Sway-dependent modulation of the triceps surae H-reflex during standing

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More recently, the neurophysiological control of human standing posture has been examined by eliciting the Hoffmann (H)-reflex in the soleus (Sol) and medial gastrocnemius (MG) muscles (19). The H-reflex is primarily elicited through the activation of the group Ia afferents; however, contributions from other afferent pathways cannot be ruled out completely (3). Using the H-reflex technique, we recently observed that the efficacy of the spinal pathway between the Ia afferents and the α-motoneurons from the triceps surae varied between different positions of postural sway during quiet standing (19). When subjects were in a forward compared with backward position of sway, larger H-reflex responses occurred in both the Sol and MG. The authors suggested that this phase-dependent modulation of the H-reflex ensured a greater likelihood for depolarization of the Sol and MG motoneuron pool via synaptic transmission of the Ia afferents when additional plantar flexor torque was required, such is the case when the body is in a more forward position of sway. While the study was the first to describe such a modulation during the postural sway of standing, the relative contributions of sway position and direction were not examined.

Therefore, the purpose of this study was to determine the contributions of sway position and sway direction on the modulation of the Ia pathway during quiet standing. Given the previous findings of a significant change to the H-reflex during experimentally controlled ankle displacements and velocities (2, 14–16), as well as the results from our previous study (19), it was hypothesized that the triceps surae H-reflex would be greater when subjects were swaying in a forward compared with a backward position, as well as in a forward compared with a backward direction. Both forward sway position and sway direction are likely to be associated with an overall decrease in muscle length (11), which, under experimentally controlled tasks, involves an increase in the H-reflex amplitude (11, 13).

Two experiments were conducted to test this hypothesis. The initial experiment (experiment 1) examined whether the direction of sway affected the size of the H-reflex by recording Sol and MG H-reflex recruitment curves at two different directions, but from the same position, of sway during standing. Because a direction-dependent modulation of the triceps surae H-reflex was observed, a subsequent experiment (exp-
imemt 2) was conducted to further determine whether the effects of sway position and direction to the 1a pathway occurred independently of each other.

**METHODS**

**Subjects**

Eight men (31 ± 6 yr, 175 ± 4 cm, 71 ± 8 kg) and 10 men (29 ± 6 yr, 177 ± 3 cm, and 71 ± 10 kg) participated in experiments 1 and 2, respectively. All procedures were conducted in accordance with the Declaration of Helsinki and were approved by the local university ethics committee.

**Subject Setup**

For experiments 1 and 2, pairs of surface electrodes (5-mm diameter, 2-cm interelectrode distance, Ag-AgCl, Meditrace) were placed in a bipolar configuration over the subject’s right tibialis anterior (TA), Sol, and MG to measure the muscle’s background electromyogram (bEMG) activity. These EMG recordings were amplified 400 times (MA300, Motion Lab Systems) and low-pass filtered at 750 Hz. Additional pairs of electrodes (same material as above) were placed in a belly-tendon configuration over the right Sol and MG to measure the H-reflex and M-wave amplitudes. Signals from the Sol and MG were amplified 200 and 100 times (NL844, Digitimer), respectively, and low-pass filtered at 500 Hz (NL135, Digitimer). All EMG recordings were sampled at 10 kHz using a 16-bit Power 1401 and Spike2 data collection system (Cambridge Electronics Design). In addition to the electrodes used for recording EMG, electrical stimuli were delivered through an anode electrode (5.08-cm × 10.2-cm carbon rubber pad; Empi) placed proximal to the patella on the lower anterior aspect of the thigh, and a cathode electrode (5-mm diameter, Ag-AgCl, Meditrace) placed at a position in the popliteal fossa that gave the largest H-reflex response for a given electrical current, while subjects were lying prone on a bench.

For experiment 2, movements of the right leg during the experimental trials were tracked using a six-camera motion analysis system (ProReflex, Qualisys, Sweden). Kinematic data for one subject were not collected. Single reflective markers were placed on the greater trochanter, medial and lateral knee joint line, medial and lateral malleoli, and the first and fifth metatarsal heads to define the proximal and distal aspects of the thigh, shank, and foot segments. Clusters of four reflective markers, mounted on a rigid plate, were placed on the lateral aspect of the right thigh and shank, as well as on the dorsum of the right foot, and were used to track the three-dimensional movements of the lower limb segments. The sampling frequency of the motion data, synchronized in time with the analog data, was 100 Hz.

**Experimental Conditions**

Subjects stood quietly on a force platform (OR6-5-2000, Advanced Mechanical Technology) that was flush mounted with the ground. Subjects selected their initial foot position, and this position was kept constant throughout the duration of the test by tracing the initial foot position on the force platform. Subjects stood with their arms by their sides, facing forward with their eyes open, and fixated on a target 5 m in front at eye level.

**Experiment 1** commenced with an initial 90-s quiet standing period. From this quiet standing period, the mean baseline COP position in the A-P direction was calculated by using the force and moment signals from the force platform (sampling rate of 1 kHz using CED Power 1401 and Spike2 software, Cambridge Electronic Design). The COP position and direction parameters for two experimental conditions were then determined as either 1) COP moving in the positive direction (i.e., swaying forward) at the mean baseline COP position; and 2) COP moving in the negative direction (i.e., swaying backward) at the mean COP baseline position.

Throughout the experiment, the position and direction of the COP in the A-P direction were monitored online such that, when the COP moved through the mean position in the desired direction, as determined randomly by the experimenter, an electrical stimulus to the posterior tibial nerve was applied via an outgoing signal from the computer. Each stimulus, delivered from a constant-current stimulator (DS7A, Digitimer), was 1 ms in duration, and its intensity was gradually increased until the maximal M-wave response (Mmax) was observed. Interstimulus duration was no less than 15 s to minimize the effect of postactivation depression (4). Each experimental condition comprised an average of 29 (range of 22–42) stimulation intensities (trials) to generate an H-reflex recruitment curve.

For experiment 2, H-reflex recruitment curves from the Sol and MG were initially measured while the subject stood with his back against a wall to minimize the amount of postural sway and any resultant effects to the H-reflex amplitude. This setup, a prelude to the main protocol of experiment 2, ensured that an appropriate reflex response could be elicited in the subject, to determine the intensity at which the maximal H-reflex response (Hmax) is elicited during standing, and to determine the Mmax response of the Sol and MG.

Once the preliminary data were collected, the main protocol of experiment 2 commenced. Subjects performed a 90-s quiet-standing trial, without wall support, to determine the mean and SD of the COP position and velocity in the A-P direction. From this, the COP position and direction parameters for the four experimental conditions of experiment 2 were determined: COP at the mean + 1.6 SD position and moving in the positive (i.e., forward) direction (condition A); COP at the mean + 1.6 SD position and moving in the positive direction (condition B); COP at the mean + 1.6 SD position and moving in the negative (i.e., backward) direction (condition C); and COP at the mean – 1.6 SD position and moving in the negative direction (condition D).

The position and velocity of the COP in the A-P direction were monitored online such that, when the two COP parameters satisfied the criteria for the particular experimental condition, an electrical stimulus was applied to the posterior tibial nerve. To allow for some differentiation between direction conditions, a positive or negative direction was deemed to occur if the velocity of the COP was no less than ±5 mm/s. The intensity of each stimulus was set to elicit a reflex response that was ~90% of Hmax, as determined from the H-reflex recruitment curve data obtained while subjects stood against a wall. Using such an intensity results in a large M-wave amplitude without the H-reflex being on the descending part of the recruitment curve. Using such an intensity results in a large M-wave amplitude without the H-reflex being on the descending part of the recruitment curve (9, 22). Trials in which the movement of the COM did not conform to the desired position and direction occurred independently of each other. The COP position and direction were then determined by using the force and moment signals from the force platform (sampling rate of 1 kHz using CED Power 1401 and Spike2 software, Cambridge Electronic Design). The COP position and direction parameters for two experimental conditions were then determined as either 1) COP moving in the positive direction (i.e., swaying forward) at the mean baseline COP position; and 2) COP moving in the negative direction (i.e., swaying backward) at the mean COP baseline position.

**Data Analysis**

The two experiments of this study involved the use of electrical stimuli at predetermined COP position and velocity thresholds. The COP signal is, however, a measure of the position of the ground reaction force rather than postural sway itself. Thus, to ensure that the responses to the electrical stimuli were also related to different sway positions and/or directions, the position and velocity of the center of mass (COM) were calculated offline using the zero point-to-point double integration technique (9, 22). Trials in which the movement of the COM did not conform to the desired position and direction parameters for each condition were omitted from analysis. Data from one subject of experiment 2 were subsequently removed from statis-
tical analyses due to the absence of trials from one experimental condition.

For each trial of experiments 1 and 2, the bEMG amplitude of the TA, Sol, and MG were calculated as the root mean square of the 50 ms before the delivery of each electrical stimulus. The peak-to-peak amplitude of the H-reflex and M-wave from the Sol and MG were determined from the electrodes placed in the belly-tendon configuration. For experiment 1, the maximum peak-to-peak amplitude of the M-wave (M\text{max}) was identified from the Sol and MG recruitment curves obtained for each experimental condition. The M\text{max} amplitude, normalized to each condition’s M\text{max}, was determined as the average of the three largest H-reflex amplitudes for each condition.

For experiment 2, the H-reflex and M-wave amplitudes from each stimulation were normalized to the amplitude of M\text{max} obtained during the supported standing condition. M\text{max} was assumed to be of the same magnitude between all experimental conditions based on previous work, which found that the size of M\text{max} does not significantly differ between standing postures (19). The lack of change in M\text{max} amplitude between the two experimental conditions of experiment 1 of the present study also supports this rationale.

Statistical Analysis

For experiment 1, two-way repeated-measures ANOVAs with muscle (Sol vs. MG) and COP direction (negative vs. positive) as factors were conducted to analyze the H\text{max} and M\text{max} values. For analyzing the bEMG data, a third muscle condition (i.e., TA) was added to the repeated-measures ANOVA. For experiment 2, three-way repeated-measures ANOVAs with muscle (Sol vs. MG), COP position (mean ± 1.6 SD vs. mean ± 1.6 SD), and COP direction (negative vs. positive) as factors were conducted to compare the amplitudes of the H-reflex and M-wave between the different sway positions and directions. Three-way repeated-measures ANOVAs were also used to analyze the bEMG data, with a third condition (i.e., TA) added for the muscle factor.

Statistical analyses were performed using commercially available software (SPSS). Significance for all statistical tests was set at \( P \leq 0.05 \), and trends were considered at \( 0.05 < P \leq 0.10 \).

RESULTS

Experiment 1

COP and COM at the time of stimulus. The COP velocity was different between the negative (backward) and positive (forward) COP direction conditions (−9.1 ± 1.5 vs. 10.7 ± 2.1 mm/s). Similarly, COM velocity was different between COP direction conditions (−5.1 vs. 4.0 ± 0.7 mm/s), but smaller in magnitude than the COP velocity. No differences were observed in the position of the COP (<1 mm difference) and the COM (<1 mm difference) between the two COP direction conditions. Based on the similarities in the velocity and position of the COP and COM (also observed in experiment 2, see below), the COP direction and position conditions for the two experiments will be referred to as sway direction and position conditions, respectively.

Amplitude of the H-reflex and M-wave. H-reflex-to-M-wave recruitment curves from a representative subject are shown in Fig. 1. When the data were grouped across all subjects, there was a significant main effect of sway direction \([F(1,7) = 13.65; P = 0.008]\) for the H\text{max}-to-M\text{max} ratio. The ratio, when averaged between the Sol and MG, was 9.2 ± 3.1% greater during the positive compared with the negative direction condition. This difference was not accompanied by any changes to the M\text{max} amplitude \((P = 0.948)\).

bEMG activity. There was a significant muscle × direction interaction effect \([F(2,14) = 15.15; P < 0.001]\) for the level of bEMG. Post hoc analyses indicated that there was a 3.4 ± 0.2 and 13.1 ± 3.0 μV increase in the Sol \((P = 0.035)\) and MG \((P = 0.001)\) bEMG activity, respectively, during the positive compared with the negative sway direction condition. Furthermore, the bEMG TA tended to increase (0.3 ± 0.2 μV; \( P = 0.058\)) during the positive compared with the negative sway direction condition. Despite the statistical findings, the magnitude of bEMG change between sway conditions is small relative to the muscle’s maximal contraction capability.

Experiment 2

COP, COM, and body kinematics at the time of stimulus. As shown in Fig. 2, the position and velocity components of the A-P COP corresponded to the criteria set out for the four experimental conditions. The differences in the COP position...
and velocity parameters between experimental conditions were also accompanied by parallel changes to the linear and angular kinematics of the COM and ankle joint, respectively (Fig. 2). There were significant COM position \[ F(1,8) = 23.62; P = 0.001 \] and ankle position \[ F(1,6) = 4.86; P = 0.07 \] main effects between the sway position conditions. The COM was in a more anterior position, along with greater ankle dorsiflexion during the forward compared with the backward sway position condition. There was a significant COM velocity \[ F(1,8) = 43.21; P = 0.001 \] main effect, as well as a trend toward an ankle velocity main effect \[ F(1,6) = 4.86; P = 0.07 \] for sway direction. When swaying in the forward compared with the backward direction, the ankle was undergoing a greater rate of dorsiflexion, along with a forward direction movement of the COM. In contrast to the kinematics of the ankle joint and the COM, the angular kinematics of the knee joint were not different between the sway position and velocity conditions (\( P \) values ranged between 0.186 and 0.823). There was less than a 0.24° and a 0.03°/s difference in the knee angle and angular velocity, respectively, between any two experimental conditions.

Amplitude of the H-reflex and M-wave. Sway position and direction main effects from a representative subject and across all subjects are presented in Figs. 3 and 4, respectively. The figures illustrate several findings. First, there was a trend for a greater H-reflex amplitude during the forward compared with the backward sway position condition [mean difference of 8.9 ± 3.7%; \( F(1,8) = 4.19; P = 0.075 \); Figs. 3 and 4]. Second, the direction of sway significantly affected the size of the H-reflex, whereby larger H-reflexes occurred during trials with a positive compared with a negative sway direction [mean difference of 14.6 ± 6.2%; \( F(1,8) = 10.32; P = 0.012 \); Figs. 3 and 4]. The observed changes in the H-reflex amplitude between sway position and direction conditions were not a result of a change in stimulus intensity, because no differences were found in the amplitude of the M-wave between sway position (\( P = 0.758 \)) and direction (\( P = 0.486 \)) conditions.

bEMG activity. The level of background activity exhibited significant muscle × sway position \[ F(2,16) = 9.48; P = 0.002 \] and muscle × sway direction \[ F(2,16) = 11.57; P = 0.001 \] interaction effects (Table 1). Post hoc analyses indicated that, for the Sol, the magnitude of the bEMG tended to be greater (\( P = 0.061 \)) when subjects were in a more forward compared with a backward sway position, but was not different between sway direction conditions (\( P = 0.373 \)). For the MG, bEMG was different between sway position (\( P < 0.001 \)) and direction (\( P = 0.005 \)) conditions. Not only was the level of MG bEMG activity larger when subjects were positioned in a more forward (mean + 1.6 SD) compared with a backward (mean − 1.6 SD) position, the level of activity was also greater when the swaying was in a positive compared with a negative direction. The bEMG for the TA was not different between any of the experimental conditions (\( P = 0.505 \) for position effect, \( P = 0.350 \) for direction effect).

Fig. 2. The mean ± SD of the linear or angular position (left) and velocity (right) of the intended center of pressure (COP), actual COP, center of mass (COM), and ankle joint at the time of stimulus. A–D along the horizontal axis represent the four different experimental conditions: the COP at the mean − 1.6 SD position and moving in the positive (i.e., forward) direction (A), the COP at the mean + 1.6 SD position and moving in the positive (i.e., forward) direction (A), the COP at the mean + 1.6 SD position and moving in the positive direction (B), the COP at the mean + 1.6 SD position and moving in the negative direction (C), and the COP at the mean − 1.6 SD position and moving in the negative direction (D). The position of the COM is relative to the center of the force platform. Positive angular values indicate dorsiflexion.
DISCUSSION

The purpose of this study was to determine whether the direction and/or position of postural sway influence the efficacy of the Ia pathway during quiet standing. Based on the results of previous studies that have investigated the modulation of the triceps surae H-reflex under various static and dynamic conditions, it was hypothesized that both sway parameters would affect the efficacy of the Ia pathway. The results of this study support this hypothesis, as the amplitude of the triceps surae H-reflex was influenced by the direction and, to some extent, the position ($P = 0.075$) of the subject’s postural sway. The presence of a direction- and, to a lesser extent, a position-dependent modulation on the efficacy of the Ia pathway may explain the differences found between the results of this study and a previous study examining changes to the triceps surae during standing (19). In the present study, the independent effect of sway direction resulted in a 9.2–14.6% difference in the H-reflex amplitude, whereas sway position alone resulted in an 8.9% change. The magnitude of these changes is slightly less than the 12–23% difference that was previously reported (19). This may be explained by the fact that the experimental conditions examined in the previous study differed in terms of both sway position and direction. Thus the between-study differences highlight the importance of considering the independent effects of both sway direction and position on alterations in spinal excitability.

In both experiments 1 and 2, the direction of sway had a significant effect on the efficacy of the Ia pathway. Regardless of sway position, an increased efficacy of the Ia pathway, as reflected by the larger amplitude of the H-reflex, occurred in the muscles of the triceps surae when the body was swaying in a positive (forward) compared with a negative (backward) direction. It is most probable that this direction-dependent modulation of the spinal pathway occurred as a result of an
altered level of presynaptic inhibition acting on the Ia afferent terminals and not through other neural mechanisms. For example, the lack of difference observed in the level of TA bEMG activity between the sway conditions of experiment 2 suggests that the amount of reciprocal inhibition was unlikely to have been altered between experimental conditions. Furthermore, the tendency for an increase in the TA bEMG activity during the forward direction compared with the backward direction of experiment 1 would have only served to reduce the size of the triceps surae H-reflex and, therefore, cannot explain the observed increase in the Ia efficacy when swaying in the forward direction compared with the backward direction. The effect of an altered level of motoneuron excitability between conditions is likely to be minimal in this study. Although statistically significant changes in the level of the Sol and MG bEMG activity were observed between experimental conditions, a previous study has shown that the absolute magnitude of bEMG change that occurs during standing is too small to affect the size of the H-reflex when H-reflexes are elicited with subjects in a standing posture (19).

In some regards, the 8.9–14.6% change in the H-reflex observed between experimental conditions may be considered small. However, these differences are similar in magnitude to that found during larger and faster ankle movements. Nordlund et al. (14) examined the modulation of the H-reflex during ankle joint rotations against an ankle torque motor using a 30° ankle range of motion and an ankle angular velocity of ±5°/s while subjects lay prone on a bench. Despite the use of a 30-fold increase in ankle range of motion and the fivefold increase in ankle velocity compared with what occurs during standing, Nordlund et al. (14) also observed a difference of ~9% in the Sol H_{max}-to-M_{max} ratio between contraction types. Therefore, the finding of a sway direction, and a possible position-dependent modulation of the spinal Ia pathway, as reflected by triceps surae H-reflex, is likely of great significance in the control of upright stance.

The results, averaged over many trials within each subject, exhibited significant effects with regard to the direction of postural sway. However, it is possible that the observed changes in spinal excitability are indirectly affected by additional events associated with the various phases of the sway cycle. One such possibility is the effect of muscle length. It has previously been shown that, when a subject is in a sitting or lying posture and his ankle movement is experimentally controlled via a torque motor, a greater amount of presynaptic inhibition, as reflected by a smaller H-reflex, is found during muscle lengthening (i.e., dorsiflexion) compared with shortening (i.e., plantar flexion) actions (14–16). During situations involving a passive change in muscle length, the decrease in the H-reflex amplitude during lengthening compared with shortening actions has been attributed to the increase in afferent firing rates, leading to a greater amount of homosynaptic postactivation depression (15, 21). Homosynaptic postactivation depression is, however, not believed to play a major role in regulating presynaptic inhibition during tasks requiring actively contracting muscles (18). The muscle action-dependent changes to the H-reflex amplitude are, therefore, more likely to be influenced by presynaptic inhibition induced by primary afferent depolarization.

If a similar relationship between contraction type and Ia efficacy is to occur during quiet standing, a smaller H-reflex would be expected during events in the sway cycle when the muscle is lengthening. Although this cannot be determined conclusively from this study, as muscle length measurements were not collected, it appears that the modulation of the triceps surae H-reflex is occurring in accordance with the recent findings of a “paradoxical” change in muscle length in the triceps surae during standing. Using ultrasound imaging to record changes in muscle fascicle length, subjects with an intrinsic ankle stiffness less than the load stiffness exhibited a decrease in muscle fascicle length (i.e., shortening) of the Sol and MG during forward sway (10, 11). The small changes in fascicle length were also strongly related to the fluctuations in ankle torque (10). In the present study, the H-reflexes were grouped based on the movements of the COM (i.e., body sway), but were triggered at specific COP positions and COP directions. Given that the intrinsic ankle stiffness is normally less than the load stiffness, this study’s results put forth the possibility that, during the forward sway direction condition, the Sol and MG were shortening at the time of the electrical stimulus. Consequently, a larger H-reflex was observed. In contrast, when the muscles comprising the triceps surae were most likely to be lengthening, such as during instances with a backward sway direction, the H-reflex was found to be reduced.

The mechanisms by which muscle actions of the triceps surae act onto the Ia pathway are not known. In one study involving passive ankle rotations, modulation of the H-reflex was found to occur <60 ms after the initiation of the movement (15). Such an early onset in the change of Ia efficacy would strongly suggest that the muscle length-specific modulation to the Ia pathway is mediated via spinal level mechanisms. The size of the H-reflex, however, can also be affected by supraspinal processes, particularly during tasks involving actively contracting muscles. Using transcranial magnetic stimulation, Sekiguchi et al. (17) suggested that there was an increase in the inhibitory component from the corticospinal volley during controlled lengthening compared with shortening contractions. Specifically, the increase in inhibition from supraspinal centers would act to reduce the H-reflex amplitude during lengthening contractions. In the case of quiet standing, which requires the contraction of the triceps surae muscles,
changes to the H-reflex amplitude were found to correspond with the expected muscle actions (i.e., shortening vs. lengthening) within the various phases of postural sway. These associations, therefore, raise the possibility of a corticospinal contribution to the control of upright stance. The corticospinal contribution is, however, unlikely to be monosynaptic, based on the findings of weak or absent short-latency facilitation of the ankle plantar flexors by transcranial magnetic stimulation in weak isometric contractions (1) and the absence of short-latency synchronization of Sol motor units during standing (13).

In conclusion, the present study found a significant sway direction-dependent and a trend toward a position-dependent modulation of the triceps surae H-reflex during the postural sway of quiet standing. The two sway parameters have independent effects on the triceps surae Ia pathway. It is possible, but cannot be determined from the current protocol, that the changes in reflex excitability may be related to other neuromuscular events, such as the length changes to the Sol and MG muscles, relating to standing sway.

GRANTS

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REFERENCES

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