Adapting Locomotion to Different Surface Compliances: Neuromuscular Responses and Changes in Movement Dynamics

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Marigold, Daniel S. and Aftab E. Patla. Adapting locomotion to different surface compliances: neuromuscular responses and changes in movement dynamics. J Neurophysiol 94: 1733–1750, 2005. First published May 11, 2005; doi:10.1152/jn.00019.2005. Knowledge of how the nervous system deals with surfaces with different physical properties such as compliance that challenge balance during locomotion is of importance as we are constantly faced with these situations every day. The purpose of this study was to examine the control of center of mass (COM) and lower limb dynamics and recovery response modulation of muscle activity during locomotion across an unexpected compliant surface and in particular, scaling behavior across different levels of compliance. Eight young adults walked along a walkway and stepped on an unexpected compliant surface in the middle of the travel path. There were three different levels of surface compliance, and participants experienced either no compliant surface or one of the three compliant surfaces during each trial that were presented in a blocked or random fashion. Whole body kinematics were collected along with surface electromyography (EMG) of selected bilateral lower limb and trunk muscles. The recovery response to the first compliant-surface trial demonstrated muscle onset latencies between 97 and 175 ms, and activity was modulated while on the compliant surface. Vertical COM trajectory was not preserved after contact with the compliant surface: peak vertical COM, while on the compliant surface was lower than when on stable ground. Perturbed-limb knee flexion after toe-off increased with increased surface compliance, which enabled toe clearance with the ground to be similar to control trials. The results suggest that stepping off of a compliant surface is actively modulated by the CNS and is geared toward maintaining dynamic stability.

INTRODUCTION

Fundamental to locomotion across unstable terrain is maintaining dynamic stability. Dynamic stability entails controlling the body center of mass (COM) within a moving base of support (Marigold and Patla 2002). Any movement that directly (e.g., trunk pitch or roll motion, stance limb knee flexion) or indirectly (e.g., an unexpected trip or slip) affects COM movement can adversely affect stability. Understanding how the CNS deals with different surfaces that challenge balance during locomotion is of importance as we are constantly faced with such situations in everyday life. Changes in surface compliance (or stiffness) disturb normal movement dynamics, and strategies to accommodate such disturbances must be readily available. Knowledge of the strategies utilized may become even more important when considering that stability on irregular terrain may be compromised in older adults at risk for falls (Menz et al. 2003a).

Individuals during running and hopping strive to maintain vertical COM motions across damped/compliant surfaces: changes in lower limb dynamics appear to allow them to accommodate to such surfaces (Farley et al. 1998; Ferris and Farley 1997; Ferris et al. 1998, 1999; Moritz and Farley 2003). For example, runners are able to maintain their vertical COM across a range of compliant surfaces by altering their leg stiffness (Ferris et al. 1998; Kerdok et al. 2002). Individuals hopping on a damped/compliant surface maintain similar peak upward COM displacement despite greater surface depression as surface damping increases and surface stiffness decreases (Moritz and Farley 2003). This is the result of greater work done by the legs (i.e., muscles perform 24-fold more net work) to replace the energy lost by the damped surface and ensure the upward COM displacement is constant (Moritz and Farley 2003; Moritz et al. 2004).

The tasks of hopping and running involve primary or dominant changes in the vertical COM movement during an aerial phase component. Any alterations in vertical COM movement would directly affect the duration of the free flight phase and hence the movement itself. Therefore it is understandable that the CNS adopts strategies to minimize changes in vertical COM movement. During walking, the primary goal is not simply to maintain vertical motion but rather a combination of vertical and horizontal movement of the COM. Furthermore, there is a time when both lower limbs are in contact with the ground (i.e., double support phase) in a staggered posture, which provides a larger base of support and greater range of recovery strategies if necessary. How the COM is controlled after an abrupt change in surface compliance during walking is largely unknown. A recent study of stepping onto an unexpected ankle inverting platform demonstrated that walking on a treadmill has shown short-latency (∼40 ms) and longer-latency (after 100 ms) responses in a range of muscles (Nieuwenhuijzen et al. 2002).

Phase-dependent modulation of reflexive responses during locomotion has been demonstrated with electrical stimulation (Belanger and Patla 1987; Duyssens et al. 1990, 1992; Yang and Stein 1990; Zehr et al. 1997) and with perturbations including tripping (Eng et al. 1994; Schillings et al. 1999, 2000) and slipping (Tang and Woollacott 1999). This strategy of modulating muscle activity depending on the phase of the gait cycle serves, in part, to maintain dynamic stability in the face of an unexpected destabilizing force. While our paradigm does not manipulate the timing of the gait perturbation, the nature of the compliant surface provides a perturbation throughout the
stance phase, and thus response characteristics must be adjusted continually. We expect a similar phase-dependent modulation of muscle activity to occur in response to stepping on a compliant surface; we refer to this as recovery response modulation, which will depend on the level of surface compliance.

The goal of this study was to examine the control of COM and lower limb dynamics and recovery response modulation of muscle activity during locomotion across an unexpected compliant surface and in particular, scaling behavior across different levels of compliance. Previous studies on gait perturbations have shown that responses differ between randomly and consecutively (i.e., blocked) presented trials (Marigold and Patla 2002; Marigold et al. 2003); thus we choose to present compliant-surface trials in blocked and random fashion to see if differences occur for this type of gait perturbation. Furthermore, we were particularly interested in the first exposure to a compliant surface as the first response to a gait perturbation is different from subsequent responses (Marigold and Patla 2002; Marigold et al. 2003).

METHODS

Participants

Eight University of Waterloo students [3 male and 5 female; age: 24.5 ± 1.9 yr; height: 172.6 ± 9.8 cm; mass: 66.5 ± 11.3 kg (means ± SD); all right-leg dominant determined from a questionnaire] volunteered for this study. Participants did not have any neurological, muscular, or joint disorder that could affect their performance and/or behavior in this study. The study was approved by the Office of Research Ethics at the University of Waterloo and informed written consent was received from all participants.

Compliant-surface apparatus

The compliant-surface apparatus (0.51 m long, 0.46 m wide, and 0.10 m high) consisted of one of three pieces of different density foam or a solid wooden block (each 0.066 m high) sandwiched between a thin (0.017 m) steel base with guide wires (0.01 m diam) projecting vertically from the four corners of the surface and a thin (0.017 m) piece of wood with linear bearings mounted in the four corners to receive the guide wires (see Fig. 1). When the solid wood block was placed in the middle, the surface acted as stable, solid ground (i.e., the control trials). When one of the pieces of foam was placed in the middle of the apparatus, the top wooden board and foam were depressed when loaded.

Loads ranging from 0 to 100 kg were rested on the compliant-surface apparatus for each piece of foam to determine force-displacement curves for each compliant surface (see Fig. 1). One Optotrak camera (Northern Digital, Waterloo, Ontario, Canada) recorded three infrared emitting diodes (IREDs) placed on the surface of the compliant-surface apparatus. The loads were placed in the center of the compliant-surface apparatus, which was on a force plate. The average displacement from the three IREDs was used to determine the displacement caused by the load. The vertical force (minus the 0 load value) from the force plate was used as the force value for the curves. A fourth-order polynomial regression was performed on these curves and $R^2$ values were 0.98, 0.98, and 0.99 for the most-, medium-, and least-compliant-surface conditions, respectively. The surface stiffness for each piece of foam was determined by resting a 100-kg mass on the top and recording the amount of depression. The stiffness of each surface was 25.9, 32.9, and 65.7 kN/m and subsequently will be referred to as most compliant, medium compliant, and least compliant, respectively.

The linear bearings and guide wires mounted in the apparatus acted to prevent the top wooden board from sliding in any direction. However, when the surface was loaded, it was free to tilt (see Fig. 1), and this rotation depended on how the participant stepped on the surface. The maximum downward tilt possible in the frontal plane for all compliant surfaces was 5.5°. In the sagittal plane, the maximum downward tilt possible for all compliant surfaces was 6.5°.

Protocol

Participants walked along an 8 m long, 1.2 m wide, and 0.1 m elevated wooden walkway with the compliant-surface apparatus mounted on a force plate (AMTI, Arlington, VA) and flush with the walkway and positioned midway along the path. A second force plate was positioned after the compliant surface with a solid wooden block mounted on top and flush with the walkway. Participants walked along the walkway such that they stepped on the compliant-surface apparatus with their left foot (i.e., perturbed limb) and the second force plate with their right foot (i.e., unperturbed limb). Participants were given practice trials (when the compliant-surface apparatus was stable and did not depress) to adjust their starting position so as to ensure they stepped on each of the plates. Although the top wooden board of the compliant-surface apparatus was similar to the rest of the walkway, the linear bearings mounted in the four corners were visible. Participants were not told when the compliant surface could depress (i.e., foam placed inside rather than a solid wooden block) or which type of foam was present but were aware that the surface could depress when stepped on. Trials were presented in two different fashions: blocked and random. Each participant experienced the blocked trials first followed by the random trials. For the blocked trials, the first 10 trials acted as controls (baseline controls) in that the compliant-surface apparatus provided a stable surface (i.e., a solid wooden block instead of a piece of foam). Subsequently, participants experienced five consecutive trials of the most-compliant surface followed by five consecutive trials of the medium-compliant surface and five consecutive trials of the least-compliant surface. This sequence of 15 compliant-surface trials was then repeated such that the total number of trials (control and compliant) for blocked trials was 40. For the random trials, the first 10 trials (presented after the blocked trials) acted as control trials (baseline controls). Subsequently, participants experienced five trials of each compliant surface and five control trials (controls) randomly presented for a total of 30 trials. Thus there were four compliant-surface conditions for the blocked trials (i.e., baseline controls, most compliant, medium compliant, and least compliant) and five compliant-surface conditions for the random trials (i.e., baseline controls, controls, most compliant, medium compliant, and least compliant).

Three Optotrak cameras were used to collect whole body kinematics (sampling frequency of 60 Hz and sampling duration of 6 s) and a video camera (Panasonic Canada, Mississauga, Ontario, Canada) recorded the walking trials from the left side of the participant’s body for qualitative observations. A total of 21 IREDs were placed bilaterally on the heel, fifth metatarsal, ankle, knee, greater trochanter, iliac crest, acromion, elbow, wrist, ear, and the xyphoid process of each participant.

Surface electromyography (EMG) (Bortec, Calgary, Alberta, Canada) were collected from bilateral tibialis anterior (TA), the medial head of gastrocnemius (MG), soleus (SOL), rectus femoris (RF), biceps femoris (BF), and erector spinae (ES) using self-adhesive electrodes (Ag/AgCl) (Kendall Medi-Trace, Chicopee, MA) placed
~2 cm apart and longitudinally on the belly of the muscle. The signals were band-pass filtered (10–1,000 Hz) and sampled at 1,200 Hz for 6 s along with force plate data. The common mode rejection of the EMG system was 115 db and the input impedance was 10 GΩ.

Data analysis

Force plate data were low-pass filtered at 50 Hz (0 lag, 2nd-order, Butterworth algorithm) and used to determine foot contacts and toe-offs on the compliant surface and subsequent force plate. A vertical force that exceeded a 15 N threshold represented foot contact, and toe-off was defined as when the vertical force fell below this same threshold. For foot contacts and toe-offs when not stepping on the force plates, the ankle markers were used to estimate these events. Subsequently, the total time on the compliant surface, single support phase on the compliant surface, and the double support phase before (i.e., double support phase 1: when the perturbed limb was in contact with the compliant surface and the unperturbed limb was in contact with the ground behind) and after (i.e., double support phase 2: when the perturbed limb was in contact with the compliant surface and the unperturbed limb was in contact with the ground ahead) the compliant surface were determined. All profiles were aligned to the initial foot contact on the compliant surface except for the joint powers, which were aligned to toe-off from the compliant surface.

A custom-written program in MATLAB (Mathworks, Natick, MA) low-pass filtered the position data for all IRED markers at 6 Hz (using a 2nd-order, dual-pass, Butterworth algorithm) and processed all kinetic and kinematic data. A 12-linked segment model was used for calculating the total body COM, where anthropometric data were from Winter (2005), and segment definitions were as described in Marigold and Patla (2002) with the addition of bilateral arm and forearm segments. Perturbed-limb knee angle, trunk pitch and roll angle, and toe clearance during the step off the compliant surface were also determined. Full knee extension was 180° with values less than this angle representing knee flexion. Trunk pitch was calculated as the angle between a vertical line (orthogonal to the plane of progression) and a line joining the bisection of the iliac crest IREDs and bisection of the acromion IREDs in the sagittal plane. Trunk roll was calculated as the angle between a vertical line (orthogonal to the plane of progression) and a line joining the bisection of the iliac crest IREDs and bisection of the acromion IREDs in the frontal plane. Toe clearance was defined as the vertical distance from the ground to the ankle marker on the perturbed limb at the point where this marker reached the edge of the compliant surface and met the stable walkway (i.e., where the depression of the compliant surface creates an obstacle with the remainder of the walkway) during early swing phase of this limb.

For the vertical COM and perturbed-limb knee-angle profiles (see Fig. 2), the first minimum values after foot contact on the compliant surface (vertical COM minimum 1 and perturbed-limb knee-angle minimum 1, respectively) were determined along with the peak values (peak vertical COM and peak perturbed-limb knee angle, respectively) and the second minimum values (vertical COM minimum 2 and perturbed-limb knee-angle minimum 2, respectively). These values were determined on a trial-to-trial basis and then averaged for each set of compliant-surface and control trials. Additionally, the vertical COM profiles for the control trials were ensemble averaged and the time to deviate from 2 SD of the ensemble averaged profiles was determined for each compliant-surface trial.

Using a standard inverse dynamic approach (Winter 2005), ankle, knee, and hip joint moments were calculated for the perturbed limb following toe-off from the compliant surface (i.e., swing phase). Subsequently, ankle, knee, and hip joint power was determined from the product of the joint moment and joint angular velocity (Winter 2005). The area under the joint power curves (i.e., joint work) for the first half of the swing phase following toe-off from the compliant surface was determined using the trapezoidal integration technique for each trial and subsequently averaged for each set of compliant-surface and control trials.

We were interested in three different aspects of the response to encountering a compliant surface in the pathway during locomotion including: step-on phase, overall stability during the single support phase on the compliant surface, and step-off phase. The step on phase represents the initial and subsequent loading of the compliant surface and is characterized by the vertical COM and perturbed-limb knee-angle minimum 1 as well as the peak vertical COM and peak perturbed-limb knee-angle measures. The vertical COM time to deviate from baseline values is also used to categorize the step on phase. Overall stability during the single support phase on the compliant surface was assessed by the trunk pitch and roll angle root-mean-square (RMS) values, which were determined on a trial-by-trial basis and subsequently averaged for each set of compliant-surface and control trials. Finally, the step off phase represented the unloading phase off the compliant surface and the early swing phase of the perturbed limb. The vertical COM, perturbed-limb knee-angle mini-
maximum 2, toe clearance, and ankle, knee, and hip joint power measures were analyzed to characterize the response during this phase.

EMG was full-wave rectified and low-pass filtered at 10 Hz (0 lag, 2nd-order, Butterworth algorithm). All EMG data processing used a custom-written program. Muscle response profiles for each compliant-surface trial were determined by subtracting the ensemble averaged profile of the control trials (initial 10 control trials for the blocked trial protocol and 10 control trials prior to random trial protocol) from the compliant-surface trial. The presence of a recovery muscle response burst (i.e., muscle onset latency) was defined as an increase in muscle activity that exceeded 2 SD (for an excitatory burst) or fell below 2 SD (for an inhibitory burst) of the mean muscle activity prior to foot contact on the compliant surface for ≥30 ms and was determined by a combination of visual inspection and computer algorithm via an interactive program (Marigold and Patla 2002). Muscles for the onset latency analysis were only used when greater than half the participants activated the muscle for recovery. The onset latencies for compliant-surface trials after the initial one were not determined because they were too difficult to isolate due to a large variability of muscle activity prior to contact with the compliant-surface apparatus and/or reduced recovery response magnitude that masked the timing of the muscle activity after contact with the surface.

The average time on the compliant surface was determined for each set of compliant-surface trials (1st compliant-surface trial separate) and divided into four equal bins (150-ms duration) such that it characterized four different phases. The first two phases characterized the early response on the compliant surface, whereas the second two phases characterized the late response and preparation for toe-off from the compliant surface. This analysis allowed us to characterize the recovery response modulation. The mean amplitude of the muscle responses for each bin was then determined. Subsequently, the mean amplitude was normalized with respect to the mean amplitude of the corresponding bin of the control trials.

Statistical analysis

Because each compliant surface set of trials was presented twice in the blocked trial protocol, it is possible that the participants changed their response in the second block for each surface. None of the outcome measures demonstrated a block effect (P < 0.05) except for the vertical COM minimum 2 (P = 0.021), knee-joint work (P = 0.043), and perturbed-limb SOL amplitude (P = 0.013). The difference for the vertical COM minimum 2 was only 0.2% (or 0.19 cm), and we considered this negligible so both blocks were pooled for further analysis. Because the differences between blocks were too large for the knee-joint work and perturbed-limb SOL amplitude measures, only the first block was used in subsequent analyses, and for the remainder of the outcome measures, blocks of each compliant-surface condition were pooled for further analysis.

The alpha level was 0.05 for all statistical analyses. A one-way (condition) repeated-measures ANOVA was performed for each kinematic and kinetic measure. When significant, Bonferroni posthoc comparisons were performed. Because the first exposure to an unexpected compliant surface represents the true reactive response in that no prior experience or knowledge about the surface is available (Marigold and Patla 2002), paired t-test compared the first compliant-surface trial (i.e., 1st exposure to the most-compliant condition) in the blocked trials with the baseline control trials for each measure.

A one-way (muscle) ANOVA examined the differences in muscle onset latencies for the first compliant-surface trial. Furthermore, a one-way (phase) ANOVA compared the differences in muscle amplitude across the four phases (on the compliant surface) for the first compliant-surface trial for each muscle. For the blocked and random trials, a two-way (condition and phase) repeated-measures ANOVA compared the mean muscle amplitude for each muscle across compliant-surface conditions and the four phases on the compliant surface. The EMG data were ranked transformed prior to these analyses because the data were not normally distributed. In addition, for muscle amplitude analyses only the perturbed-limb muscles were included because we were particularly interested in how this limb was controlled (note the kinematic and kinetic measures were only from this limb as well).

RESULTS

All participants were able to complete the task: no falls occurred during the compliant-surface trials. Each compliance surface allowed a certain amount of depression to occur. The ankle marker vertical position provides a good indication of the amount of depression as it is close to the ground and the few degrees of freedom available to the CNS at this level ensure minimal compensation at this point in the linked segments of the body. Ankle marker peak depression values (i.e., difference from controls trials) for the most-compliant, medium-compliant, and least-compliant surfaces in the blocked trials were 2.02 ± 0.54, 1.54 ± 0.55, 1.39 ± 0.67 cm, respectively. Ankle marker peak depression values for the most-compliant, medium-compliant, and least-compliant surfaces in the random trials were 2.10 ± 0.59, 1.59 ± 0.64, 1.28 ± 0.62 cm, respectively. Figure 3 shows a sample vertical ankle marker trajectory.

The first exposure to the unexpected compliant surface represents the true reactive response in that no prior experience or knowledge about the surface is available (Marigold and Patla 2002) as participants had not yet experienced the compliant surface and were not aware that on this trial the surface could be depressed. We describe the response to this trial first for all measures followed by the responses seen in the blocked and random trials.

The total time on the compliant surface was longer by ∼55 ms in the first exposure compared with controls (Table 1). This was neither due to changes in the duration of double support phase 1 nor changes in single support duration (Table 1). Rather exposure to the compliant surface for the first time led to an ∼35-ms longer duration of double support phase 2 (i.e., when the perturbed limb was in contact with the compliant surface and the unperturbed limb was in contact with the ground ahead), which may explain the longer total time on the compliant surface (Table 1).

![Figure 3](http://jn.physiology.org/DownloadedFrom/10.1152/jn.00006.2005)
For the blocked $[F(3,24) = 17.90, P < 0.0001]$ and random $[F(4,32) = 19.62, P < 0.0001]$ protocols, the ANOVAs demonstrated that the total time on the compliant surface was significantly different among the surface conditions (Table 1). Post hoc tests showed that the total time on the compliant surface was longer for only the most-compliant surface compared with control trials. This same pattern was also true for the duration of double support phase 2 for both the blocked $[F(3,24) = 21.96, P < 0.0001]$ and random $[F(4,32) = 17.39, P < 0.0001]$ protocols (Table 1). While the ANOVA suggested a significant difference in the duration of double support phase 1 for the random trials $[F(4,32) = 2.95, P = 0.038]$, Bonferroni post hoc tests failed to show differences between the conditions. There were no differences in the duration of double support phase 1 $[F(3,24) = 0.44, P = 0.729]$ and single support phase $[F(3,24) = 0.44, P = 0.729]$ for the blocked trials and no differences in the duration of single support phase $[F(4,32) = 1.58, P = 0.206]$ for the random trials (Table 1).

Muscle responses after the first compliant-surface trial are clearly different as demonstrated in Fig. 7 showing the subtracted EMG traces for the same individual as in Figs. 4 and 5. Subsequent compliant-surface trials show attenuated responses in almost all muscles (which make determining muscle onset latencies difficult after the 1st compliant-surface trial). In addition, muscle activity is even suppressed after the first compliant-surface trial as evident in the perturbed-limb RF for this individual.

The ANOVAs for the first compliant-surface trial showed that muscle amplitude of the perturbed-limb TA $[F(3,18) = 7.84, P = 0.002]$, MG $[F(3,18) = 3.37, P = 0.042]$, RF $[F(3,18) = 6.84, P = 0.003]$, BF $[F(3,18) = 4.40, P = 0.017]$, and ES $[F(3,18) = 7.28, P = 0.002]$ was different depending on the phase on the compliant surface. Amplitude was greatest in the second phase for the TA, MG, and ES, the third phase for the RF, and the fourth phase for the BF (see Fig. 8). In contrast, there were no differences in muscle amplitude for the perturbed-limb SOL $[F(3,18) = 1.65, P = 0.213]$. The mean muscle amplitude values for the four phases and three compliant-surface conditions are also summarized in Fig. 8. All muscles on the perturbed limb demonstrated a condition $\times$ phase interaction for the blocked trials [TA: $F(6,42) = 3.73, P = 0.005]$; SOL: $F(6,42) = 2.90, P = 0.019$; MG: $F(6,42) = 3.32, P = 0.009$; BF: $F(6,42) = 4.30, P = 0.002$; ES: $F(6,42) = 3.61, P = 0.006$] except the RF $[F(6,42) = 1.37, P = 0.251]$. In contrast, only the perturbed-limb TA $[F(6,42) = 2.96, P = 0.017]$ and MG $[F(6,41) = 5.33, P = 0.004]$ showed an interaction for the random trials [no significant differences for SOL: $F(6,42) = 1.92, P = 0.100$; RF: $F(6,42) = 1.78, P = 0.127$; BF: $F(6,42) = 1.62, P = 0.166$; ES: $F(6,42) = 2.08, P = 0.076$]. There were phase main effects for the perturbed-limb TA $[F(3,21) = 6.58, P = 0.003]$ and ES $[F(3,21) = 4.58, P = 0.013]$ in the random trials and the BF $[F(3,21) = 6.06, P = 0.004]$ for the blocked trials. In particular, muscle amplitude was less in phase 1 compared with the other phases for the TA in the random trials; similar between phase 1-3 and 2-4 for the ES in the random trials; and similar between phase 1-3 and 1, 2, and 4 for the BF in the blocked trials. In addition, there was a condition main effect for the perturbed-limb MG $[F(2,14) = 15.25, P = 0.0003]$ for the
FIG. 4. Typical full-wave rectified and filtered EMG responses of a control trial and the 1st compliant-surface trial for 1 participant. Perturbed-limb tibialis anterior (TA), soleus (SOL), medial head of gastrocnemius (MG), rectus femoris (RF), and erector spinae (ES) are shown along with the unperturbed-limb TA and ES. FC, foot contact on the compliant-surface apparatus.
FIG. 5. Typical muscle response profiles (i.e., ensemble averaged control trials from unperturbed walking subtracted out) for the 1st compliant-surface trial for one participant showing the perturbed-limb TA, SOL, MG, RF, and ES and unperturbed-limb TA and ES.
movement dynamics on a compliant surface: stepping onto the compliant surface

The arms were not used in the recovery response to any of the compliant-surface trials except for two participants who moved their arms up and outward in response to the first compliant-surface trial. The arm response in these two participants was similar to those observed in slipping studies (Marigold and Patla 2002; Marigold et al. 2003).

A stick figure representation of walking on the compliant surface is illustrated in Fig. 9. In this figure, the response to a control trial and the first compliant-surface trial are shown. One noticeable difference between these two trials is the trunk pitch angle: the trunk is pitched more forward in response to the first compliant-surface trial. In addition, the perturbed-limb knee angle is more flexed as this limb begins swing phase (i.e., after toe-off from the compliant surface).

In response to compliant-surface trials (1st, blocked, and random trials), vertical COM and perturbed-limb knee-angle trajectories deviated from control trials. The time to deviate for these kinematic measures was, in large part, prior to the onset of noticeable muscle activity or too soon after to be affected (see Fig. 6). The vertical COM deviated from the control trials trajectory after ~109 ms and the perturbed-limb knee angle after ~198 ms for the first compliant-surface trial. In contrast, the vertical COM trajectories for the blocked trials deviated from the control trials between 71 and 85 ms after foot contact on the compliant-surface apparatus: no differences were found between compliant-surface conditions \( F(2,20) = 0.73, P = 0.501 \). Perturbed-limb knee angle deviated from control trials between 135 and 175 ms with no differences between compliant-surface conditions \( F(2,15) = 3.51, P = 0.063 \). For the random trials, the vertical COM deviated later in the trial between 116 and 147 ms after foot contact on the compliant-surface apparatus: no differences were found between compliant-surface conditions \( F(2,16) = 1.84, P = 0.195 \). Perturbed-limb knee angle deviated from control trials between 120 and 129 ms after foot contact on the compliant surface with no differences between compliant-surface conditions \( F(2,15) = 2.49, P = 0.163 \).

Figure 10 illustrates the differences among conditions for the step onto the compliant-surface apparatus measures for the first compliant-surface trial, blocked trials, and random trials. Although there was no difference in the vertical COM minimum 1 value between controls and the first compliant-surface trial, the peak vertical COM was ~1.3 cm less than controls. The profiles of the vertical COM and perturbed-limb knee-angle trajectories for the blocked trials are shown in Fig. 11. Responses appear to be scaled to the amount of surface compliance. This is also evident among the random trials (see Fig. 11). Results from the ANOVAs demonstrated that both the vertical COM minimum 1 \( F(3,24) = 17.85, P < 0.0001 \) and the peak vertical COM \( F(3,24) = 47.55, P < 0.0001 \) were different among the conditions for the blocked trials. This was also the case for the random trials [vertical COM minimum 1: \( F(4,32) = 3.52, P = 0.019 \); peak vertical COM: \( F(4,32) = 71.42, P < 0.0001 \)]. The vertical COM minimum 1 was lower among the compliant-surface conditions compared with the control trials for both blocked and random trials. Furthermore, the peak vertical COM decreased as compliance increased (Fig. 10).

The perturbed-limb knee angle was significantly more extended in response to the first compliant-surface trial in the initial loading phase (perturbed-limb knee-angle minimum 1) and subsequently more flexed than controls at its peak (peak perturbed-limb knee angle: see Fig. 10). The ANOVA showed no differences in perturbed-limb knee-angle minimum 1 \( F(3,24) = 2.67, P = 0.074 \) among the conditions for the blocked trials: this knee angle was ~162–163° for each condition. In contrast, the perturbed-limb knee-angle minimum 1 \( F(4,32) = 19.47, P < 0.0001 \) was different among the conditions for the random trials. In particular, the knee was flexed to a greater extent as compliance increased (Figs. 10 and 11). The peak perturbed-limb knee angle remained the same...
FIG. 7. Typical muscle response profiles (i.e., ensemble averaged control trials from unperturbed walking subtracted out) for the 1st 3 compliant-surface trials for 1 participant showing the changes in response amplitude after the 1st exposure to the compliant surface. Muscle abbreviations are the same as in previous figures. FC, foot contact on the compliant surface apparatus.
FIG. 8. Muscle amplitude (normalized to appropriate control trials phase) for the perturbed-limb muscles for the 1st compliant-surface trial and the different levels of surface compliance for the blocked and random trials. The 4 phases correspond to equal bins (~150 ms) while the participant’s perturbed limb was in contact with the compliant-surface apparatus. The 4 phases are also shown graphically in Fig. 2. Muscle abbreviations are the same as in previous figures. Error bars are SD.
Among the conditions for both the blocked $[F(3,24) = 0.04, P = 0.99]$ and random $[F(4,32) = 0.96, P = 0.443]$ trials.

**Movement dynamics on a compliant surface: stepping off the compliant surface**

The most noticeable change when experiencing the first compliant-surface trial after a series of control trials was the $\sim 12^\circ$ increase in perturbed-limb knee flexion after toe-off on the compliant surface (perturbed-limb knee-angle minimum 2, Fig. 12). Accompanying this knee flexion was a lower vertical COM (vertical COM minimum 2), no change in toe clearance, greater power absorption at the ankle, and less power generation at the hip joint (Fig. 12). Interestingly, knee-joint work demonstrated no differences between the control trials and the first compliant-surface trial.

The differences among the compliant-surface conditions (blocked and random trials) for the step off the compliant-surface apparatus are also illustrated in Fig. 12. The ANOVAs demonstrated that the vertical COM around toe-off from the compliant surface (vertical COM minimum 2) was significantly different among conditions for both the blocked $[F(3,24) = 15.32, P < 0.0001]$ and random $[F(4,32) = 29.00, P < 0.0001]$ trials. More specifically, the vertical COM was lower in the most-compliant condition compared with the other compliant-surface conditions and controls.

As compliance increased, the perturbed-limb knee angle after toe-off (perturbed-limb knee-angle minimum 2) was flexed to a greater extent for both the blocked $[F(3,24) = 25.90, P < 0.0001]$ and random $[F(4,32) = 15.75, P < 0.0001]$ trials. In fact, the knee was flexed by nearly $8^\circ$ more in the most-compliant condition compared with the control conditions for both blocked and random trials (Figs. 11 and 12). The greater knee flexion may have been to preserve toe clearance (Fig. 12) during the step off the compliant surface. This was confirmed by analyzing toe clearance. There was no difference in toe clearance between compliant-surface conditions for both the blocked $[F(3,24) = 2.45, P = 0.092]$ and random trials $[F(4,32) = 1.99, P = 0.123]$.

Figures 12 and 13 demonstrate the effect of the compliant-surface conditions on ankle-, knee-, and hip-joint power. The ankle-joint work was different across the conditions for both the blocked $[F(3,21) = 4.30, P = 0.019]$ and random $[F(4,28) = 5.92, P = 0.002]$ trials. Ankle-joint work decreased as compliance increased. Hip-joint work was different across the conditions for both the blocked $[F(3,21) = 16.20, P < 0.0001]$ and random $[F(4,28) = 14.93, P < 0.0001]$ trials with work also decreasing as compliance increased. In contrast, although knee-joint work was different across the conditions for both the blocked $[F(3,21) = 7.22, P = 0.002]$ and random $[F(4,28) = 10.03, P < 0.0001]$ trials, work done increased as compliance increased.

**Overall stability during single support on the compliant surface**

The trunk pitch angle RMS was significantly increased in the first compliant-surface trial compared with controls (Table 2), suggesting that control over the trunk angle is more difficult when encountering a compliant surface during walking. This is evident in Fig. 9, which shows the trunk pitches more forward in response to a compliant surface. Although the trunk roll angle RMS was larger than the pitch RMS, there was no difference between controls and the first compliant-surface trial (Table 2).

Similar to the results of the first exposure to the compliant surface, trunk pitch angle RMS (blocked trials: $F(3,24) = 14.50, P < 0.0001$; random trials: $F(4,32) = 18.31, P < 0.0001$) but not roll angle RMS (blocked trials: $F(3,24) = 0.56, P = 0.649$; random trials: $F(4,32) = 0.52, P = 0.72$) demonstrated a significant difference as assessed by an ANOVA (Table 2). Post hoc tests showed that trunk pitch angle RMS was larger when stepping on the compliant surfaces (most, medium, and least compliant) compared with controls for both the blocked and random trials. Specifically, the Bonferroni tests demonstrated that the RMS was significantly larger for the most-compliant surface compared with all other surfaces but the medium- and least-compliant surfaces were not different.

**Discussion**

Terrestrial animals have to be able to compensate for perturbations to locomotion induced by different surfaces whether
they are slippery, uneven, or compliant. The CNS has the job of modulating muscle activity and hence limb movements to ensure that dynamic stability is maintained. The aim of this study was to examine the control of COM and lower limb dynamics and recovery response modulation of muscle activity during locomotion across an unexpected compliant surface and, in particular, scaling behavior across different levels of surface compliance. Our results suggest recovery response modulation of muscle activity and changes in movement dynamics affecting the vertical COM. While the initial loading of the compliant surface is passively controlled, stepping off the surface is actively modulated to prevent tripping by maintaining toe clearance and to ensure safe forward progression. Furthermore, the range of vertical COM trajectories was not maintained.

An additional goal of this study was to determine whether compliant-surface conditions presented in a blocked versus random design influenced the strategies for negotiating the compliant surface. The majority of the measures showed similar patterns between the two protocols. It is possible that the compliant-surface perturbation was not destabilizing enough to elicit differences between blocked and random trials together.

As the recovery response to the first compliant-surface trial elucidates the truly reactive response to negotiating a compliant surface, our discussion will focus on this response and use later trials to illustrate the effects of varying the level of compliance.

Neuromuscular response to an unexpected compliant surface

Long-latency reflexes (between 97 and 175 ms) were elicited in response to stepping on an unexpected compliant surface. The timing of these reflexes is consistent with previous studies of slipping (Marigold and Patla 2002; Marigold et al. 2003; Tang and Woollacott 1999: Tang et al. 1998), tripping (Eng et al. 1994; Schillings et al. 2000), and walking on an ankle inverting platform (Nieuwenhuijzen et al. 2002). Although studies of slipping and tripping have shown distinct flexor and extensor synergies for recovering balance (Eng et al. 1994; Marigold and Patla 2002; Marigold et al. 2003; Tang et al. 1998), there was no clear flexor/extensor strategy observed for our compliant-surface perturbation. Thus reflexes appear to be modulated such that they are functionally appropriate for the type of perturbation encountered (e.g., slip, trip, or compliant surface).

When cats step in an unexpected hole during locomotion (i.e., foot-in-hole experiments), ankle extensor muscle activity in the first 30 ms after passing ground level is not different from control conditions (i.e., solid, level ground support) (Gorassini et al. 1994). These authors argue that the lack of change during this time is because the activity is preprogrammed. Studies of landing movements where the person falls through a “false platform” after jumping from a height also show that ankle muscle activity is not altered in the initial 30 ms after passing ground level (Duncan and McDonagh 2000). Our results as illustrated in Figs. 4 and 5 demonstrate that the ankle extensors had little or no change in muscle activity during the initial 30-ms period after stepping on the compliant surface. Thus our results are consistent with these studies suggesting that the initial ankle extensor activity is preprogrammed for landing.

Although ankle extensor muscle activity is not altered in the initial 30 ms after passing ground level in the foot-in-hole trials, it is reduced between 30 and 200 ms, and there is a
strong corrective flexor response to lift the cat’s leg out from the hole in the walking surface (Gorassini et al. 1994). In response to stepping on a compliant surface in the present study, a large perturbed-limb ankle flexor burst is seen ~175 ms in response to the first compliant-surface trial (see Fig. 5) without a concomitant flexion response of lifting the leg. A flexor response to lift the leg off the compliant surface during this phase (which corresponds roughly to single support) would not be possible. Instead a flexor muscle response is seen later in the step cycle (for example the large increase in activity of BF and concurrent decrease in RF in Fig. 8) with increased knee flexion to step off the compliant surface and clear the obstacle created by the depression of the surface.

The trigger for this flexor response has been argued to be a result of the absence of afferent input such as load or cutaneous information (Gorassini et al. 1994; Hiebert et al. 1995). For example, stimulating group I afferents of ankle extensor muscles when the cat’s paw was in the hole resulted in a suppression of the corrective flexor bursts and extensor activity was maintained for the duration of stimulation (Hiebert et al. 1995). The premise that the absence of afferent information can alter the muscle response after an unexpected event has also been argued to contribute to the doubling of muscle activity seen after landing in the false-platform studies (McDonagh and Duncan 2002).

The response seen after contact on the compliant surface is not due to an absence of afferent input, but rather the altered surface property provides a different stimulus than normally present during solid ground support. Also the sudden unexpected lowering of the body represents an unloading response (ground reaction force less than body weight resulting in downward acceleration of the body COM) altering afferent input. In addition, it may have stimulated the vestibulospinal apparatus, and hence the vestibulospinal tract may have been involved in the reflexive responses. In fact, an otolith-spinal reflex contributes to muscle bursts when falling from a sudden drop from a height in cats (Watt 1976). The altered foot-surface interaction on the compliant surface may modify plantar cutaneous and/or ankle proprioceptive input, which in turn may have evoked the reflexes and shaped the recovery response. Studies using electrical nerve stimulation on healthy individuals and those with sensory polyneuropathy demonstrate the importance of cutaneous afferent information on reflex response modulation during locomotion (Van Wezel et al. 1997, 2000). Furthermore, false-platform studies suggest that landing ankle muscle activity results from stretch reflexes triggered by ankle rotation (Duncan and McDonagh 2000; Santello 2005). It is highly plausible that ankle stretch induced by the tilt of the compliant-surface apparatus when loaded contributes to the muscle recovery response.

Functional role of muscle responses

What functional roles do the muscle activation patterns play in responding to an unexpected compliant surface? The perturbed-limb SOL and MG may be activated because loading the compliant surface changes when and how the shank rotates over the foot. The initial response in these muscles may be triggered by plantarflexor stretch caused when the foot contacts the compliant surface and the surface closer to the individual depresses under the weight of the body. The perturbed-limb TA responds later (although still during the plantarflexor activity) to provide co-contraction and hence stabilize the ankle joint, which is being challenged by the foot–compliant-surface interaction (imagine stepping on a piece of foam). The unperturbed-limb TA is activated early to prevent tripping of the limb beginning swing phase (lowering of the body from stepping on the compliant surface means the swing limb foot must be dorsiflexed to prevent scapping the toes on the ground). Bilateral ES muscles are activated to control trunk motion. Finally, the unperturbed-limb RF is activated and may play a role in preventing knee collapse as the weight of the body is accepted and the rate of force increases from rapid depression of the compliant surface.

Stability requirements differ depending on the phase of the gait cycle and because the perturbation caused by the change in surface compliance is ongoing during contact with this surface, modifications in muscle responses and/or more global kinematic strategies are not only possible but expected. Indeed, changes in muscle response amplitude across the different phases of contact with the compliant surface were observed and suggest recovery response modulation.

In response to the first compliant-surface trial, perturbed-limb ankle muscle amplitude (TA, SOL, and MG) is increased
in the first two phases (see Fig. 8), suggesting a stiffening response at the ankle to stabilize the limb in contact with unstable surface. Proximal musculature is more active later in stance on the compliant surface such that the perturbed-limb RF demonstrates greater muscle activity in the third phase possibly to prevent further knee collapse after the body is lowered on the compliant surface. Activity in this muscle is subsequently decreased in the fourth phase with a concomitant increase in perturbed-limb BF activity. This strategy, which is also seen in the blocked and random trials (particularly with the most-compliant condition), may serve to facilitate the knee flexion response at toe-off to clear the obstacle created by the depression of the compliant surface. This would also allow toe clearance to be maintained as seen in Fig. 12.

For the most part, the greatest muscle activity was seen for the most-compliant condition compared with the medium- and least-compliant conditions for the blocked and random trials. Further work is needed to understand the effect of complex muscle activation patterns during this locomotor task.

**Initial response to stepping on a compliant surface is passively controlled**

Small changes in ground support may alter lower limb segments too rapidly for any neural response component to be efficient. Thus the CNS may be less concerned with the initial step on the altered terrain and more alert to subsequent phases to minimize the destabilizing effects on stability (i.e., prevent tripping and falling and maintain forward progression with appropriate foot placement). The first minimum of the vertical COM is not different between control trials and the first compliant-surface trial, which may be due to increased perturbed-limb knee extension (see Fig. 10). This knee extension appears to be passive in that the depression from the compliant surface forces the knee into extension before full weight acceptance occurs. Interestingly, the greater knee extension as a response to initial loading of the compliant surface is not present in the blocked compliant-surface trials but does happen during the random compliant-surface trials. The random trials...
better represent an unexpected perturbation similar to the first exposure to the compliant surface, whereas the ability to predict a compliant-surface trial is easier during the blocked trial protocol. In the blocked trials, individuals may choose a strategy to “ride” the surface as it depresses.

This passive mechanism of knee extension is supported by the fact that muscle onset latencies occur too late (between 97 and 175 ms) to affect the initial loading of the surface: deviations in vertical COM trajectory occurs ~100 ms after foot contact on the compliant surface, and the first minimum of the vertical COM occurs ~56 ms after contact in response to the first compliant-surface trial. Furthermore, the muscle activity during the initial loading (1st bin: ~150 ms) of the compliant surface is relatively small and not different from prior to foot contact with the exception of the perturbed-limb SOL and MG. However, activity is increased in this bin since both these muscles are activated at ~100 ms (within the temporal boundaries of the bin), which is still too late to make a difference. In addition, stepping on an unstable surface may trigger the CNS to modulate the time spent in double support (i.e., double support phase 1) or single support such that double support is increased to prolong contact with a stable surface or single support is shorter to quickly get off the unstable surface. However, there were no differences in either temporal parameter between control trials and compliant-surface conditions, further suggesting no modulation during the initial loading of the compliant surface. Moritz and Farley (2004) also argue that changes in leg and joint dynamics result from passive mechanisms in response to hopping on an unexpected hard surface after hopping on a compliant surface: changes in leg stiffness occurred prior to any muscle activation suggesting that the CNS relies in part on reactive forces and/or intrinsic muscle properties rather than active muscle control.

Knowledge about and experience with a surface enables the CNS to better anticipate the destabilizing effects of such surfaces. For example, despite not being informed of an impending slip perturbation during gait, individuals respond differently after the initial slip trial (Marigold and Patla 2002). In addition, anticipation of a change in surface stiffness during hopping in place leads to earlier muscle activation and changes in COM and knee angle dynamics (Moritz and Farley 2004). Experience with the compliant surface may explain why the vertical COM first minimum is lower in response to the compliant conditions versus the control conditions for both blocked and random trials despite no difference in the first exposure (see Fig. 10). Anticipatory strategies can also be seen in the present study. For example, the time for the vertical COM to deviate from baseline control trials occurs earlier in the blocked trials compared with the first compliant-surface trial.
trial. Furthermore, muscle recovery response amplitude is reduced after the first compliant-surface trial.

Farley and colleagues (Farley et al. 1998; Ferris and Farley 1997; Ferris et al. 1998, 1999; Moritz and Farley 2003) have argued that changes made by the CNS in lower limb dynamics (such as leg stiffness, joint angles, and muscle-activation patterns) allows the individual to preserve vertical COM motion when encountering a damped/compliant surface. However, a recent study of hopping has shown downward COM is not preserved when individuals encounter abrupt changes in surface stiffness (e.g., in surprise or expected conditions): COM is changed by ≤4 cm (Moritz and Farley 2004). Our findings demonstrate that peak vertical COM is depressed compared with the control condition, suggesting that the range of COM motion in the vertical direction is not preserved. This is despite muscle activation early enough to affect this phase. Menz et al. (2003b) suggest that one of the primary goals of the postural control system is to stabilize head movements during gait. Head stabilization is important during gait as it stabilizes the visual apparatus during goal-directed movement. Although stable vertical COM motions may keep the head and thus the eyes from being disturbed, a variety of nonvisual and visual reflexes are available to stabilize eye movements in case the head is perturbed as in when stepping on a compliant surface. It is possible that the abrupt change in surface compliance in our study for only a single step changes the control mechanisms adopted by the CNS. In addition, in a hopping task the vertical COM is more important to the overall goal versus in locomotion, where the vertical and horizontal (i.e., movement in the plane of progression) motion of the COM is important. Therefore the goal of the CNS may be to adjust lower limb dynamics (and thereby vertical COM) for the subsequent step (i.e., onto stable ground) rather than attempt to correct for the perturbation. This is in line with the assumption that dynamic stability is paramount to locomotor tasks.

CNS actively ensures dynamic stability after the initial loading of an unexpected compliant surface

The challenge evoked by stepping on an unexpected compliant surface must be dealt with efficiently to preserve stability and maintain forward progression. The perturbed limb (reflected in the vertical displacement of the ankle marker) and subsequently the vertical COM are lowered when stepping on a compliant surface. Additionally, a large trunk pitch ensues from increased horizontal trunk velocity (contributing to increased trunk pitch RMS). Trunk pitch RMS increases as compliance increases, suggesting that at least trunk stability (and as a result trunk COM) is compromised to a greater extent. Bilateral ES muscles are eccentrically activated to counter the effect of the trunk pitch. This strategy may be crucial in preventing the forward trunk COM from deviating too far forward and causing a fall. For example, increased trunk pitch at toe-off after a perturbation (treadmill acceleration) applied during gait led to failed recovery attempts versus less trunk pitch (Owings et al. 2001). Although the BF muscle did not exhibit a burst in the first compliant-surface trial, there was increased activity in the blocked and random trials, and thus a hip extensor moment may also facilitated in controlling trunk pitch to decrease angular momentum similar to the response after a trip during locomotion (Pijnappels et al. 2005).

To maintain dynamic stability, the CNS must not only deal with the step onto an unstable surface but also manage the step off onto more stable ground. In general, stability during dynamic movements such as locomotion requires controlling the COM within changing size and moving base of support. COM movements are heavily influenced by trunk movement forward/backwards (pitch) or sideways (roll): the larger the pitch or roll motion, the greater the challenge to the CNS to control stability. An unexpected trip on the lip created by the depression of the compliant surface can indirectly affect COM movements (Eng et al. 1994; Pijnappels et al. 2005). Therefore it is important to maintain adequate toe clearance over the temporary obstacle created by the depression of the compliant surface to ensure stability. The results of this study suggest that the recovery response to a compliant-surface perturbation is geared toward maintaining dynamic stability. Research on other types of gait perturbations has demonstrated this as well (Belanger and Patla 1987; Eng et al. 1994; Marigold and Patla 2002; Marigold et al. 2003; Schillings et al. 1999, 2000; Tang et al. 1998).

Despite sufficient time to adjust the vertical COM trajectory during mid-stance, our findings demonstrated that increasing compliance resulted in lower peak vertical COM. Thus the CNS does not seem to be overly concerned with attempting to realign COM trajectory but rather getting off the unstable surface. This can be seen with increases in knee flexion after toe-off with increases in the level of compliance to accommodate the imposed obstacle and prevent tripping: the vertical COM is lower too, which further increases the risk of tripping. This increased knee flexion as compliance increases allows toe clearance to be maintained in early swing phase of the perturbed limb. Cats exhibit a strong flexor response contributing to exaggerated knee and ankle flexion in response to the ground support being removed (i.e., foot-in-hole experiments) during locomotion (Gorassini et al. 1994). In the present study, knee flexion is the result of active control (modulation) of the perturbed-limb toe-off and early swing phase as evident from alterations in temporal gait parameters, modulation of the perturbed-limb knee angle with different levels of compliance, and changes in joint power at the ankle, knee, and hip. Furthermore, the recovery response modulation observed for the perturbed-limb RF and BF such that RF activity is decreased in phase 4 and BF activity is increased suggests facilitation toward knee flexion at toe-off from the compliant surface.

Individuals increased their time on the compliant-surface apparatus for each level of compliance. This change was not due to changes in the first double support phase or single support but rather a longer duration of double support phase 2. In other words, individuals spent a greater amount of time with their unperturbed limb in front of the compliant surface and perturbed limb in contact with the surface suggesting that changes in movement dynamics may have been occurring that necessitated the longer duration. In fact, knee angle is modulated with the different compliant surfaces: as surface compliance increases and the body is further lowered, flexion of the perturbed-limb knee is increased and toe clearance is maintained.

While the knee generates more power, the ankle absorbs more power and the hip joint generates less power (see Figs. 12 and 13) after toe-off from the compliant surface. Control over
the knee–joint power is similar to that found when people step over obstacles on solid, level ground (Patla and Prentice 1995) and when recovering from a trip during walking (Eng et al. 1997). Joint-power analyses capture the resultant effect of muscle activity changes.

Conclusion

The results of this study suggest that the recovery response to a perturbation induced by stepping on a compliant surface is geared toward maintaining dynamic stability. Although vertical COM motion is not preserved in response to stepping on an unexpected compliant surface, muscle activity is modulated throughout the recovery response, and changes in movement dynamics are specific to stepping off to the compliant surface. This finding emphasizes the importance of investigating the step off of unstable ground support and subsequent steps in the recovery phase (Cordero et al. 2003; Oddsson et al. 2004).

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REFERENCES


