Muscle Reflexes as Modulated Preparatory Neuromuscular Activation Levels

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Abstract—Mechanical stimulation of the soles can result in lower limb muscle contraction. This suggests that controlled stimulation to the soles may be used to "drive" muscle activation that can assist in maintaining the functional integrity of lower limb muscles during extended-duration space flight. A Dynamic Foot Stimulus device, (DFS) composed of multiple solenoids, was used to stimulate the right sole of seated subjects. To modify muscle spindle input, in advance of the stimulus, ankle angle was varied across stimulation conditions while other another condition involved vibration of the Achilles tendon. Surface electromyography (EMG) revealed that stimulation led to significant neuromuscular responses in the ankle musculature that were influenced by the amount of muscle spindle input related to ankle muscle length and tendon vibration. These results provide important information that can be used to guide the development of a "passive" countermeasure that relies on sole stimulation and can supplement existing exercise protocols during space flight.

The Postural unloading associated with space flight has a variety of effects on the human body. Adaptations in all physiological systems occur that are appropriate for the weightlessness of microgravity but are problematic for the health and safety of crew members returning to the 1g environment of Earth. Exposure to microgravity initiates a cascading sequence of events that ultimately results in a combination of muscle atrophy, "recalibration" of proprioceptive processes, and modifications of neuronal functioning. This phenomenon is not exclusively due to muscle "disuse"[1] but may stem from the removal of the mechanical pressure gradient on the plantar surface of the feet during gravitational unloading. Kozlovskaya and her colleagues[2-4] have suggested that removal of this stimulus sets in motion an adaptive physiological process that ultimately results in neuromotor degradation.

A recent review has extensively discussed how the development of human physiological systems is interdependent with a 1g environment and that the removal of the normal gravitational force can be expected to impact all systems.[5] Thus, it is not surprising that virtually all physiological systems that have been evaluated after space flight display significant physical or functional differences relative to preflight. These changes are even evident at the neural level with changes in the intrinsic motor unit characteristics, decreased rate of unit recruitment,[6] and clonic activity in limb muscles.[7] Of particular interest to our research group are the obvious negative functional consequences of neuromotor degradation on the control of postflight posture, locomotion,[8-10] and activities of daily living.

To date, the primary methods used to counter neuromotor degradation during flight consist of modified exercises traditionally performed in 1g. These include treadmills, bicycle ergometers, bungy cords, and modified resistance exercise devices. By using these exercise devices, astronauts maintain cardiovascular and skeletal-musculature fitness. However, even in combination, these exercises are not completely effective in preventing the negative consequences of unloading on the neuromotor system. Additionally, performing these exercises is time consuming, thereby preventing the crew members from completing important operational tasks.

Passive neuromotor countermeasures

Recently, there has been interest in the development of a new generation of neuromotor countermeasures intended to maintain adequate functioning of somatosensory receptors, central nervous system mechanisms and associated motor units. In particular, Vinogradova et al.[11] have reported on the use of a device that provides mechanical stimulation to the soles. These authors contend that this stimulation helps stem the neurophysiological processes associated with gravitational unloading that ultimately result in neuromotor degradation. One advantage of such a "passive" countermeasure is that crew members would have the opportunity to carry out other critical on-board tasks while using the device. It is envisioned that these neuromotor countermeasures would serve as a *supplement* to the more traditional exercise devices.

Previous work by Layne and colleagues[12,13] has shown that stimulation of the feet during microgravity leads to a restoration of neuromuscular activity normally associated with rapid arm movement in 1g but absent without foot stimulation in 0g. Further, Layne et. al.[14] have demonstrated that this enhanced neuromuscular response remains present during extended space flight missions of up to six months. During a ground-based experiment in which the soles were stimulated using inflatable bladders, researchers again demonstrated that neuromuscular activation could be enhanced with mechanical stimulation.[15] This increased activation could serve as a necessary precursor for the physiological processes necessary to attenuate the degradation of neuromotor functioning associated with space flight. Consistent with this idea is the evidence presented by De-Doncker et al.[16] and Kyparos et al.[17] who have demonstrated that the application of mechanical stimulation to the soles of rats undergoing hindlimb suspension results in a large attenuation of the muscle atrophy normally observed during hindlimb suspension. Additionally, Hernandez-Korwo et al.[18] reported that a crewmember who intermittently used "shoes" that provided stimulation to the feet during a mission aboard the Salyut-6 space station, performed significantly better during postflight testing of muscle strength and locomotion relative to his fellow crewmember who was not exposed to increased foot stimulation. Thus, there is accumulating evidence that mechanical stimulation of the feet can function to greatly attenuate the loss of muscle mass and functionality associated with the removal of weight bearing activities during space flight. This evidence suggests that a device that stimulates the foot somatosensory receptors can serve as the basis of an inflight neuromotor countermeasure. In fact, De-Doncker et. al.[16] suggest that stimulation of the soles may provide an "effective means of preventing muscular atrophy and the associated post-flight motor control deficits experienced by astronauts" (p. 2350).

We have recently developed a dynamic foot pressure device (DFS) that provides mechanical stimulation to the soles with the use of solenoids (see methods for further description). Stimulation provided by the DFS generally results in short-latency neuromuscular responses in the ankle musculature. These responses are similar to those reported by other investigators who have employed either mechanical or electrical stimuli directly to nerves and/or muscle or cutaneous receptors.[15,19,20] DFS can be used to determine if a spatial and temporal pattern of sole stimulation exists that results in a maximal level of increased neuromuscular activation. The device can also be used to explore underlying neurophysiological mechanisms related to the neuromuscular responses to dynamic foot stimulation.

Spatial Influence of Sole Stimulation

Kavounoudias et al.[21] investigated the effect of stimulus location on neuromuscular responses by applying vibration to the fore foot and rear sole of the foot. In response to these two stimulations, they measured opposite center of pressure traces along the anterior-posterior axis for the sites. This suggests that the antagonistic muscles of the lower limb were enhanced differently with different stimulation sites. Sonnenborg et.

al.[22] performed an extensive exploration of the sole of the foot applying electrical stimulation to 16 different sites on the human sole during voluntary contraction of the tibialis anterior and soleus. They reported that soleus activity was generally inhibited with electrical stimulation, but the tibialis anterior response included an early excitatory activity, particularly for the sites located in the arch and along the medial site of the sole. Additionally, Andersen et al.[23] also reported differential neuromuscular responses to stimulation of different sites on the sole. These data suggest that spatial factors play a significant role in the subsequent response to foot stimuli.

Patterns of Stimulation

In addition to a possible optimal stimulus site, there may also be a pattern of stimulation, with specific temporal and spatial characteristics, that results in neuromuscular responses that exceed those found for a single stimulus. For example, the stimulation of one site may effect additional pulses.[24,25] Mela et al.[25] stimulated the peroneal nerve with four pulses, which facilitate or inhibit the response to a second stimulus at the same site or a different site. There may be refractory periods or adaptation to the stimuli. Optimizing patterns of electrical stimulation have been investigated by applying stimulation directly to a nerve, varying the number of pulses and the interval between the interpulse intervals ranging from 4 ms to 54 ms. They found an initial short interval, with longer subsequent intervals maximized the activity of tibialis anterior. Kavounoudias et al.[21] found the magnitude of the postural response to mechanical stimulation (vibration) increased as the frequency of the stimulation increased. This frequency dependent response to vibration further suggests that foot pressure stimulation patterns may have an influence on the response. However, there have been no studies that vary spatial characteristics during mechanical stimulation patterns. Identifying spatial and temporal patterns of stimulation that result in increased neuromuscular responses provides a solid foundation on which to develop a countermeasure that functions to attenuate neuromotor degradation during space flight.

Finally, some authors have suggested that neuromuscular responses to stimulation of the sole are the result of spinal reflexes.[26-28] If accurate, this suggests that varying muscle spindle input may influence the magnitude of the responses by altering spinal cord neuronal properties. Thus, it also becomes important to investigate the possible influence of ankle muscle angle and associated spindle input on responses to DFS prior to the full-scale development of a neuromotor countermeasure.

Methods

Dynamic Foot Stimulator (DFS) Protocol

Data reported below were collected during two different experiments utilizing two different groups of subjects. The first experiment consisted of investigations designed to address questions of whether stimulating different areas of the sole and temporally coupling two stimuli impacted the neuromuscular response. The second experiment was conducted to determine if varying muscle spindle input by manipulating ankle angle impacted the responses. Both experiments utilized 10 right-handed male and female volunteers between the ages of 18-35. All were free of any muscular or neurological medical conditions. Handedness was determined by administering the Edinburgh Handedness Inventory. All subjects provided informed consent as required by the University of Houston's Institutional Review Board. The basic protocol for both experiments involved the subjects being seated with their right foot resting comfortably and strapped to the DFS. The DFS uses small solenoids embedded within an aluminum frame to provide mechanical stimuli to the sole (Fig. 1).

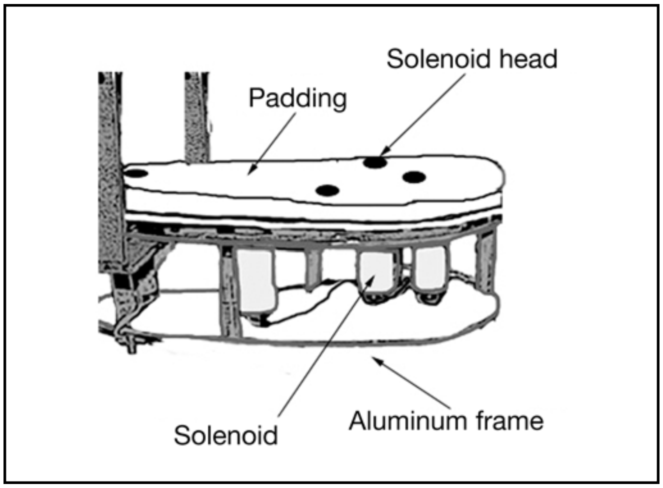

Figure 1. Schematic of the Dynamic Foot Stimulator

The solenoids are computer-controlled and can be independently operated to provide varying spatial and temporal stimulation patterns. The surface areas of the solenoids are 2.5 cm. The magnitude of the stimulus was 25 psi. Each stimulus consisted of the solenoid applying pressure to the sole for 250 milliseconds. Chair height and distance was set for ankle and knee angles at 90 degrees. The left foot was positioned comfortably at the same height as the right foot. The subjects were instructed to relax their muscles throughout the testing. To acclimatize the subjects to the sensation, they received several stimulations prior to the beginning of testing. Pilot testing indicated that the level of attention subjects devoted to the stimuli influenced the neuromuscular responsiveness to the stimuli. To control for attention levels, during the testing the subjects read aloud a series of random numbers from a sheet that was placed in front of them at a distance of three meters. The subjects were instructed to keep their muscle "relaxed" during testing; muscle electrical silence was monitored on-line during the testing.

EMG Data Collection

Root mean square (RMS) surface EMG was obtained from the soleus (SO), lateral gastrocnemius (LG), and tibialis anterior (TA) of the right shank. After cleaning the skin, the preamplifier electrodes (Therapeutics Unlimited, Iowa City, Iowa, USA) were attached to the skin over the muscles midway between the muscle belly and the distal tendon. In the case of the soleus, the electrode was positioned along the lateral aspect of the muscle just distal to the gastrocnemius. The ground lead was secured proximal to the lateral malleolus with a comfortably fitting elastic strap. During all testing the EMG and the electrical signals from the DFS, indicating the time and duration of solenoid activation, were sampled at 1000 Hz, A/D converted, and then stored on a desktop computer.

Experiment One Protocol

In this experiment, each subject experienced nine different sole stimulation conditions. Three of the nine conditions consisted of a single mechanical stimulation applied to one of three different sites on the sole. Those sites were the heel, lateral ridge, and the medial metatarsal, and are specifically defined in Table 1. The stimulation sites are schematically presented in Fig. 2. The remaining six conditions were different spatial patterns of stimulation using combinations of the three stimulus sites defined above. Each pattern consisted of two stimulation sites separated by 250 ms between solenoid initiations. The patterns are listed in Table 1.

Each condition involved 20 stimulations (single site or pattern) within a 1-minute period, with unpredictable inter-stimulation intervals to prevent event anticipation and sensory receptor habituation. The subject rested for two minutes between each condition to reduce possible fatigue. The order of conditions was also randomized to reduce any order effect.

Experiment One Data Analysis

The data were initially analyzed by identifying the stimulus 250 ms "windows" during which the stimulus was applied to the sole. Using an automatic detection script, the peak amplitude and positive integrated area (PIA) were obtained for each muscle of each subject for each condition. The first response for all conditions was disregarded due to possible startle response, but the subsequent 20 response windows were assessed for potential neuromuscular responses. Only one analysis window, defined by the second stimulation, was assessed for the pattern conditions. The first response for all conditions was disregarded due to possible startle response, but the subsequent 20 response windows were assessed for potential neuromuscular responses. Correlations between peak amplitude and the positive integrated area for a given analysis window were calculated for each muscle for each condition. The peak amplitudes were then used for subsequent analysis, as a consequence of PIA and peak being strongly correlated. The data were not compared with the magnitude maximal voluntary contractions because the fundamental question being asked is whether sensory input from the sole can produce activation in muscle that are electrically "silent." Thus, the important comparisons involve assessing the response to the stimulus relative to "baseline" EMG measures. Peak data were transformed with a natural log transformation to facilitate a normal distribution. Differences in EMG response to single stimulation sites were compared using repeated-measures ANOVA. There were two within subject factors: sites (heel, medial, lateral) and muscles (SO, LG and TA). A second repeated measures analysis was performed that included the pattern conditions along with the single stimulus data. Each pattern condition was grouped with the same single site as the second stimulation in the pattern. For example, single site heel was grouped with pattern 3 and pattern 5. This analysis had one measure representing the groupings (heels, meds, and lats) and two within subject factors, subsite (single site, and the two pattern conditions), and muscles (SO, LG, and TA). A probability value of 0.05 was adopted for all statistical testing.

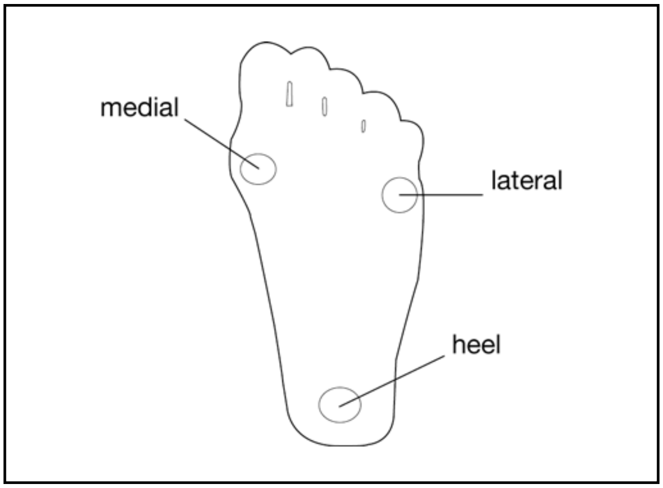

Figure 2. Schematic of the Sites of Sole Stimulation

Table 1. Stimulation Patterns used during the experimental protocol

Pattern	1st stimulation	2nd stimulation
1	Medial	Lateral
2	Lateral	Medial
3	Medial	Heel
4	Heel	Medial
5	Lateral	Heel
6	Heel	Lateral

Experiment Two Protocol

In this experiment, the stimulus consisted of the activation of a single solenoid applied under the fifth metatarsal of the right foot. Muscle spindle input was modulated in two ways. The first method involved changing ankle angle prior to the administration of the stimuli. In this protocol, three blocks consisting of 22-24 stimulations were tested. One block of stimulations was applied when the ankle angle was at 90° (C90), another with the ankle at 110° (C110), and a third condition with the ankle at 70° (C70). A fourth condition involved applying 100 Hz vibration to the Achilles tendon with the ankle at 90° (CVIB). Tendon vibration was applied using cylindrically-shaped vibrators weighing 150 g that were secured with a rubber strap (Dynatronic, Valence, France). The order of the conditions was randomized and a two-minute rest period was provided between conditions.

Experiment Two Data Analysis

As in Experiment One, peak amplitude and positive integrated area (PIA) were obtained for each muscle, of each subject for each condition within the 250 ms data analysis “window.” Initial statistical assessment demonstrated that neither the PIA nor peak data were normally distributed, so the data were converted to their natural log prior to statistical analysis. The peak value of 1000 ms of baseline data was used as comparator with the peak amplitude measures obtained within the response window. One-way analysis of variance with repeated measures was used to test for overall statistical significance. Tukey’s post-hoc comparisons were performed when significance was found. As in Experiment One, PIA and peak amplitude were highly correlated. Results from statistical testing of the peak amplitude data are reported here.

Results

Experiment One

Across all muscles, stimulation of the lateral site elicited the greatest neuromuscular response ($F_{1,9}$ = 10.65, p = 0.010). The medial site elicited a greater neuromuscular response than the heel ($F_{1,9}$ = 10.60, p = 0.010), with the heel response being no different from the baseline. Refer to Fig. 3 for a representation of the combined muscle response to each stimulation site.

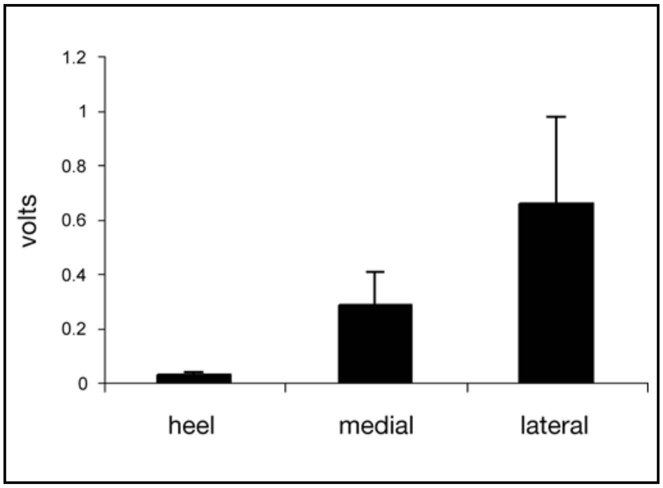

Figure 3. The Mean Peak Amplitude Muscle Responses to Three Foot Stimulation Sites (+SEM)

The LG and SO demonstrated no significant difference between their patterns of responses for each site stimulated. The TA responded in a similar manner to the LG and SO for the heel and medial locations, but did not follow the trend of increased response for the lateral stimulation ($F_{1,9}$ = 14.51, p = 0.004). Fig. 4 illustrates an exemplar subject response, typifying the different SO responses for each of the stimulation sites.

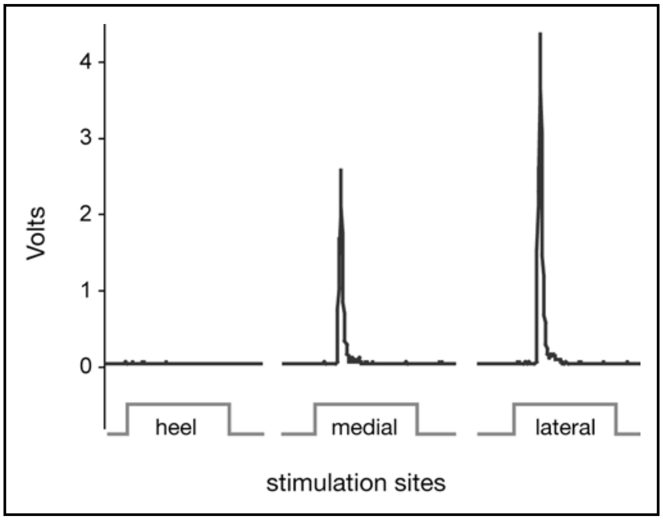

Figure 4. An Exemplar SO Waveform Response for Heel, Medial and Lateral Single Site Stimulation

Experiment One—Pattern Analysis

For this analysis, pattern conditions with the same last stimulation site were grouped together with the corresponding single site stimulations. Fig. 5 illustrates that across all muscles, a stimulus preceding each stimulation site resulted in a different response than if the site were stimulated alone. The only exception was the heel stimulation preceded by lateral stimulation. The heel site response was increased when preceded by a medial stimulation ($F_{1,9}$ = 5.54, p = 0.043). The medial and lateral site responses were inhibited relative to single stimulations by both preceding stimulations in their comparable patterns.

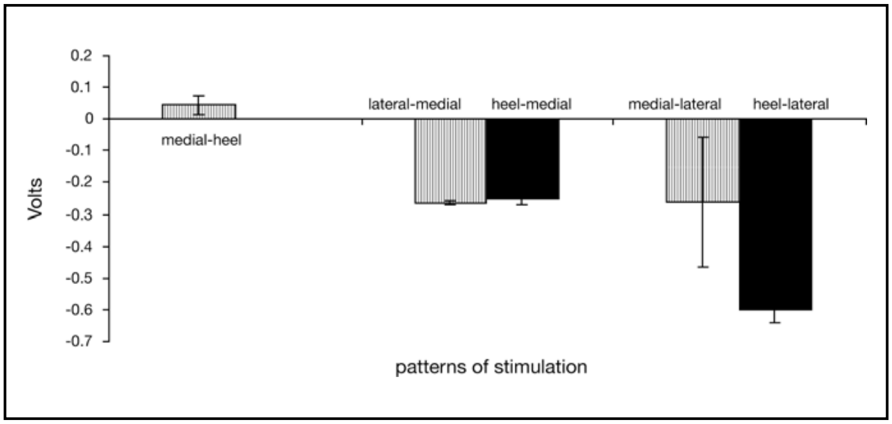

Figure 5. Effect of preceding stimulus upon the neuromuscular response to DFS. Values below *0* indicate that a preceding stimulus served to inhibit the subsequent response relative to the baseline voltage value.

Medial site responses were inhibited by prior lateral ($F_{1,9}$ = 12.96, p = 0.006) and heel stimulation ($F_{1,9}$ = 13.92, p = 0.005). The lateral responses were inhibited by prior medial ($F_{1,9}$ = 9.27, p = 0.014) and heel stimulation ($F_{1,9}$ = 35.42, p < 0.0001).

Comparisons of the muscles indicate that the LG and SO respond in the same direction to a preceding stimulus application. However, the TA differed from those responses for three of the six pattern conditions. When the heel was preceded by medial stimulation, the TA response was unchanged whereas the

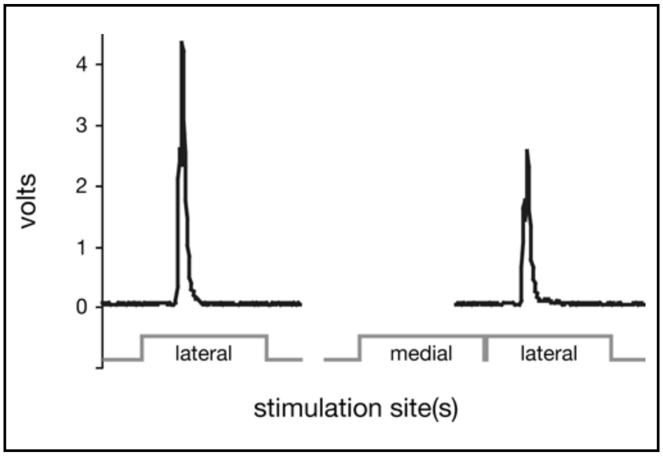

Figure 6. Exemplar waveform displaying inhibition of the lateral soleus response relative to baseline when preceded by stimulation at the medial site.

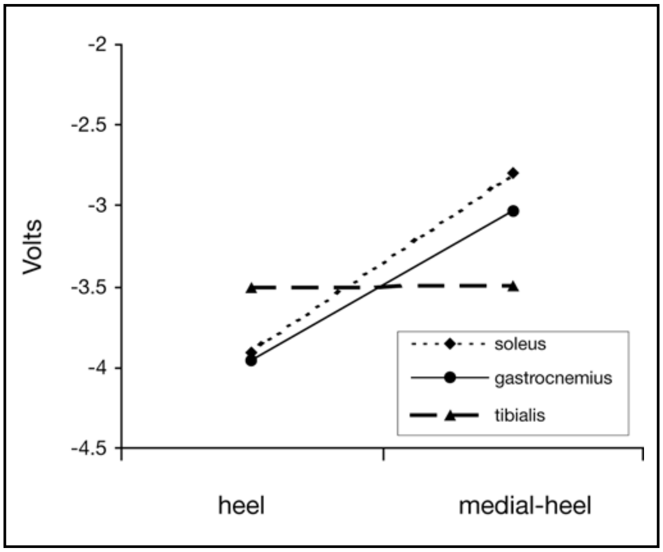

Figure 7. Differences in muscle in response to heel stimulation when paired with medial sole stimulation. Note that the response of the tibialis anterior in unaffected by "patterned" stimulation relative to baseline.

LG and SO increased their response to heel stimulation ($F_{1,9} = 10.17$, $p = 0.011$); see Fig. 7.

The TA was not as greatly inhibited as the LG and SO when a medial stimulus was preceded by a heel stimulus ($F_{1,9} = 10.17$, $p = 0.011$). Significant differences between the antagonist muscles were also found for the response to lateral stimulus preceded by heel, primarily due to the differences in single lateral stimulation responses described above ($F_{1,9} = 95.82$, $p < 0.0001$).

Experiment Two

In response to mechanical stimulation of the sole under the fifth metatarsal, there was a significant overall increase peak amplitude in both the SO and LG, ($p < 0.05$). Figure 8 A-B provides individual exemplar responses for both muscles. As expected, peak SO and LG responses for each condition were significantly greater than baseline. Peak responses were largest in C70, followed by C90, then C110, with CVIB displaying the lowest peak amplitude.

As was found for the plantarflexors, there was an overall significant effect of applying a stimulus to the sole for the peak amplitude measures of the TA ($p < 0.05$). Exemplar data from a single subject is presented in Fig. 9. Post-hoc testing revealed there were significant differences between all conditions with responses being largest in C110, followed by C90, then C70. Similar to the responses observed in the plantarflexors, the application of vibration to the Achilles tendon virtually eliminated responses to sole stimulation. The findings from both the plantarflexor and dorsiflexors indicate that when a particular muscle is in a lengthened position, the response to sole stimulation is greater.

Discussion

The general purpose of this investigation was to determine if spatially patterned mechanical stimulation to the sole generates neuromuscular responses in the relaxed ankle musculature of seated subjects and whether differing levels of muscle spindle activity modified these responses. The data clearly show that short-latency neuromuscular activity can consistently be generated using mechanical stimulation of relatively short duration (250 ms) and that different responses are observed for different stimulation sites and patterns. Further, varying spindle input modifies the response in a manner that indicates that enhanced responses are observed when the muscle is stretched prior to stimulation.

Responses in Electrically "Quiet" Muscles

The DFS protocol resulted in neuromuscular responses to sole mechanical stimulation in electrically "quiet" muscles, as evidenced by the significant differences between the EMG baseline activity and the activity in all experimental conditions. This is an important finding as previous reports concerning responses to electrical or mechanical stimulation indicate that muscles must first be voluntarily activated prior to stimulation for a response to occur,[19,29] unless a noxious stimulus is applied. It has been reported that the level of neuromuscular activation of some ankle musculature over the course of 24 hours during flight exceeds that recording during 24 hours on Earth. Consistent with the previous work, we can therefore expect that DFS stimulation applied during flight will result in neuromuscular activation of greater magnitude than that reported here.

The increased activity over the course of 24 hours reported by Edgerton et al.[1] indicates a level of hyperactivity that may be related to the patterns of muscle use associated with the unique functional tasks during space flight. This finding suggests that the atrophy prevention observed by both De-Doncker et al.[16] and Kyparos et al.[17] is not exclusively a function of increased neuromuscular activation resulting from DFS. It is more likely that controlled stimulation of the sole restores, to some extent, the afference associated with gravitational loading experienced on the soles, thereby attenuating the adaptive process that leads to neuromotor degradation following the removal of this sensory input. Additionally, the DFS protocol was able to generate neuromuscular responses in muscles that were not directly subjected to the stimulus. This indicates that the neuromuscular responses reported here are not simply stretch reflexes. This finding has broad implications for the use of sensory stimulation countermeasures.

Responses spatially patterned stimulation

Muscle activity of the lower limb was enhanced to different degrees depending on the location of the stimulus. The lateral stimulation site yielded the greatest muscle response, followed by the medial and no significant response from the heel site. All of these responses were modified by a preceding stimulus: facilitating the heel response and drastically inhibiting the medial and lateral responses.

The response most similar to the current findings is the plantar reflex. This is the normal response to the Babinski test, where a stroke of the foot sole elicits a curling of the toes and possible plantar flexion. Similar to the findings above, the plantar reflex is best elicited from the lateral aspect of the foot sole.[30] As a result, the response to mechanical foot stimulation in this study may share some of the same pathways as the plantar reflex.

The neurophysiological mechanism underlying the responses may involve a number of factors at a variety of organizational layers. The properties of cutaneous mechanoreceptors may provide the first level for differentiating the response. The distribution of receptor fields for cutaneous mechanoreceptors is not uniform across the sole of the foot. Kennedy and Inglis[31] identified receptor fields on the sole of the foot for slow adapting cutaneous mechanoreceptor units and fast adapting units. The heel stimulus used in this study would only stimulate four to five slow adapting unit receptor fields; the medial site would possibly stimulate one slow adapting unit and two or three fast adapting units while the lateral site could potentially activate two slow activating units and six fast activating units.[31] These findings would suggest that stimulation of a greater number of fast activating cutaneous mechanoreceptor units yields an

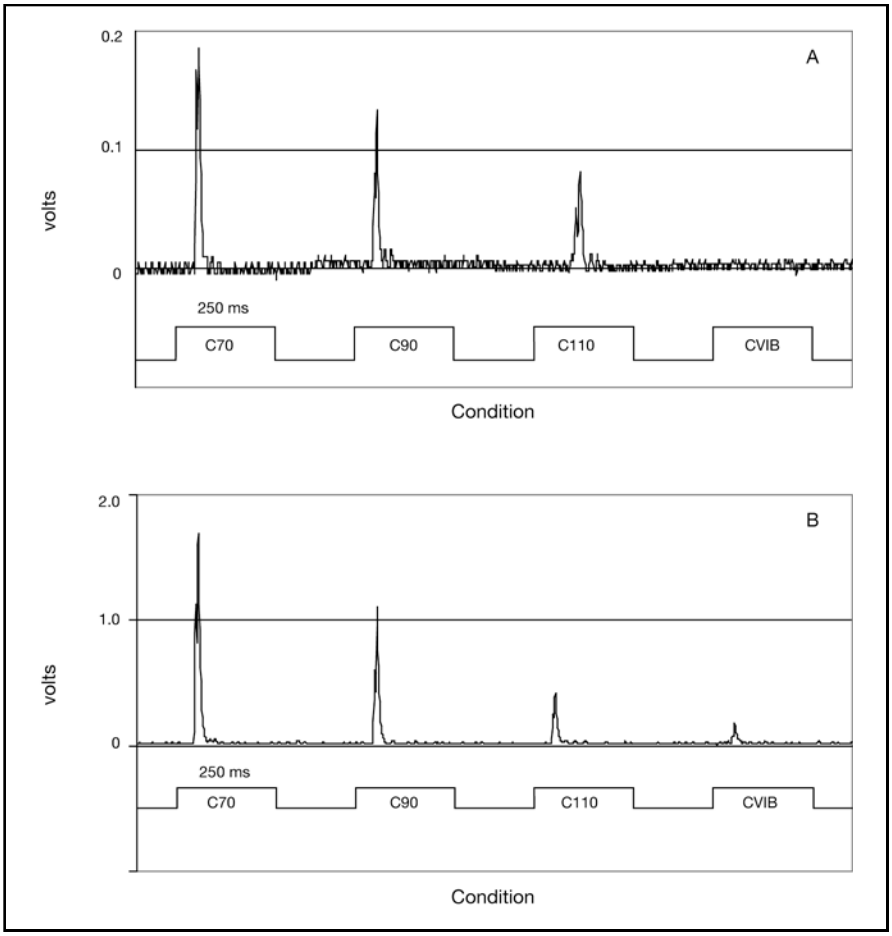

Figure 8. Single subject exemplar neuromuscular responses of the SO (A), (Subject 2) and LG (B), (Subject 3), from each experimental condition.

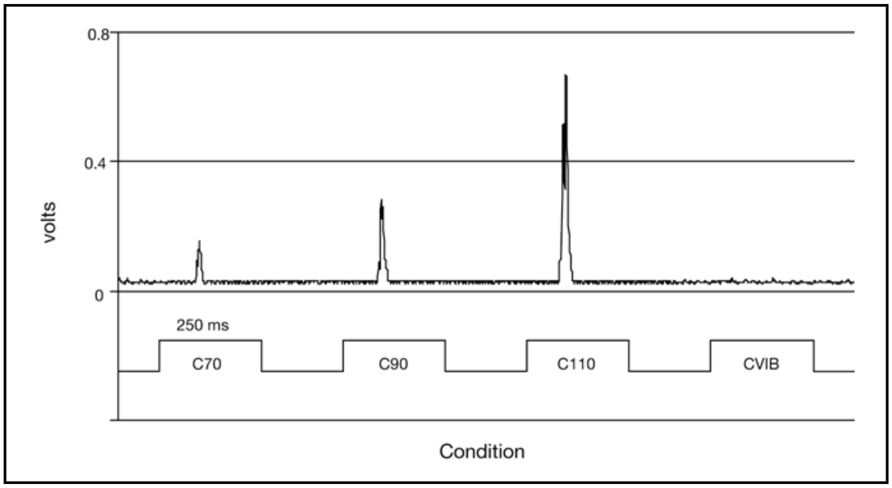

Figure 9. Single subject exemplar neuromuscular responses of the TA. Note, the pattern of amplitude responses is reversed from the responses observed in the SO and LG.

increased response to mechanical foot stimulation. The fast adapting units also have the lowest threshold. However, the density and distribution appear to be of more importance than threshold levels because the threshold levels of the cutaneous mechanoreceptors do not vary for different locations on the foot sole.[31]

The next level of organization differentiates between regions of the foot sole by nerve innervation territories. The medial calcaneal, medial, and lateral plantar nerve branches from the tibial nerve innervate the heel, medial three quarters and lateral quarter of the foot sole, respectively. The sural nerve also includes glabrous skin on the lateral side of the foot and heel, extending into the sole.[32] Further divisions can be determined with specific fascicular receptor fields. Nine fascicular receptor fields have been identified for the plantar nerves,[31] two of which include just the heel site in our study, three include just the medial site, and one includes just the lateral site. Another fascicular receptor field includes both medial and lateral sites. The sural nerve has three receptor fields that extend into the foot sole, possibly contributing to lateral and/or heel site. These specifically defined fascicular receptor fields, representing regions analogous to the stimulation sites of this study, may account for possible variations in response to stimulation of those sites.

The tibal and sural nerves are also organized into the spinal cord through specific spinal roots of a vertebrate segment. Consequently, receptor fields for a single spinal root are created, known as dermatomes. There are three dermatomes, with a certain degree of overlap, that influence the foot sole: L4, L5, and S1. The lateral site may be included in S1 and/or L5 dermatome, the medial site may be included in L5 and/or L4, and the heel may be included in L5 and/or S1. The significance of foot sole locations being represented by different dermatomes is that different spinal cord segments may have varying interneuron environments, altering their influence on the response.

Organizational features of cutaneous afferents, listed above, may also provide explanations for the observed changes in response to pattern stimuli. Activation of receptor fields, at the receptor, nerve, or dermatome level may inhibit or facilitate responses from other receptor fields. Whatever the mechanism(s) associated with the observed responses, the duration of influence from the first stimulus must last approximately 200 ms if they are to impact the neuromuscular responses observed in the second stimulus window. This criterion rules out a number of stretch reflexes and reciprocal inhibition.

Responses to Varying Afferent Input

The data indicate that the magnitudes of the neuromuscular responses are sensitive to changes in muscle spindle afference. This is illustrated by the fact that the greatest response amplitudes were found in the experimental condition in which the muscles were at their greatest length, i.e., C70. Conversely, when the plantarflexors were at their shortest length, the responses displayed the least amplitude. This basic pattern was the same for the dorsiflexor. Overall, conditions that led to a stretch of the sensory region of the muscle spindle and, subsequently, increased spindle afference, were associated with the greatest responses in the stretched muscles. Current data are consistent with the results of Bawa and Stein[33] who reported the reflex effects in the soleus muscle were modified as ankle angle was varied.

As mentioned, cutaneous input contributes to the neuromuscular activation, it seems likely that the full expression (i.e., greatest amplitude) of the response requires the muscle spindle input associated with the stimulus. Solenoids in the DFS press slightly into the skin of the sole that causes a stretch on the intrinsic muscles underneath. Given that the stimulus produces a quick stretch of the foot musculature, it is expected that Ia input dominates the afferent volley associated with the stimulus.[20]

Impact of vibration

Current data show that when vibration was imposed with the ankle at 90° (CVIB), the magnitude of neuromuscular responses was greatly reduced or completely eliminated relative to responses in other conditions. This finding suggests that primary spindle input is important to the generation of the responses observed in this study. The reduction in magnitude of neuromuscular responses in response to vibration is consistent with many reports in which vibration was used to modify the neural environment.[28,34] Primary spindling endings are particularly effective in responding to vibration. Therefore, the inhibitory effects on neuromuscular activation during vibration protocols are commonly attributed to the changes in Ia input. This is reasonable considering that early investigations reported that, during vibration, primary endings produce smaller responses to tendon taps,[35] and Ia excitation thresholds are increased[36] relative to conditions without vibration. Additionally, secondary spindle fibers and Golgi tendon organs are generally insensitive to vibration in relaxed muscles, such as those in the current study.[37] It should be noted, however, that disruption in cutaneous receptor signaling may have also contributed to the reduced responses observed in CVIB.[38]

Conclusion

The precise mechanisms underlying the responses reported here are beyond the scope of this investigation. However, the importance of stimulus location and pattern and level of muscle afference on the response have been demonstrated. Before a usable countermeasure for space flight can be developed, however, the basic stimulus response parameters surrounding neuromuscular response to mechanical stimulation of the sole must first be answered. With the knowledge gained from these investigations, future studies designed to identify stimulation patterns that function to optimally attenuate the neuromotor degradation experienced by crew members can ultimately be conducted. Whether it is a series of single stimulations or a complex pattern of varied stimuli, the replacement of absent cutaneous loading afferent could be used as a supplementary countermeasure to the negative consequences of space flight.

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Layne, C. S., K. E. Forth, A. F. Abercromby. "Spatial Factors and Muscle Spindle Input Influence the Generation of Neuromuscular Responses to Stimulation of the Human Foot," *Acta Astronautica* 56/9-12 (2005): 809-19.

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Forth, K. E. and C. S. Layne. "The Neuromuscular Response to Context-Specific Foot Stimulation" Houston Society for Engineering in Medicine and Biology, 22nd Annual Houston Conference on Biomedical Engineering Research, Feb., 2005.

Forth, K. E. and C. S. Layne. "Spatial and Temporal Mechanical Foot Stimulation Parameters Influence Neuromuscular Responses in the Lower Limbs," Sigma Xi Student Research Day, University of Houston, April, 2004.

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Layne, C. S., K. E. Forth, and A. F. Abercromby. "Does Varying Muscle Spindle Input Modify Neuromuscular Responses to Foot Stimulation?" 14th Humans in Space Conference, Banff, Alberta, Canada, May, 2003.

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Clarke, M. S. F., C. S. Layne, and W. Boling. "Development of New Technologies for Assessing the Effects of Physical Activity on Skeletal Muscle Function and Physical Fitness in Field-Based Situations," Grants to Enhance and Advance Research (GEAR), University of Houston, May, 2003, $23,284.

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