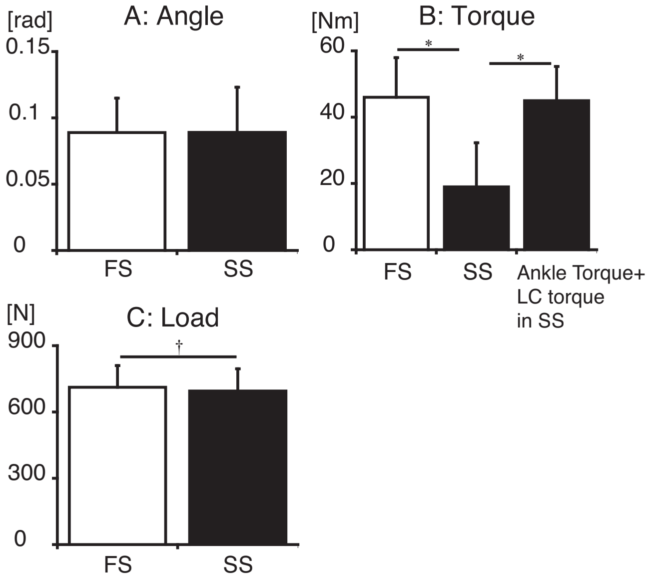

Fig. 2. A: Comparison of the mean angle for FS and SS (A), the ankle torque for FS and SS, and the ankle torque + LC torque during SS (B), and the load on the foot soles for FS and SS (C). The values indicate the group averages and the error bars indicate the standard deviations of the group. $^*p < 0.05$ between tasks according to the post hoc test, and $^\dagger p < 0.05$ between tasks according to the t-test.

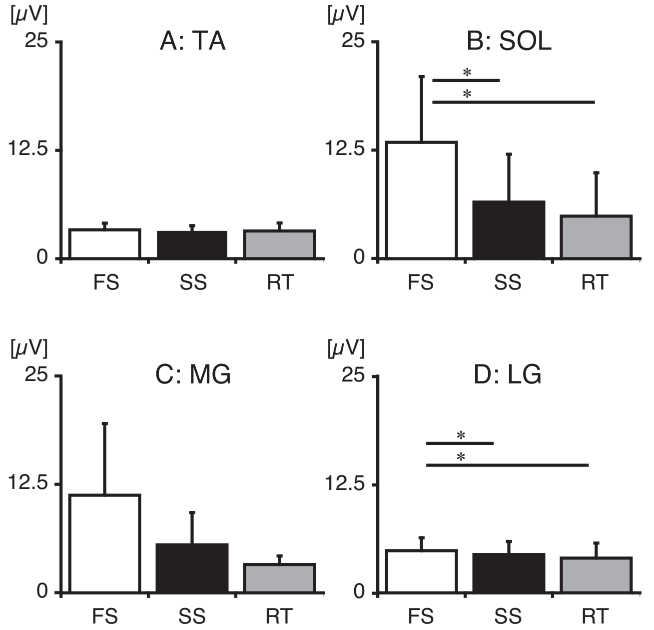

Fig. 3. Comparison of the root mean squares of EMGs among FS, SS, and RT for TA (A), SOL (B), MG (C), and LG (D). The values indicate the group averages and the error bars indicate the standard deviations of the group. $^*p < 0.05$ between tasks according to the post hoc tests.

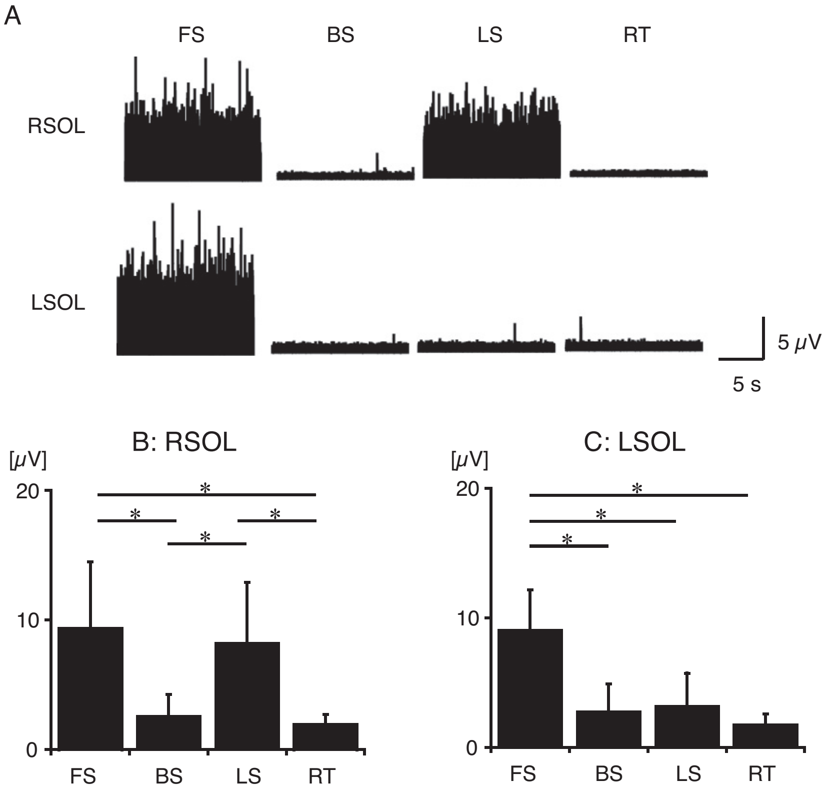

Fig. 4. Results of Experiment 2. A: Example recording for RSOL and LSOL for one subject during each condition. B and C: Comparison of the root mean squares of EMGs among FS, BS, LS, and RT for RSOL (B) and LSOL (C). The values indicate the group averages and the error bars indicate the standard deviations of the group. $^*p < 0.05$ between tasks according to the post hoc tests.

RT, while the LSOL activity was not different among BS, LS, and RT. For RTA and LTA, the ANOVA tests did not show any significant differences among the conditions ($p = 0.420$ and $p = 0.458$ for RTA and LTA, respectively).

4. Discussion

During SS, it was demonstrated that the plantarflexor activity was attenuated to the level of the resting condition even when keeping the vertical load approximately the same as during natural standing (Figs. 2 and 3). Additionally, this attenuated plantarflexor activity (for SOL) was found only in one side when the ipsilateral leg was supported, while the soleus activity in the other leg was the same as that during quiet standing (Fig. 4). During the supported tasks, the subject did not change his/her voluntary effort to stand naturally, implying that the attenuation of the muscle activity occurred automatically.

We attempted to maintain the vertical load equivalent during SS and FS by attaching the support device as horizontal as possible, minimizing the contribution of a vertical support force. As a result, the vertical reaction force was almost equivalent between the tasks (Fig. 2C), although a minute reduction of the vertical force ($2.52 \pm 1.40\%$) was still measured. Thus, we can assume that the functional requirement of ankle joint torque was completely eliminated (Fig. 2B), while keeping the sensory information on the gravity direction at the same level for FS and SS. Therefore, we can conclude that the functional requirement of the ankle joint torque, rather than the vertical load, appears to elicit the plantarflexor activity. Consequently, to induce sufficient muscle activity in the anti-gravity muscles, the present study suggests that a torque requirement is a necessary condition.

The neural circuit responsible for this phenomenon is not understood. It is not clear where and how the continuous muscle activity in the anti-gravity muscles is triggered. In decerebrated cats, electrical stimulation of the pons and pontine in the brain stem can induce continuous muscle activity in the legs and, hence, facilitate standing posture [3]. A similar neural mechanism may be at work in humans that can elicit a patterned muscle activity in the anti-gravity muscles, including the plantarflexor activity during standing. This motor command triggered by the brain stem activity must be inhibited in the plantarflexors in case of SS. At this stage, we cannot suggest any specific neural mechanism that realizes the inhibition, as most of the sensory information related to postural control was kept equivalent to the one during FS.

It is well documented that the plantarflexor activity is *regulated* by various sensory inputs [27]. However, for the purpose of rehabilitation of muscle atrophy related to neuromuscular disorders and/or to exposure to microgravity, it is worthy to investigate how sufficient muscle activity can be *induced* in the anti-gravity muscles. For example, muscle atrophy in anti-gravity muscles is a serious problem among astronauts, considering that their resident time in space stations is increasing. Numerous studies conducted by Kozlovskaya's research team demonstrated the potential effectiveness of dynamic mechanical stimulation of the feet on the attenuation of neuromotor degradation associated with unloading [19,21,23]. Specifically, the results suggest that dynamic foot stimulation to the plantar surfaces of the feet may be a useful supplement to more traditional exercise countermeasures during space flights. However, up to date, there is no direct evidence that such device can be effective in *inducing* continuous muscle activity in anti-gravity muscles. This can be easily understood given the results of the current study: Providing pressure on the foot soles alone may not be sufficient for inducing muscle activity in anti-gravity muscles if a torque requirement is not present.

In conclusion, we demonstrated that the plantarflexor activity was attenuated to the level of the resting condition when the ankle torque requirement was eliminated, while keeping the vertical load the same as during the natural standing condition. Also, this attenuated plantarflexor activity was found only in one side when the ipsilateral leg was supported. The results suggest that the vertical load is not fundamental in inducing the continuous muscle activity in the anti-gravity muscles, but that the activity depends on the required joint torque needed to oppose the gravity toppling torque.

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Conflict of interest statement

The authors declare they have no conflict of interest.

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