Neuromuscular Responses to Mechanical Foot Stimulation: The Influence of Loading and Postural Context

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Introduction: Recent work indicates mechanical stimulation of soles may attenuate muscle atrophy initiated by gravitational unloading, including that experienced during spaceflight. The aim of the present study was to determine the modulating effect of unloading and body configurations on the neuromuscular response to mechanical foot stimulation. ***Methods:*** A solenoid (2.5-cm^2 surface area) embedded within a platform provided non-noxious stimulation to the lateral foot sole: 100 ms duration, 3-mm protrusion. Stimulation was applied while measuring root mean square electromyography of the soleus and lateral gastrocnemius. Experiment 1 compared seated and standing conditions, as well as different levels of gravitational unloading created by suspension. Experiment 2 altered postural stability by varying leg stance widths during a static stepping posture. Either the foot of the support leg or the nonsupport leg was stimulated. Reduced levels of loading further altered the level of postural challenge and support while maintaining the same body configuration. ***Results:*** In both experiments, loading was not a modulating factor to the response, supporting the use of mechanical foot pressure as a countermeasure for spaceflight. Body configuration and postural instability both modulated the response, independently of load. ***Discussion:*** In conclusion, an application of dynamic foot stimulation could be used to elicit neuromuscular activity without the need of background muscle activity or gravitational loading. However, the body configuration of the user with respect to postural stability needs to be considered in the application, and may provide further scope of benefits extending to the activation of postural synergies.

Keywords: atrophy, spaceflight, countermeasure, electromyography.

HUMAN BIPEDAL POSTURE is specifically designed around gravity (8,40), and prolonged exposure to an absent gravity vector, such as during spaceflight, is well documented for compromising terrestrial postural control upon return from flight. These changes are attributed to neuromuscular modifications and postflight deficiencies, including a loss in antigravity extensor muscle mass (12), altered muscle spindle sensitivity, and shifts in sensory accuracy and dominance (10,22,36). A new direction in the development of countermeasures for spaceflight-induced muscle atrophy and neuromuscular degradation focuses on producing in-flight neuromuscular responses by stimulating load afferents with mechanical stimuli (see 23). Load sensory afferents are especially effective for altering antigravity extensor neuromuscular activity (9), and thus would target the affected musculature.

To stimulate the load afference in the foot, mechanical stimulation could be applied within a specialized "boot," providing a countermeasure that could be worn during daily activities and/or during exercise regimes (17). Different types of mechanical foot stimulation have been used to elicit enhanced neuromuscular responses, and/or attenuate muscle atrophy in both humans and animals. They include static pressure applied to the whole human sole (1,17,24,42), dynamic pressure applied to the plantar surface of the hind feet in hind limb suspended rats (6,21), dynamic pressure applied to the human forefoot and heel (25), small area dynamic pressure (13,26), small area progressive dynamic pressure (30), and dynamic pressure in the form of vibration in humans (18) and rats (11).

While favorable responses for attenuating muscle atrophy from plantar mechanical stimulation and vibration have been demonstrated in rat hind limb suspension models (6,11,21), and during dry immersion studies in humans (20,27,33,35), the role of gravitational unloading in the response to dynamic foot stimulation in humans, and thus direct applicability as a countermeasure to spaceflight-induced muscle loss, is still to be fully understood. Currently, load dependence for human muscle activity has been established for locomotion and postural perturbation responses (9), and Bastiaanse et al. (4) demonstrated an increased cutaneous reflex amplitude response with body unloading. This cutaneous reflex was elicited from electrical stimulation of cutaneous nerves radiating from areas of the feet and the load effect was especially strong for antigravity extensor muscles, and not purely a function of background muscular activity (4). In contrast, mechanical foot stimulation has triggered postural responses with a complete loss of gravitational loading, as experienced in microgravity (24), but the relationship between mechanical stimulation responses and partial loading has yet to be identified.

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Moreover, body configurations which influence localized lower limb loading and/or postural stability may also influence the response to plantar stimulation. Indeed, whole body postural responses still occur in microgravity, including responses to antereoposterior center of mass displacements (3,29,41), and body adjustments to align with the vertical axis while astronauts' feet are strapped to the floor (2). Thus, any modulation of response to cutaneous stimulation normally associated with a terrestrial postural context may be preserved in spaceflight if similar body configurations are maintained. We further separate body configuration into two postural control categories that are extremely relevant in 1 g: 1) the level to which postural stability is challenged. Burke et al. (5) demonstrated body postures with a greater postural challenge inhibited tibialis anterior responses to sural nerve, non-noxious electrical stimulation. These authors also demonstrated this task dependency was not purely a function of muscle contraction levels prior to stimulation. 2) The support role of the stimulated foot and corresponding leg. A reduction in cutaneous reflexes of the lower limb also occurs during a contraction associated with a supporting or postural role rather than voluntary contraction (5,14). Therefore, both the degree of postural challenge and the supporting role of the stimulated foot and corresponding leg are expected to reduce the neuromuscular response to mechanical foot stimulation.

This investigation included two experiments each designed to elucidate the role of gravitational loading and the related contexts of support and postural stability in the neuromuscular response to dynamic mechanical foot stimulation. Experiment 1 investigated the role of gravitational loading, comparing neuromuscular responses for seated and standing conditions, as well as different levels of gravitational unloading created by suspension. Experiment 2 examined the influence of contexts relating to postural instability and support context on the neuromuscular response to foot stimulation. The postural instability was altered with varied leg widths during a maintained stepping posture. The support context was also differentiated, as the foot on either the supporting leg or the non-supporting leg was stimulated, depending upon experimental condition. Reduced levels of loading were included to alter the level of postural challenge and support while maintaining the same body configuration. We hypothesized the neuromuscular response to foot stimulation would increase with unloading, and reduce with greater postural instability and support role of the stimulated foot and corresponding leg.

METHODS

Both experiments involved a non-noxious mechanical stimulation to the lateral portion of the sole of the foot during different levels of loading and different body configurations. The neuromuscular responses were measured with electromyography of the soleus and lateral gastrocnemius. Experiments were performed in the Laboratory of Integrated Physiology, University of Houston, on different groups ($N = 15$ per group) of right-handed healthy subjects (mean ± SD; Experiment 1: 25.7 ± 4.1 yr; Experiment 2: 24.6 ± 3.9 yr) weighing less than 76 kg (Experiment 1: 65 ± 8 kg; Experiment 2: 68 ± 6.8 kg). All were free from any known muscular or neurological medical conditions. The study protocol was approved in advance by the University of Houston's Committee for the Protection of Human Subjects. Each subject provided written informed consent before participating. Subjects were recruited from the University community.

Foot Stimulation

The Dynamic Foot Stimulation device (DFS) contained one solenoid (surface area 2.5 cm^2), embedded within a custom-built wooden platform and was controlled through customized software (LabView, National Instrument Corp, Austin, TX). Velcro straps, fed through narrow slits in the platform either side of the foot, secured the foot in place, thereby maintaining the subject's sole in contact with the DFS throughout the testing and prevented ankle flexion, which eliminated triceps surae stretch reflex responses. Each condition, in both experiments, consisted of a single trial of stimulation applied to the sole of the foot under the fifth metatarsal joint for 100 ms at 20 psi, 3-mm protrusion, 21 times within a 2-min period. A variable interstimulus interval and 2-min rest period between each trial was used to counter event anticipation and sensory receptor habituation. In order to control mental attention, subjects were required to slowly read aloud a series of random numbers displayed a meter in front of the subject at head height during stimulation periods (38).

Unloading Device—The Pneu-lift™

Suspension was provided with the Pneu-lift™ (Pneumex, Inc., Sandpoint, ID). A harness was tightly fitted around the subject's waist and legs, adjusted for comfort, and attached to the cross bar. The harness was also worn under non-suspension conditions. During unloading using the Pneu-lift™, subjects' feet were positioned to align the natural balance of the subject to create only a vertical unloading force by the device. Electromyography (EMG) of the soleus (SOL) and lateral gastrocnemius (GA) was monitored to ensure there was no background activity. Unloading was applied for only 2-4 min at a time with normal loading between trials and conditions. Differential loading levels were confirmed by foot pressure distribution records of each condition in both experiments using F-Scan® pressure sensors (Tekscan, Inc., Boston, MA) (**Fig. 1**). Theses sensors were placed under the feet.

General Subject Preparation

The subjects were barefoot, and their right foot was properly positioned for a stimulation location underneath the fifth metatarsal joint, and secured in place with elastic Velcro straps. This plantar stimulation site

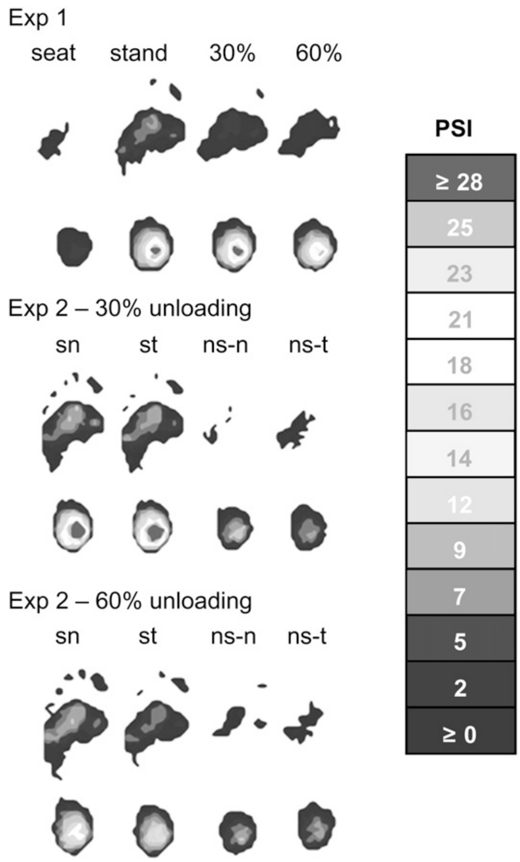

Fig. 1. Single subject examples of foot pressure distributions measured during each condition of Experiment 1 and 2. During all conditions of both experiments the sole was in contact with the ground at all times. sn = support leg, regular stance, st = support leg, tandem stance, ns-N = non-support leg, regular stance, ns-t = non-support leg, tandem stance.

was selected because it elicited the greatest neuromuscular response to dynamic stimulation in a passive soleus and lateral gastrocnemius (26). The subjects were familiarized with and experienced the stimulation prior to testing. Surface electrode sites were located, prepared, and electrodes positioned over the belly of the SOL and GA (see EMG collection procedure below). The experimental environment for all experiments minimized external stimulation such as noise, light, and distractions.

EMG Data Collection

After light abrasion and cleaning of the skin with alcohol, a silver-silver chloride preamplifier electrode (Therapeutics Unlimited, Iowa City, IA) was attached to the SOL and GA. Surgical tape was used as needed to ensure the electrode maintained its position on the skin over the belly of the respective muscle. The ground lead was placed just above the right ankle and secured with an elastic strap. Sampling rates were preset to 1000 Hz. Both the EMG root mean squared data from the SOL and GA (5.5-ms time constant) and solenoid activation signal were simultaneously collected by the Enhanced Graphics Acquisition and Analysis board (R.C. Electronics Inc., Santa Barbara, CA), in order to synchronize stimulus and response data for the analysis. Background EMG was monitored during each trial to ensure baseline levels were maintained.

Experiment 1

This experiment investigated the neuromuscular responses for seated and standing conditions, as well as different levels of gravitational unloading created by suspension. Each subject experienced four conditions: 1) seated, sitting with normal loading; 2) stand, standing with normal loading; 3) stand30, standing with 30% bodyweight unloaded; and 4) stand60, standing with 60% bodyweight unloaded (Fig. 1). The order of the conditions was randomized across subjects to eliminate any possible order effect.

All standing conditions required use of the Pneu-lift™, and the appropriate suspension level set relative to the subject's weight. For the seated condition, the chair was adjusted for a 100° ankle angle and a 110° knee angle. The right foot and right knee, in the seated condition, were stabilized with elastic bands to facilitate a relaxed leg. After the subject was relaxed, the foot stimulation was applied.

Experiment 2

This experiment consisted of a variety of static "stepping" postures, during which the right leg was stimulated. The postural instability was altered with varied leg widths, and the possible effect of support context was altered by simulating either the support or non-support leg. **Fig. 2** schematically represents the postures assumed by the subjects and which foot received the stimulus. Reduced levels of loading were included to alter the level of postural challenge and support while maintaining the same stepping posture. All conditions required the use of the Pneu-lift™, and the appropriate suspension level set relative to the subject's weight.

The stepping posture was defined by the position of two platform levels, one for the support leg and one for the non-support leg (stepping leg). The platforms were finely adjusted and positioned relative to the unloading frame to facilitate the most comfortable and "natural" posture. The subjects were instructed to stand with the majority of their weight on the supporting leg. This was confirmed with verbal communication and with the F-Scan® pressure sensors (Tekscan, Inc., Boston, MA) (Fig. 1). In the tandem conditions the feet (support and stepping) were positioned in a tandem line, while in the regular stance conditions the feet were positioned shoulder width apart. Subjects were instructed to hold their own weight and support themselves; they were also informed the harness could not support their full weight in the event of loss of balance, to facilitate the full perceptual significance of the less stable conditions. The platforms were reconfigured for each condition to stimulate the right foot, and the right foot was stabilized with elastic bands to the DFS to facilitate consistent stimulation. **Table I** provides summary information about each condition in Experiment 2. The order of the conditions was randomized to eliminate any possible

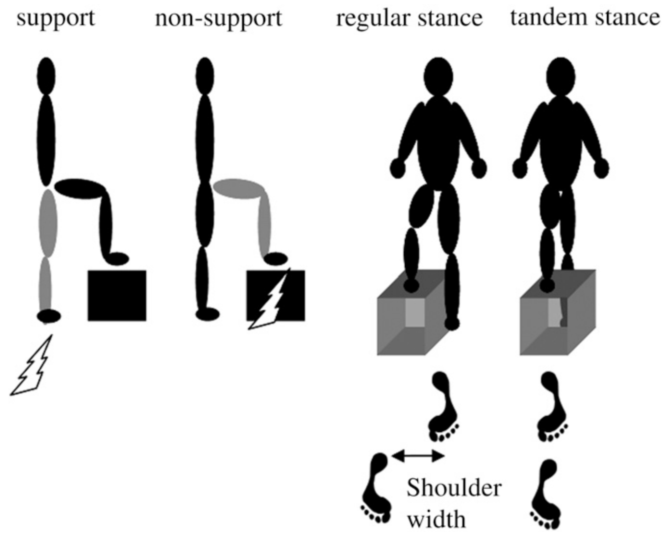

Fig. 2. In each condition of Experiment 2 the right leg (in gray) was stimulated, and that leg was either in the support or non-support position of the static stepping posture. Also, the stepping posture had two varied stances, regular and tandem stance.

order effects. The foot stimulation was applied after subjects were relaxed and comfortable.

Data Analysis

For both experiments, a 100-ms data analysis window was defined for each stimulation by the initiation of the stimulus and the following 100 ms. A custom-written Excel program (Microsoft Corporation, Redmond, WA) identified the peak amplitude in the root mean squared records and calculated the positive integrated area (PIA) for the 20 analysis windows in each trial. The first response was disregarded to minimize effects of a potential startle response. The peak response and PIA for both the SOL and GA were significantly correlated for all conditions in both experiments ($P < 0.001$). Correlation coefficients ranged from 0.972 to 0.995 in Experiment 1, and 0.921 to 0.994 in Experiment 2. As such, peak amplitude values rather than PIA were then used for subsequent analysis. The data were transformed with a square root function to adjust for a mild distribution skew, and to facilitate a normal distribution. Repeated measures analysis tested for differences between experimental conditions. Experiment 1 had one within-subject factor: condition. Experiment 2 had three within-subject factors: stance, load, and stimulation site. Greenhouse-Geissner adjustments were made when the covariance matrix circularity assumption was violated. A priori contrasts were used to test planned comparisons. Mean response latencies for each condition were calculated from latency values identified visually on an averaged waveform of the 20 stimulation responses for each subject. The response latency was defined from the onset of the stimulus to initiation of the response. The peak latency was defined from the onset of the stimulus to the peak of the response.

TABLE I. EXPERIMENTAL CONDITIONS FOR EXPERIMENT 2.

Condition	Stance	Unloading (% Body Unload)	Stimulation Site (Lateral Plantar)
Step30S	Regular	30%	support leg
Step30NS	Regular	30%	non-support leg
Step60S	Regular	60%	support leg
Step60NS	Regular	60%	non-support leg
T30S	Tandem	30%	support leg
T30NS	Tandem	30%	non-support leg
T60S	Tandem	60%	support leg
T60NS	Tandem	60%	non-support leg

RESULTS

Experiment 1

The purpose of this experiment was to elucidate the difference in the neuromuscular response to foot stimulation during varied levels of unloading, and between seated and standing conditions.

Basic neuromuscular response: In both the SOL and GA, the basic neuromuscular response to the applied stimulation was consistent in waveform pattern, latency, and duration, regardless of experimental condition. **Fig. 3** is an example of a typical plantar stimulation response of the soleus for each of the four conditions. Across all conditions, the response latency was 48.4 ± 3.5 ms after the onset of the stimulus, with response duration 21.2 ± 4.3 ms. The peak latency of the response occurred at 56.8 ± 3.3 ms after stimulus onset. The onset of the response relative to the stimulation, the duration of response, and temporal location of the peak amplitude were consistent features for all conditions.

Peak amplitude of response: While temporal characteristics of the neuromuscular response to foot stimulation were consistent, substantial variation between conditions was observed in the peak amplitude of the response. In the SOL, there were significant differences in the peak amplitude for the conditions (Greenhouse-Geissner adjustment: $F_{1.75, 24.5} = 4.996$, $P = 0.018$), with a greater neuromuscular response for all standing conditions than the seated condition ($P \leq 0.05$). The GA followed the same trend; however, significant differences were only measured between the seated condition and the two standing conditions with reduced load ($P < 0.05$) (**Fig. 4**). In both the SOL and GA, there was no

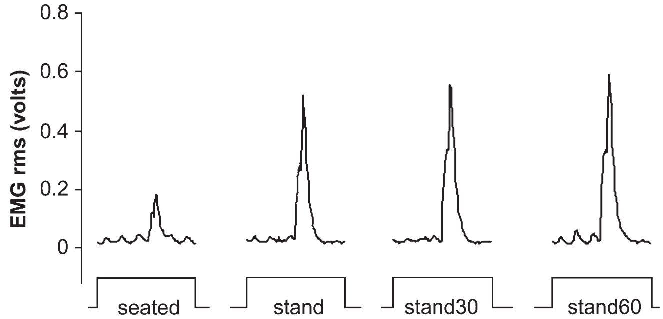

Fig. 3. A typical single SOL response to mechanical foot stimulation for each contextual condition of Experiment 1: seated, standing with full load (stand), standing with 30% reduced load (stand30), and standing with 60% reduced load (stand60).

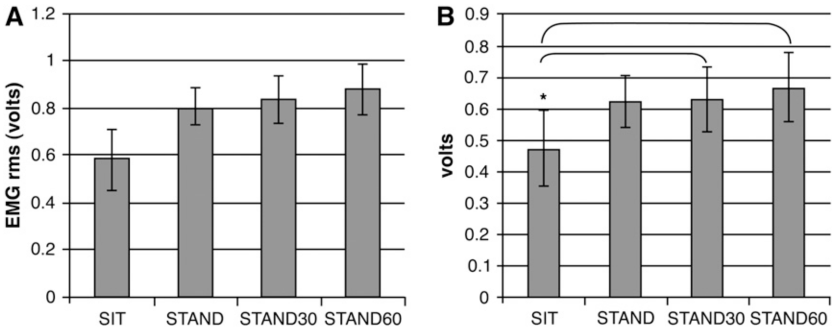

Fig. 4. A) The SOL mean peak response (± SE) to foot stimulation while seated, standing, and standing with 30% and 60% reduced load. B) The GA mean peak response (± SE) to foot stimulation while seated, standing, and standing with 30% and 60% reduced load. * Significance at $P \leq 0.05$.

significant difference between the standing conditions (i.e., those involving normal standing and standing during unloading with the Pneu-lift™), suggesting gravitational load alone did not influence the amplitude of the response. Fig. 3 provides an example of a single SOL response to the foot stimulation for the differences in amplitudes for each contextual condition.

Experiment 2

The purpose of this experiment was to elucidate differences in the neuromuscular response to foot stimulation during different body configurations which alter the postural stability and support context of the lower limbs. Different levels of unloading were also used to alter both postural stability and support contexts while maintaining the same body configuration.

The basic neuromuscular response in Experiment 2 was very similar to Experiment 1 and previously reported responses (21) for both the SOL and GA, demonstrating the same consistent temporal features: waveform pattern, latency, and duration, regardless of experimental condition. Also, as in Experiment 1, the peak amplitude varied between conditions in Experiment 2. In both the SOL and GA there was a significant interaction between the stimulation site (support context) and the stance (postural position) for the peak amplitude measured. Specifically, the stimulation response in the nonsupport leg was significantly less than in the support leg when feet were shoulder width apart, but not when feet were in tandem ($P \leq 0.01$). This finding was independent of load as there was no general load effect (SOL: $P = 0.76$; GA: $P = 0.785$) on the neuromuscular response to foot stimulation. In Experiment 2, the configuration of the right leg during the non-support and support leg conditions (regular stance) was analogous to the configuration of the right leg in Experiment 1, seated and standing conditions, respectively. Specifically, in both the non-support leg (Experiment 2) and seated (Experiment 1), the right leg was flexed to an approximately 110° knee angle, while the support leg (Experiment 2) and standing conditions (Experiment 1) both had the right leg extended. Experiment 2 results were consistent with the findings of Experiment 1 as again, conditions with the support leg (standing) configuration exhibited a greater response than the non-support leg (seated) configuration, independent of load.

DISCUSSION

The aim of this study was to determine the modulating effect of unloading and body configurations on the neuromuscular response to mechanical foot stimulation and thus further assess the applicability of a plantar stimulation countermeasure for spaceflight-generated neuromuscular alternations. In both the SOL and GA the neuromuscular responses to dynamic lateral foot stimulation were consistent and predictable in temporal features: waveform pattern, latency, and duration, while the peak amplitude of the response was dependent upon experimental condition. The consistent and short response latency of 48 ms suggests an oligosynaptic spinal path. Cutaneous mechanoreceptors of the foot sole and muscle spindles of intrinsic foot muscle are the receptors expected to be stimulated, resulting in the activation of neuronal pathways, including those involved in previously identified cutaneous and stretch reflexes (14,15), although neither wholly match the response features described above.

Regardless of the specific neurophysiological processes underlying the response, our data unequivocally show the response to foot stimulation remains intact under a variety of unloading and postural contextual conditions. This includes generating a response in passive antigravity muscles. As antigravity extensor muscles are often electrically quiet and demonstrate the most substantial atrophy in microgravity, this is highly desirable for any muscle atrophy countermeasure developed for use during spaceflight.

In both experiments, gravitational unloading was not a modulating factor to the response. The absence of influence from short-term unloading supports the use of mechanical foot pressure as a countermeasure for spaceflight, as it implies responses will be maintained in microgravity. This is consistent with Layne et al. (24), who successfully applied mechanical foot stimulation to the soles of free-floating astronauts and elicited the same neuromuscular responses during 105 d of spaceflight.

The lack of load dependence in the present study is in contrast to a load dependency displayed by cutaneous reflex responses to sural stimulation during locomotion (4), as well as a general reduction in whole body postural responses with reduced load (7,8). The absence of load dependency in the present response may be a result of required load afference being replaced by the same mechanical stimulation, and/ or by the presence of static foot stimulation resulting from contact with the base platform. This contact provided a constant source of afference to the spinal cord and may be a required precursor to the full expression of the observed response. Conversely, electrically induced cutaneous stimulation only stimulates part of the foot region and also bypasses specific impulse coding from sensory properties. Both features may dissociate electrically induced cutaneous stimulation from being interpreted as load afference and, in turn, expose the response to modulations from load levels. The same phenomenon may exist for the soleus stretch reflex. A load dependency has been demonstrated with the H Reflex (32,34), but when a soleus stretch reflex was elicited mechanically, which includes a full sole stimulation, the stretch reflex was unaffected by unloading (16).

In the present study, however, the relationship between plantar stimulation and the resultant neuromuscular response was revealed to be more complex. In addition to a lack of load dependence, the response exhibited a dependence on body configurations of the support and postural stability contexts, both of which are a function of load, i.e., a reduced load reduces the level of required support and makes a position more stable. The apparent incongruence of this finding may be explained by examining identified postural mechanisms. Well-established postural muscle synergies exist for common postures of standing and stepping. We suspect the development of these postural muscle synergies includes the linking of the defining gravity vector to the body configuration, enabling an associative muscle synergy response from particular body configurations independent of the original gravity vector. Hence, the body configuration of an unstable or support posture in full gravitational loading could still elicit the same responses even when the stability threat or support need is diminished. However, body configuration alone is not usually sufficient to generate terrestrial postural synergies. In microgravity or during terrestrial unloading, the combination of static foot pressure, analogous to contact with a surface, along with the appropriate body configurations, may provide sufficient afference to “trigger” postural synergies in microgravity. Ting and MacPhearson (39) demonstrated in cats that the ground reaction force angle, a function of loading force and slip force and the cutaneous receptors that detect them, was the critical determinant for automatic postural responses. In microgravity when feet are fixed to a surface, shear receptor detection will still be operational and load force will be minimally represented by the contact. In a foot with no contact or loading, background activity of any cutaneous receptors in the sole will be absent (19), thus suggesting afference from the sole requires mechanical stimulation of the receptors, which in turn contributes to the initiation of postural responses.

Terrestrial postural synergies observed in microgravity have all included the astronaut’s feet strapped to a surface (2,3,29). Moreover, two studies illustrate the absence of postural responses in free-floating subjects, and the restoration of those responses from the addition of mechanical foot stimulation. Dietz and Colombo (8) showed this phenomenon with C7 level water immersion during a pulling and pushing task. Terrestrial postural patterns were absent in free floating and reestablished when subjects were standing on a platform. Layne et al. (24) also demonstrated free-floating astronauts failed to exhibit anticipatory postural responses during a rapid arm raise, but restored them with the application of static foot stimulation. The level of static foot pressure applied was equivalent to that experienced in 1-g stance (24), and thereby artificially provided cutaneous stimulation for the load force component of ground reaction force angle. In the current study, the contact with the base platform would have provided some load force afferent input, but the load-detecting receptors in the specific lateral site would have also been stimulated (to equal levels across all conditions) from the dynamic mechanical foot stimulation.

During the foot stimulation, the body configurations used in the present study included seated, standing, and standing in a variety of static stepping positions. The response was greatly reduced while sitting relative to standing. This was true even in the standing condition that had the most similar loading pattern as that of the seated condition (i.e., 60% unloading, Experiment 1). Aside from loading, contextual differences between seated and standing include a variety of kinesthetic afferent from the knee, hip, and surrounding musculature that may drive different responses. Background muscle activity levels of the lower leg can modulate neuromuscular responses to mechanical foot stimulation (13), and could be argued as the facilitating factor for the standing condition. Yet background activity levels of the SOL and GA were monitored and minimized during this study, and if background activity was the driving force for the facilitated response, seated and stand60 would be expected to be comparable. Instead, stand60 was the condition with the greatest response amplitude, and seated with the smallest response for both the SOL and GA.

A further contextual difference between seated and standing is an increased supporting role of the legs and a less stable postural configuration for the standing condition. In addition, the stepping positions in experiment 2 were varied specifically to alter the level of support role for the legs and the postural stability of the position. Overall, a greater response was measured in the leg with a greater postural supporting role and in positions of greater postural instability.

This direction of an increased response in support legs and positions of greater instability is unusual and unexpected as it produces potentially destabilizing influences to posture. Indeed, spinal reflex reductions have been associated with increased postural instability for the H reflex (28,31) and responses to noxious cutaneous stimulation (37). However, if foot stimulation (non-noxious) contributes to postural synergies, it is possible the response is associated with posture conserving mechanisms rather than being interpreted as a destabilizing force. In such a case, any response from the mechanical foot stimulation would be potentially exempt from inhibition, or even facilitated in less stable postures. This may also hold true for the soleus stretch reflex, which is also associated with postural control, and has been shown to be greater during walking then pedaling and sitting (15).

It is apparent, however, that an application of dynamic foot stimulation, individually or in combination with other types of pressure patterns, could be used to trigger SOL and GA contractions without the need of muscle activity or loading. These contractions may attenuate, to some degree, the lower limb muscle atrophy and neuromuscular degradation associated with extended stays in microgravity. Moreover, the body configuration of the user with respect to support and postural stability needs to be considered in the application, and may provide further scope of benefits extending to the activation of postural synergies.

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REFERENCES

1. Abbruzzese M, Rubino V, Schieppati M. Task-dependent effects evoked by foot muscle afferents on leg muscle activity in humans. Electroencephalogr Clin Neurophysiol 1996; 101:339–48.
2. Baroni G, Ferrigno G, Rabuffetti M, Pedotti A, Massion J. Long-term adaptation of postural control in microgravity. Exp Brain Res 1999; 128:410–6.
3. Baroni G, Pedrocchi A, Ferrigno G, Massion J, Pedotti A. Static and dynamic postural control in long-term microgravity: evidence of a dual adaptation. J Appl Physiol 2001; 90:205–15.
4. Bastiaanse CM, Duysens J, Dietz V. Modulation of cutaneous reflexes by load receptor input during human walking. Exp Brain Res 2000; 135:189–98.
5. Burke D, Dickson HG, Skuse NF. Task-dependent changes in the responses to low-threshold cutaneous afferent volleys in the human lower limb. J Physiol 1991; 432:445–58.
6. De-Doncker L, Picquet F, Falempin M. Effects of cutaneous receptor stimulation on muscular atrophy developed in hindlimb unloading condition. J Appl Physiol 2000; 89:2344–51.
7. Dietz V, Horstmann GA, Trippel M, Gollhofer A. Human postural reflexes and gravity–an under water simulation. Neurosci Lett 1989; 106:350–5.
8. Dietz V, Colombo G. Effects of body immersion on postural adjustments to voluntary arm movements in humans: role of load receptor input. J Physiol 1996; 497(Pt. 3):849–56.
9. Dietz V, Duysens J. Significance of load receptor input during locomotion: a review. Gait Posture 2000; 11:102–10.
10. Edgerton VR, Roy RR. Neuromuscular adaptation to actual and simulated spaceflight. In: Handbook of physiology: environmental physiology. III The gravitational environment. New York: Oxford University Press; 1996.
11. Falempin M, In-Albon SF. Influence of brief daily tendon vibration on rat soleus muscle in non-weight-bearing situation. J Appl Physiol 1999; 87:3–9.
12. Fitts RH, Riley DR, Widrick JJ. Physiology of a microgravity environment invited review: microgravity and skeletal muscle. J Appl Physiol 2000; 89:823–39.
13. Forth KE, Layne CS. Background muscle activity enhances the neuromuscular response to mechanical foot stimulation. Am J Phys Med Rehabil 2007; 86:50–6.
14. Gibbs J, Harrison LM, Stephens JA. Cutaneomuscular reflexes recorded from the lower limb in man during different tasks. J Physiol 1995; 487(Pt. 1):237–42.
15. Grey MJ, Larsen B, Sinkjaer T. A task dependent change in the medium latency component of the soleus stretch reflex. Exp Brain Res 2002; 145:316–22.
16. Grey MJ, van Doornik J, Sinkjaer T. Plantar flexor stretch reflex responses to whole body loading/unloading during human walking. Eur J Neurosci 2002; 16:2001–7.
17. Hernandez Corvo R, Kozlovskaia IB, Kreĭdich IuV, Martinez Fernandez S, Rakhmanov AS.. Effect of a 7-day space flight on the structure and function of the human locomotor apparatus. Kosm Biol Aviakosm Med 1983; 17(2):37–44.
18. Kavounoudias A, Roll R, Roll JP. Specific whole-body shifts induced by frequency-modulated vibrations of human plantar soles. Neurosci Lett 1999; 266:181–4.
19. Kennedy PM, Inglis JT. Distribution and behaviour of glabrous cutaneous receptors in the human foot sole. J Physiol 2002; 538(Pt. 3):995–1002.
20. Kozlovskaya IB, Sayenko IV, Sayenko DG, Miller TF, Khusnutdinova DR, Melnik KA. Roles of support afferentation in control of the tonic muscle activity. Acta Astronautica 2007; 60:285–94.
21. Kyparos A, Feeback DL, Layne CS, Martinez DA, Clarke MS. Mechanical stimulation of the plantar foot surface attenuates soleus muscle atrophy induced by hindlimb unloading in rats. J Appl Physiol 2005; 99:739–46.
22. Lackner JR, DiZio P. Human orientation and movement control in weightless and artificial gravity environments. Exp Brain Res 2000; 130:2–26.
23. Layne CS, Forth KE. Plantar stimulation as a possible countermeasure to microgravity-induced neuromotor degradation. Aviat Space Environ Med 2008; 79:787–94.
24. Layne CS, Mulavara AP, Pruett CJ, McDonald PV, Kozlovskaya IB, Bloomberg JJ. The use of in-flight foot pressure as a countermeasure to neuromuscular degradation. Acta Astronautica 1998; 42: 231–46.
25. Layne CS, Forth KE, Baxter MF, Houser JJ. Voluntary neuromuscular activation is enhanced when paired with a mechanical stimulus to human plantar soles. Neurosci Lett 2002; 334:75–8.
26. Layne CS, Forth KE, Abercromby AF. Spatial factors and muscle spindle input influence the generation of neuromuscular responses to stimulation of the human foot. Acta Astronaut 2005; 56:809–19.
27. Litvinova KS, Vikhlyantsev IM, Kozlovskaya IB, Podlubnaya ZA, Shenkman BS. Effects of artificial support stimulation on fiber and molecular characteristics of soleus muscle in men exposed to 7-day dry immersion. J Gravit Physiol 2004; 11:P131–2.
28. Llewellyn M, Yang JF, Prochazka A. Human H-reflexes are smaller in difficult beam walking than in normal treadmill walking. Exp Brain Res 1990; 83:22–8.
29. Massion J, Popov K, Fabre JC, Rage P, Gurfinkel V. Is the erect posture in microgravity based on the control of trunk orientation or center of mass position? Exp Brain Res 1997; 114:384–9.
30. Maurer C, Mergner T, Bolha B, Hlavacka F. Human balance control during cutaneous stimulation of the plantar soles. Neurosci Lett 2001; 302:45–8.
31. McIlroy WE, Bishop DC, Staines WR, Nelson AJ, Maki BE, Brooke JD. Modulation of afferent inflow during the control of balancing tasks using the lower limbs. Brain Res 2003; 961: 73–80.
32. Miyoshi T, Nozaki D, Sekiguchi H, Kimura T, Sato T, Komeda T, et al. Somatosensory graviception inhibits soleus H-reflex during erect posture in humans as revealed by parabolic flight experiment. Exp Brain Res 2003; 150:109–13.
33. Moukhina A, Shenkman B, Blottner D, Nemirovskaya T, Lemesheva Y, Püttmann B, Kozlovskaya I. Effects of support stimulation on human soleus fiber characteristics during exposure to “dry” immersion. J Gravit Physiol 2004; 11: P137–8.
34. Nakazawa K, Miyoshi T, Sekiguchi H, Nozaki D, Akai M, Yano H. Effects of loading and unloading of lower limb joints on the soleus H-reflex in standing humans. Clin Neurophysiol 2004; 115(6):1296–304.
35. Netreba AI, Khusnutdinova DR, Vinogradova OL, Kozlovskaya IB. Effect of dry immersion in combination with stimulation of foot support zones upon muscle force-velocity characteristics. J Gravit Physiol 2004; 11:P129–30.

36. Newman DJ, Jackson DK, Bloomberg JJ. Altered astronaut lower limb and mass center kinematics in downward jumping following space flight. Exp Brain Res 1997; 117:30–42.
37. Rossi A, Decchi B. Flexibility of lower limb reflex responses to painful cutaneous stimulation in standing humans: evidence of load-dependent modulation. J Physiol 1994; 481(Pt. 2):521–32.
38. Rossi-Durand C. The influence of increased muscle spindle sensitivity on Achilles tendon jerk and H-reflex in relaxed human subjects. Somatosens Mot Res 2002; 19:286–95.
39. Ting LH, Macpherson JM. Ratio of shear to load ground-reaction force may underlie the directional tuning of the automatic postural response to rotation and translation. J Neurophysiol 2004; 92:808–23.
40. Vaughan CL. Theories of bipedal walking: an odyssey. J Biomech 2003; 36:513–23.
41. Vernazza-Martin S, Martin N, Massion J. Kinematic synergy adaptation to microgravity during forward trunk movement. J Neurophysiol 2000; 83:453–64.
42. Wu G, Chiang JH. The significance of somatosensory stimulations to the human foot in the control of postural reflexes. Exp Brain Res 1997; 114:163–9.