Regulation of Feed-forward and Feedback Strategies at the Human Ankle during Balance Control

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Abstract

The dynamics of sway during quiet stance have often been approximated by the movement of an unstable inverted pendulum. Controlling this unstable load requires the nervous system to balance the reliance on feed-forward volitional activation and feedback mechanisms such as stretch reflexes. It has been demonstrated that reflex excitability is heightened when postural stability is threatened by destabilizing forces in the environment. However, the relationship between postural stability, volitional activation, and stretch reflex excitability remains unclear. We addressed this question by characterizing feed-forward and feedback activation strategies during balance of a simulated inverted pendulum. We hypothesized that feed-forward co-contraction and stretch reflex amplitude would scale together as the external support provided by the environment was reduced. Electromyographic (EMG) responses in 5 muscles of the lower limb were used to characterize co-contraction patterns and stretch reflex amplitude as subjects stabilized the simulated loads. Our results revealed that co-contraction magnitude did indeed scale with increasingly destabilizing torques; however reflex amplitude was attenuated as stability was reduced. These findings suggest that the contribution of feedback mechanisms to postural stability depends on both the level of stability provided by the environment and how the environment influences the pattern of volitional activation.

I. Introduction

Maintenance of stance requires minimal effort despite the fact that the nervous system must account for the complex multi-segmental dynamics of the body. This complexity is accounted for in such a way that body sway during quiet stance can be described as an inverted pendulum [1]. To balance this pendulum, torques must be generated from the combined effects of passive muscle and joint properties, feedback mechanisms such as stretch reflexes, and feed-forward volitional activation. Each of these strategies can compensate for increasingly larger disturbances, but utilizing active stabilization will require a higher energetic cost. Hence, the nervous system may consider this tradeoff when specifying the relative contributions of feedback and feed-forward strategies during postural control.
The balance of these control strategies will not only depend on the type of load being controlled, but will also be sensitive to the type of external forces provided by the environment. When postural stability is threatened by destabilizing forces, it has been reported that reflex excitability is enhanced independent of changes in volitional muscle activation [2]. However, in the absence of these forces, it has been proposed that feed-forward, predictive mechanisms may be sufficient to stabilize posture with minimal contribution from feedback mechanisms such as stretch reflexes [3]. Hence, there remains a discrepancy regarding the relative contributions of feed-forward and feedback strategies during postural control.

Evidence from studies in the upper limb has suggested that both feedback and feed-forward strategies vary in a task-specific manner. For instance, during position control of compliant loads, reflex excitability is heightened relative to torque-matching tasks requiring the same level of muscle activity [4]. When the environment is changed to generate destabilizing forces, individuals increase the magnitude of agonist-antagonist co-contraction and may also increase the amplitude of stretch reflexes [5]. While these studies addressed the independent contributions of feed-forward and feedback strategies to postural stability, it remains to be seen how these strategies are combined in lower limb when postural stability is threatened.

The goal of this study is to examine how the nervous system combines feedback and feed-forward control strategies in the lower limb to account for the level of postural support provided by the environment. As subjects balanced a simulated inverted pendulum, we hypothesized that they would increase both co-contraction magnitude and stretch reflex excitability as the level of external support was reduced. The results of this study may advance the current understanding of how the nervous system optimizes feedback and feed-forward control parameters to account for load mechanics and the level of external support.

II. Methodology

A. Equipment

Ten subjects, 24–35 years of age (4 female), were recruited for this study. All experimental procedures were approved by the Institutional Review Board of Northwestern University and complied with the principles of the Declaration of Helsinki. Informed consent was obtained prior to testing.

A brushless servomotor (BSM90N-3150AX; Baldor Electric Company, Fort Smith, AR), controlled using Matlab xPC, was used to simulate different mechanical environments and apply perturbations to the ankle joint. Forces and moments were measured using a six degree-of-freedom load cell (45E15A4-163-AF 630N80; JR3, Inc, Woodland, CA).

Subjects were seated in a Biodex chair and movement of the trunk was minimized using a set of straps placed across the torso (Fig. 1a). Each subject’s right knee was flexed 30° and the foot was secured to an aluminum footplate using straps placed across the forefoot and heel. The ankle’s center of rotation was then aligned with the axis of the motor and locked into position at an angle of 100°.

Bipolar, surface electrodes (Noraxon USA, Scottsdale, AZ) were used to record EMG activity in 5 muscles whose actions spanned the sagittal and frontal planes. These muscles were soleus (Sol), medial gastrocnemius (MG), and lateral gastrocnemius (LG), which each have primary moment arms in plantar flexion, tibialis anterior (TA) which has moment arms in dorsiflexion and inversion, and peroneus longus (PL) which has moment arms in eversion and plantar flexion. The resulting signals were amplified using a Bortec® AMT-16 system (Bortec Biomedical, Calgary, AB), with a bandwidth between 10–1000 Hz. Analog signals
were anti-alias filtered using custom-built, differential input, 5th order Bessel filters with a cutoff frequency of 500 Hz and then sampled at 2500 Hz with an 18-bit data acquisition system (NI PCI-6289; National Instruments, Corp., Austin, TX).

B. Protocol

Subjects performed a postural control task while interacting with simulated mechanical environments which provided varying levels of postural support. In the stiff (S) environment, the motor position was fixed and subjects were instructed to maintain a torque of 5 ± 2% of their maximum voluntary torque (MVT), assisted by visual feedback of the generated ankle torque. The remaining environments required subjects to modulate ankle position to balance a simulated inverted pendulum connected to support springs with varying values of stiffness. In each case, subjects were instructed to maintain a joint angle of 100 ± 0.5° using visual feedback of ankle position.

The level of postural support was controlled by varying the stiffness of supporting springs relative to the toppling torque of the pendulum. The pendulum’s mass was equal to 25% of the subject’s mass and the height was set at 1m (Fig. 1b). This configuration produces a toppling torque proportional to the sine of the angular displacement and can be described as a gravitational stiffness equal to \( mgL \) Nm/rad. For a spring stiffness of \( k \), the passive system will be stable for all \( k \geq mgL \) and unstable otherwise. For the compliant (C), unstable 1 (U1), and unstable 2 (U2) environments, the spring stiffness was set to 1.25*\( mgL \), 0.75*\( mgL \), and 0.5*\( mgL \) Nm/rad respectively. This system was simulated by commanding the motor in an admittance control mode as illustrated by Fig. 1c. In this mode, the difference between the torque exerted by the subject and the torque due to the load dynamics was used to command a change in motor position. A dorsiflexion bias torque of 5% of MVT in plantar flexion was also applied in addition to the torque due to the simulated mass. Both the mean position and bias torque were matched across all tasks.

The contribution of the feedback strategy was assessed by applying ramp and hold perturbations to elicit stretch reflexes in the plantar flexors. Each experimental trial had a duration of 2 minutes and consisted of a sequence of 20 perturbations with a velocity and amplitude of 200°/s and 10°, respectively. To minimize the probability of anticipatory reactions, the interval between perturbations was uniformly varied from 1–3 s and subjects were instructed to not react to the perturbation.

C. Data Analysis

Average rectified EMGs were used to quantify the feed-forward volitional activity and stretch reflex amplitude for all tasks. EMG amplitude was normalized to the muscle activity recorded during maximal contractions of each muscle. Both the net muscle activation magnitude and pattern of activation across muscles were used to characterize each subject’s volitional strategy. Net muscle activity was quantified by computing the mean activity in each muscle during a 100ms window prior to perturbation and summing these values. To estimate the sources of variation in muscle activity across environments, it was assumed that the observed activation patterns were composed of a torque component to produce the bias torque and a stabilizing component used to compensate for the mechanics of the environment. The torque component was approximated by averaging the background activity in each muscle during the stiff condition. The stabilizing component was then estimated by removing the torque component from the compliant and unstable trials and averaging the residual activity. Linear regression was performed to estimate the coefficients of each component and these coefficients were used to further characterize changes in the volitional strategy across tasks.
In addition to these measures of the volitional strategy, stretch reflex amplitude was used to characterize the contribution of feedback across tasks. Reflex onset was defined as the time following movement onset when the EMG exceeded three standard deviations above the average baseline activity for 5 ms. Reflex amplitude was then computed by calculating the mean amplitude of the averaged, rectified EMG during the 20ms following response onset. All trials for each subject were pooled for analyses of both feed-forward activity and reflex amplitude.

III. Results

A. Feed-forward compensation for reduced postural support

Subjects successfully performed both the torque and position maintenance tasks by varying the magnitude of volitional muscle activation. As subjects interacted with the simulated loads, the total muscle activity scaled as the level of support was reduced (Fig. 2a). The co-contraction magnitude in the U1 condition was greater than the stiff and compliant environments (p < 0.001 and p < 0.01 respectively) and the magnitude in the U2 environment was greater than all of other conditions (all p < 0.001). Despite this variation in co-contraction magnitude across environments, the bias torque produced by the subjects (Figure 2b) remained within the accepted range of targeted torque of 4–6%MVC (95% confidence interval: 4.6–5.2% MVC) and there was no significant influence of the environment on the background torque (p = 0.14).

The majority of the feed-forward muscle activation could be described using two coordination patterns: one representing the torque generating component and one representing the stabilizing component. An example of the components used for regression analysis is illustrated in Fig 3a for 3 representative subjects. Each bar is normalized to the magnitude of the activation pattern to compare the relative activation of each muscle across subjects. In each of these cases, the torque component primarily involves the plantar flexors Sol, MG, and LG while the stabilizing component involves activation of TA and PL as well as some residual activity in the plantar flexors. Although the dorsiflexion torque produced by TA could be balanced by the plantar flexors, the co-activation of TA and PL may serve to balance torques produced in the frontal plane as well.

The structure of the observed increase in co-contraction across environments can be described by a change in the relative contribution of the torque generating and stabilizing components. Fig. 3b illustrates this variability as 95% confidence ellipses for the coefficients of the torque and stabilizing components. The coefficient of the stabilizing component increased from the stiff to the compliant environment (p < 0.01) and again in the most unstable environment (p < 0.001); however the coefficient of the torque generating component remained constant (p = 0.71) across environments. Hence, the increased in muscle activity observed in the unstable environments is consistent with increased usage of a stabilizing co-contraction strategy.

B. Modulation of reflex excitability with changes in support level

Stretch reflex amplitude varied with the level of external support provided by the environment. Figure 4a illustrates the position perturbations and reflex responses from a typical subject. In each environment, the perturbations elicited a short latency stretch reflex in Sol, MG, LG, and PL without a subsequent long-latency response. To illustrate how reflex amplitude varied within subjects, the relative change in reflex amplitude with respect to the stiff conditions is presented in Fig. 4b. From these data it is clear that reflex amplitude was significantly attenuated in Sol, MG, LG, and PL during interaction with the most unstable load. The relative reduction in reflex amplitude for the U2 condition ranged from...
6.9% in LG to 27.6% in PL when compared to the stiff condition. This reduction occurred despite the fact that the level of background EMG was greatest in the most unstable condition (Figure 2a).

IV. Conclusions

This study was performed to assess how changes in load stability affect both feed-forward and feedback control of ankle posture. We hypothesized that subjects would compensate for reduced postural support by increasing the magnitude of agonist-antagonist co-contraction and also by increasing stretch reflex excitability. Our results demonstrated that as support was reduced, individuals did indeed increase the magnitude of co-contraction to stabilize the load. This co-contraction pattern could be described as the linear combination of a torque component which remained constant across tasks and a stabilizing component which was markedly increased during interaction with the most unstable loads. When posture was disturbed by a perturbation, stretch reflex excitability in the plantar flexors was attenuated during the most unstable condition in comparison to the stiff condition.

The observed reduction in reflex excitability is consistent with reported observations of H-reflex modulation during tasks involving reduced postural support. For example, when the base of support is decreased during beam walking, H-reflex amplitude is attenuated when compared to walking over ground [6]. Together, these observations suggest that the nervous system is organized in such a way as to limit the efficacy of the stretch reflex at the ankle when postural stability is compromised. However, this strategy appears to be sensitive to nature of ongoing motor activity. For instance, when destabilizing perturbations of the trunk are applied during gait, H-reflex amplitude is actually enhanced when compared to normal walking, but reduces below baseline if subjects are allowed to hold onto handrails and provide supplementary postural support [2]. This change in strategy between quiet stance and locomotion may be related to the gating of proprioceptive feedback via locomotor pattern generating circuits or a change in context-dependent input from descending sources.

Although the current results are consistent with H-reflex modulation during postural stabilization, the relationship between environmental stability, feed-forward activation, and reflex excitability appears to differ between the upper and lower limbs. During upper limb tasks when subjects are required to stabilize compliant [7] or unstable loads [8], agonist-antagonist co-contraction is heightened when compared to torque control tasks. However, if subjects are constrained to maintain the same level of activity across tasks, the nervous system appears to increase the reliance on feedback mechanisms by increasing reflex excitability [4,9]. Although our results are consistent with the reported increases in co-contraction during position control tasks, this change in feed-forward strategy was accompanied by a reduction in reflex excitability. One potential explanation for this discrepancy is the fact that the upper limb studies primarily observed modulation in the longer-latency components of the stretch reflex while the current results involve only short-latency responses.

In summary, the results of this study suggest that the influence of feed-forward strategies must be accounted for to fully understand the task-dependent contribution of feedback mechanisms in postural control. Our results demonstrate that reducing the level of support provided by the environment may lead to altered volitional coordination strategies. The combination of both the environment and the volitional strategy will then influence the nervous system’s reliance on feedback mechanisms for postural support. Although previous studies have established that reflexes are modulated in a task dependent manner, these results should be interpreted with respect to whether a task variable (e.g. torque), the volitional activation pattern, or both are constrained. In the current context, when the task
variable is the primary constraint, it appears that the system reduces its reliance on proprioceptive feedback when posture is sufficiently challenged.

Acknowledgments

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References

Fig 1.
Experimental setup and simulated loads. (a) Subjects were seated with their foot attached to a servomotor via a rigid footplate. (b) Illustration of the simulated mechanical load controlled by the ankle. (c) Diagram of the admittance controller used to simulate load dynamics.
Fig 2.
Influence of environment on co-contraction magnitude and bias torque. (a) Co-contraction magnitude for each environment. (b) Plantar flexion torque recorded prior to perturbation.
Fig 3.
Decomposition of co-contraction pattern into torque and stabilizing components. (a) Examples of torque and co-contraction patterns extracted from regression analysis for three subjects. Patterns are normalized to unit magnitude for ease of comparison. (b) Coefficients of the torque and stabilizing components for each loading condition (ellipses represent 95% confidence intervals for both coefficients).
Fig 4. Influence of load mechanics on reflex responses. (a) Representative example of perturbation traces and resulting EMG responses for each loading condition. (b) Relative change in reflex amplitude with respect to the stiff condition. As the load became increasingly unstable, the reflex responses were increasingly attenuated.