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Runners adjust leg stiffness for their first step on a new running surface

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Abstract

Human runners adjust the stiffness of their stance leg to accommodate surface stiffness during steady state running. This adjustment allows runners to maintain similar center of mass movement (e.g., ground contact time and stride frequency) regardless of surface stiffness. When runners encounter abrupt transitions in the running surface, they must either make a rapid adjustment or allow the change in the surface stiffness to disrupt their running mechanics. Our goal was to determine how quickly runners adjust leg stiffness when they encounter an abrupt but expected change in surface stiffness that they have encountered previously. Six human subjects ran at 3 m s^{-1} on a rubber track with two types of rubber surfaces: a compliant "soft" surface ($k_{\text{surf}} = 21.3$ kN m^{-1}) and a non-compliant "hard" surface ($k_{\text{surf}} = 533$ kN m^{-1}). We found that runners completely adjusted leg stiffness for their first step on the new surface after the transition. For example, runners decreased leg stiffness by 29% between the last step on the soft surface and the first step on the hard surface (from 10.7 kN m^{-1} to 7.6 kN m^{-1}, respectively). As a result, the vertical displacement of the center of mass during stance (~ 7 cm) did not change at the transition despite a reduction in surface compression from 6 cm to less than 0.25 cm. By rapidly adjusting leg stiffness, each runner made a smooth transition between surfaces so that the path of the center of mass was unaffected by the change in surface stiffness. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Biomechanics; Locomotion; Motor control; Muscle; Spring-mass model; Stiffness

1. Introduction

A simple spring-mass system models the basic mechanics of running remarkably well. The model consists of a single Hookean spring representing a runner's leg and a point mass equivalent to body mass (Blickhan, 1989; McMahon and Cheng, 1990). This simple model has proven effective in describing the mechanics of both animals and robots as they run, hop, or trot (Blickhan and Full, 1993; Farley et al., 1993; He et al., 1991; Raibert, 1986, 1990; Raibert et al., 1986, 1993). At faster speeds, animals and robots use the same leg stiffness but increase the angle swept by the leg during stance (Farley et al., 1993; He et al., 1991; Raibert et al., 1993). Increasing the angle swept by the leg at faster speeds decreases the vertical displacement of the center of mass during stance and shortens the time that the foot remains on the ground.

Although leg stiffness is independent of running speed, humans adjust leg stiffness when they run on different surfaces (Ferris et al., 1998). For surfaces of lower stiffness, runners decrease leg spring compression by increasing leg stiffness. This adjustment offsets the increased surface compression and keeps the path of a runner's center of mass the same regardless of surface stiffness. Because many biomechanical parameters depend on the combined series stiffness of the runner and surface, adjusting leg stiffness allows humans to run in a similar manner on different surface stiffnesses (Ferris et al., 1998). Stride frequency, ground contact time, and peak ground reaction force are all independent of surface stiffness (Ferris et al., 1998). All of these observations are for steady-state running on a continuous surface. It is not known how quickly runners can adjust to an abrupt change in surface stiffness.

We hypothesized that runners would adjust leg stiffness for their first step on a new surface of a different stiffness when they knowingly ran from one surface to another. We based this hypothesis on data from running quail that suggest running birds do not maintain an invariant leg stiffness when they step on small areas of different mechanical stiffnesses (Clark, 1988). In order to

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compare our experimental findings with the results that would be expected if runners did not adjust leg stiffness for the new surface stiffness, we constructed a computer simulation of a spring-mass model on a compliant surface. We used the computer simulation to assess how the global running mechanics (e.g., path of the center of mass, contact time, running speed) would be affected by the transition in surface stiffness without a concomitant leg stiffness adjustment.

2. Methods

Six healthy female subjects (body mass 52.7 ± 3.1 kg, leg length 88 ± 3.5 cm; mean ± s.d.) between 21 and 25 years of age participated in this study. The university committee for the protection of human subjects approved the experimental protocol and subjects provided informed consent. We recorded ground reaction force (1000 Hz) and high-speed video (200 Hz) as subjects ran at $3\ \mathrm{m\,s^{-1}}$ on a 17 meter rubber track with two force platforms (AMTI, Inc.) mounted beneath the middle of the track. We cut sections of rubber to match the surface area of the force platforms so that the rubber surface did not transmit force off the force platform (Fig. 1). We determined the runner's speed with two infrared sensors placed on both sides of the force platforms (3 m apart) and accepted trials if the running speed was within ± 5% of $3\ \mathrm{m\,s^{-1}}$. We also integrated the horizontal ground reaction force with respect to time to measure the change in forward speed for each step.

We used two types of rubber to create four different surface conditions for the subjects. The compliant "soft" rubber surface had a stiffness of $21.3\ \mathrm{kN\,m^{-1}}$ and the non-compliant "hard" rubber surface had a stiffness of $533\ \mathrm{kN\,m^{-1}}$. In the first two conditions, we covered the entire length of the track with either the soft rubber surface or the hard rubber surface. For the third condition, we covered the first-half of the track with the soft surface and the second-half with the hard surface (Fig. 1). For the fourth condition, we covered the first-half of the track with the hard surface and the second-half with the soft surface. We randomized the order of the surface conditions so that each subject ran on the four conditions in a different order. We collected ground reaction force data for the following steps: last step on the soft surface before transition to the hard surface (SH0), first step on the hard surface after transition from the soft surface (SH1), one step from a continuous hard track (H), last step on the hard surface before transition to the soft surface (HS0), first step on the soft surface after transition from the hard surface (HS1), and one step from a continuous soft track (S). Subjects performed as many practice trials on each surface condition as they wanted (typically 5–10 trials). We then collected data for four trials on each surface condition for each subject.

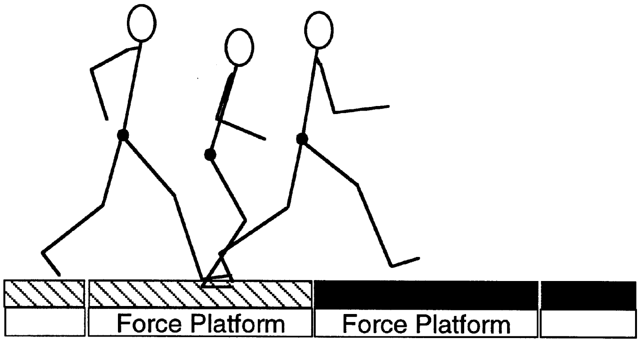

Fig. 1. Side view of the experimental set-up. Subjects ran down a track with two force platforms mounted beneath the rubber surface. For the transition trials, we covered half of the track with a compliant "soft" rubber surface (striped, $k_{\mathrm{surf}} = 21.3\ \mathrm{kN\,m^{-1}}$) and half with an extremely stiff "hard" rubber surface (black, $k_{\mathrm{surf}} = 533\ \mathrm{kN\,m^{-1}}$).

During stance, a runner's effective vertical stiffness (k_{vert}) governs the vertical motion of the center of mass (McMahon and Cheng, 1990). This effective vertical stiffness does not correspond to any physical spring in the runner or model, but is extremely important in determining the time of ground contact, the peak vertical ground reaction force, and the vertical displacement of the center of mass. On a non-compliant surface, effective vertical stiffness depends on leg stiffness (k_{leg}) and half the angle swept by the leg spring during stance (θ) (McMahon and Cheng, 1990). The effective vertical stiffness is calculated from the ratio of peak vertical ground reaction force (F_{peak}) to vertical displacement of the center of mass (Δy) at the instant when the center of mass reaches its lowest point (McMahon and Cheng, 1990).

For compliant surfaces, effective vertical stiffness also depends on surface stiffness (Ferris et al., 1998). The compression of the surface adds to the vertical displacement of the runner's center of mass. We calculated the vertical displacement of the center of mass during stance (Δy) by twice integrating the vertical acceleration of the center of mass, derived from the ground reaction force, with respect to time (Cavagna, 1975). We then calculated the vertical displacement of the center of mass relative to the surface ($\Delta y_{\mathrm{person}}$) by subtracting the surface compression (Δy_{surf}) from the vertical displacement of the center of mass (Δy). Surface compression was calculated from the ratio of the peak ground reaction force to surface stiffness.

We calculated the stiffnesses of the rubber surfaces from the average slopes of their force versus displacement relationships (linear fit $R^2 > 0.90$ for forces up to the mean peak vertical ground reaction force). We determined the force versus displacement relationships using a materials testing machine and the area of the running shoe soles. Because surface stiffness is proportional to loading area for a point elastic surface like a rubber track (Nigg and Yeadon, 1987), all subjects wore the same pair of shoes so that surface stiffness was the same for all subjects. This limited our study to subjects of approximately the same size. Although a runner's center of pressure is typically located underneath the metatarsal heads at mid-stance (Cavanagh and Lafortune, 1980), high-speed video showed that the entire shoe sole was in contact with the track when the center of mass was at its lowest point. As a result, we used the entire sole area to determine the surface stiffness using the materials testing machine. In our calculations, we used the surface stiffness value to calculate surface compression at midstance when the ground reaction force was at its peak. Using only a portion of the sole area would have led to a lower surface stiffness value, and thus a greater value for surface compression. This would have led to the calculation of a greater magnitude of leg stiffness adjustment but the same overall conclusions (Ferris et al., 1998). Thus, our use of the entire sole area to calculate surface stiffness provided the most conservative approach to testing our hypothesis because it led to calculation of the minimum possible leg stiffness adjustment for each given condition. As described in detail in a previous study (Ferris et al., 1998), we estimated surface damping properties from a series of steel shot drop tests and concluded that surface energy losses were negligible.

We used the vertical displacement of the runner's center of mass relative to the surface (Δy_{person}), leg length (L_0), and half the angle swept by the leg spring during ground contact phase (θ) to calculate the maximum compression of the leg spring (ΔL) (McMahon and Cheng, 1990)

$$\Delta L = \Delta y_{\text{person}} + L_0(1 - \cos\theta) \tag{1}$$

The distance between the greater trochanter and the ground during standing served as the leg length (L_0). We calculated half the angle swept by the leg during ground contact (θ) from forward running speed (u), ground contact time (t_c), and leg length (L_0)

$$\theta = \sin^{-1}\left(\frac{ut_c}{2L_0}\right). \tag{2}$$

Finally, we derived leg stiffness (k_{leg}) from the ratio of peak vertical ground reaction force (F_{peak}) and maximum compression of the leg spring (ΔL). Past studies describe the bases for these calculations in more detail (Farley et al., 1993; Ferris et al., 1998; He et al., 1991).

We employed a repeated measures ANOVA to determine if there were statistically significant differences among the six different steps ($p < 0.05$) for all variables in Table 2. We then used Tukey Honestly Significant Difference post-hoc tests to determine differences between specific steps (Daniel, 1995).

To determine how the mechanics would be affected if the runner did not adjust leg stiffness, we constructed a computer simulation of a spring-mass model on a vertically compliant surface (Fig. 2). Horizontal elasticity of

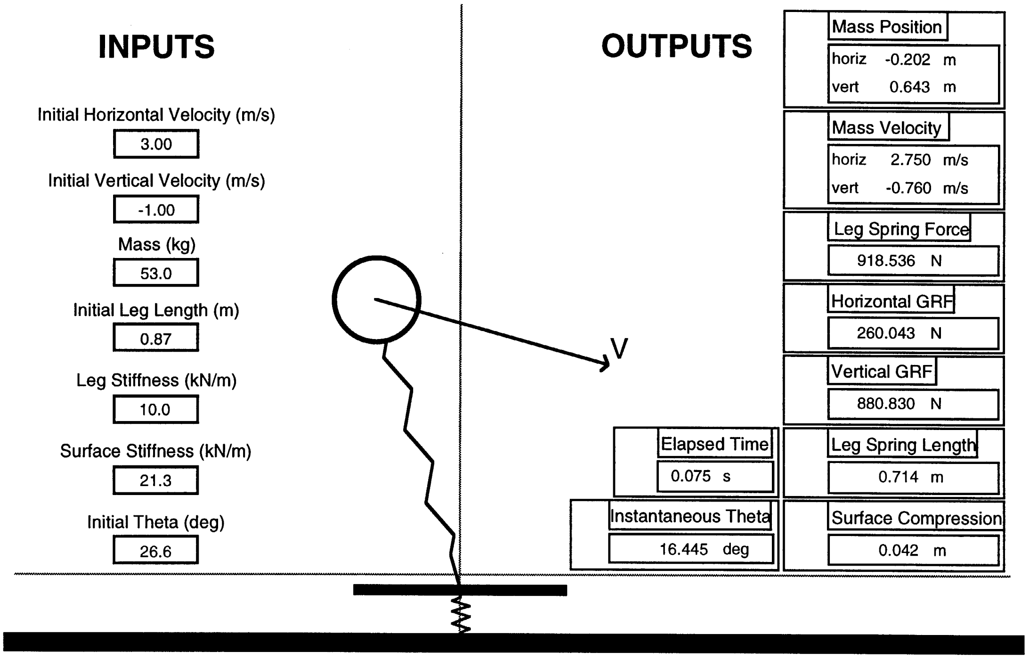

Fig. 2. Computer simulation of spring-mass model on compliant elastic surface. We used the computer simulation to determine how running mechanics would be affected if runners did not adjust leg stiffness for the abrupt transition in surface stiffness. The figure shows a single time step during one of the simulations. Input parameters are listed on the left and output parameters are listed on the right. The values displayed in the output parameter boxes are for the instantaneous time step that is shown. The arrow originating from the center of mass is the instantaneous velocity vector.

the surface could be neglected because horizontal stiffness of the surface was extremely high compared to vertical stiffness (Ferris et al., 1998). We created the simulation with Working Model 2D 4.0 (Knowledge Revolution, San Mateo, CA) using Kutta–Merson integration and a time step of 0.0001 s. We chose spring-mass system parameters corresponding to data for a typical subject (body mass 53 kg, leg length 0.87 m, initial horizontal velocity $3.0\,\mathrm{m\,s^{-1}}$, and initial vertical velocity $-1.0\,\mathrm{m\,s^{-1}}$. The magnitude of the simulation results would be expected to vary slightly for different spring-mass system parameters, [e.g., different ratios of leg stiffness to surface stiffness (Ferris and Farley, 1997; Ferris et al., 1998)], but the pattern of running dynamics would be the same.

We performed two computer simulations for each surface. The first simulation used a leg stiffness value that had been adjusted for the given surface. The second simulation used a leg stiffness value that had not been adjusted for the given surface (i.e., the leg stiffness value was appropriate for the other surface). The initial conditions were identical for the two simulations except for leg stiffness.

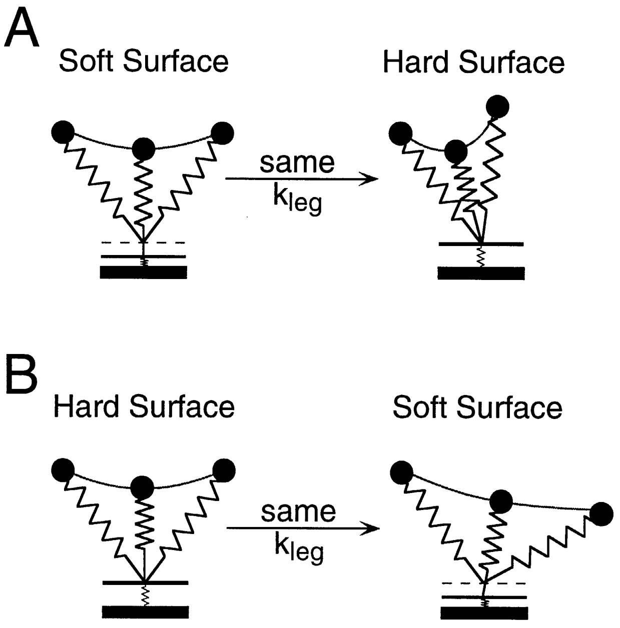

Fig. 3. Schematic representation of the computer simulation results. Each of the illustrations shows the spring-mass model at three times during stance: at initial touchdown, at the middle of the ground contact period, and at the end of ground contact. (A) When leg stiffness was not adjusted for the hard surface, the path of the center of mass was asymmetrical. The center of mass was at a higher height at the end of ground contact. (B) When leg stiffness was not adjusted for the soft surface, the path of the center of mass during ground contact was also asymmetrical. However, the center of mass was at a lower height at the end of ground contact.

3. Results

3.1. Computer simulations

The computer simulations revealed that running mechanics would be substantially altered if runners did not adjust leg stiffness (Table 1). An unadjusted leg stiffness resulted in an asymmetrical center of mass trajectory and a net change in velocity (Fig. 3). For example, when leg stiffness was not adjusted to accommodate the hard surface, the center of mass reached a higher height at the end of stance than at the beginning. Some of the initial kinetic energy was converted to gravitational potential energy. The asymmetrical center of mass trajectory also affected the direction of the center of mass velocity. Horizontal velocity decreased by 15% and vertical takeoff velocity increased by 51% between the beginning and end of ground contact (Table 1). When leg stiffness was not adjusted to accommodate the soft surface, the center of mass reached a lower height at the end of stance. The asymmetrical trajectory reflects the conversion of gravitational potential energy into kinetic energy. Horizontal velocity increased by 12% and vertical takeoff velocity decreased by 51% (Table 1). Finally, both the ground contact time and the peak ground reaction

Table 1

Results from computer simulations of spring-mass model on compliant surface. Input parameters listed in the table are surface stiffness (k_{surf}) and leg stiffness (k_{leg}). Output parameters are ground contact time (t_{c}), peak vertical ground reaction force (F_{peak}), horizontal velocity at end of stance (final horizontal velocity), and vertical velocity at end of stance (final vertical velocity)

Simulation parameters	Hard surface with adjusted leg stiffness	Hard surface with unadjusted leg stiffness	Soft surface with adjusted leg stiffness	Soft surface with unadjusted leg stiffness
k_{surf} ($\mathrm{kN\,m^{-1}}$)	533	533	21.3	21.3
k_{leg} ($\mathrm{kN\,m^{-1}}$)	6.9	10.0	10.0	6.9
t_{c} (ms)	282	240	281	310
F_{peak} (N)	1443	1721	1428	1243
Final horizontal velocity ($\mathrm{m\,s^{-1}}$)	3.00	2.56	3.00	3.37
Final vertical velocity ($\mathrm{m\,s^{-1}}$)	1.00	1.51	1.00	0.49

force differed for the two surfaces if leg stiffness was not adjusted. These results show how running dynamics should be affected if runners do not adjust leg stiffness immediately after the transition from one surface to the other surface.

3.2. Continuous running on the hard surface and the soft surface

Subjects ran with similar global mechanics on the continuous hard and soft surfaces (Fig. 4). Ground contact time, angle swept by the leg spring, peak vertical ground reaction force, vertical stiffness, and stride frequency were the same for the two surfaces (Tukey HSD, $p > 0.05$). Runners achieved the same vertical stiffness on the soft surface as on the hard surface by increasing leg stiffness (Table 2). Because the runners' legs were stiffer on the soft surface, leg compression and vertical displacement of the center of mass relative to the surface both decreased ($p < 0.05$). These effects offset the increased surface compression. As a result, vertical displacement of the center of mass was the same for the hard and soft surfaces ($p > 0.05$). In addition, the mean change in horizontal speed during stance was less than 1% for both surfaces (S: $0.1 \pm 0.5\%$ and H: $0.3 \pm 0.3\%$, mean ± s.e.m.).

3.3. Transition from the soft surface to the hard surface

Runners adjusted leg stiffness completely by the first step on the hard surface. Leg stiffness was the same for the first step after transition (SH1) as for a step on the continuous hard surface (H). As a result, runners had similar ground contact times, peak ground reaction forces, and center of mass vertical displacements (Table 2). The angle swept by the leg spring was also the same for the first step on the hard surface after the transition and the step on the continuous hard surface.

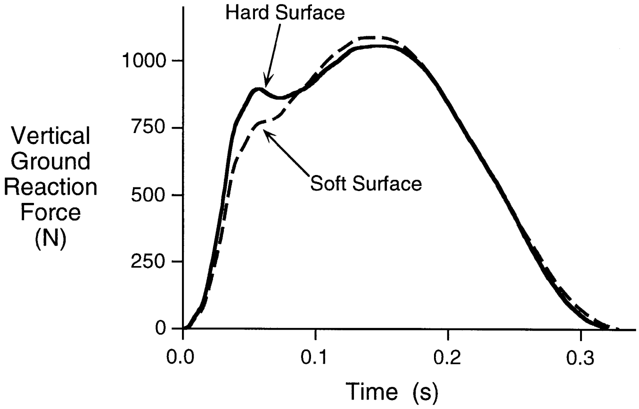

Fig. 4. Vertical ground reaction force for a subject running on the continuous hard surface and the continuous soft surface. By adjusting leg stiffness to accommodate the surface stiffness, subjects ran with similar ground reaction forces in spite of the 25-fold change in surface stiffness. The only consistent difference between surfaces was a substantial reduction in the initial impact peak on the soft surface. As previously noted, lower surface stiffnesses reduce the initial impact peak associated with the deceleration of the shank (McMahon and Greene, 1979; Nigg, 1986).

The leg stiffness adjustment did not occur before the surface transition. Runners used virtually identical leg stiffnesses and leg angles for the last step on the soft surface (SH0) as when they ran on the continuous soft surface (S). Leg stiffness was 10.7 kN m^{-1} for both steps while leg angle was 29.6 and 29.5°, respectively. All other running parameters were also the same for the two conditions (Table 2).

By rapidly reducing leg stiffness from 10.7 to 7.6 kN m^{-1}, subjects made a smooth transition from the soft to the hard surface with no disruptions to their

Table 2

Experimental data for the six surface conditions. Abbreviations for the running parameters are specified in the text. The table presents the mean values and standard errors of the means for each surface condition. An asterisk (∗) denotes a statistically significant difference between the two adjacent columns ($p < 0.05$, Tukey post hoc test). NS denotes no significant difference between the two adjacent columns. There were no significant differences between the last column (continuous soft surface, SS) and the first column (last step on soft before hard surface, SH0)

Running parameters	Last step on soft before hard surface (SH0)		First step on hard after soft surface (SH1)		Continuous hard surface (HH)		Last step on hard before soft surface (HS0)		First step on soft after hard surface (HS1)		Continuous (HS1) soft surface (SS)
F_{peak} (N)	1258 (65)	NS	1235 (65)	NS	1222 (85)	NS	1287 (76)	NS	1299 (70)	NS	1295 (63)
t_c (ms)	286 (5)	NS	270 (7)	NS	282 (1)	NS	267 (11)	∗	294 (9)	NS	282 (5)
Δy (cm)	6.8 (0.23)	NS	6.0 (0.3)	NS	6.7 (0.3)	NS	6.6 (0.5)	∗	7.8 (0.2)	NS	7.3 (0.3)
Δy_{surf} (cm)	5.9 (0.3)	∗	0.23 (0.01)	NS	0.23 (0.02)	NS	0.24 (0.01)	∗	6.1 (0.3)	NS	6.1 (0.3)
Δy_{person}	0.87 (0.31)	∗	5.8 (0.3)	NS	6.5 (0.3)	NS	6.3 (0.47)	∗	1.7 (0.3)	NS	1.2 (0.3)
ΔL (cm)	12.3 (0.86)	∗	16.5 (0.7)	NS	17.8 (1.1)	NS	16.3 (1.3)	NS	13.8 (1.2)	NS	12.6 (0.8)
θ (deg)	29.6 (0.94)	NS	28.6 (1.1)	NS	29.4 (1.4)	NS	27.5 (1.5)	∗	30.7 (1.3)	NS	29.5 (1.0)
k_{leg} (kN m^{-1})	10.7 (1.4)	∗	7.6 (0.6)	NS	7.1 (0.9)	NS	8.3 (1.1)	NS	10.0 (1.5)	NS	10.7 (1.1)
k_{vert} (kN m^{-1})	18.6 (0.95)	NS	20.7 (0.9)	NS	18.4 (1.3)	NS	20.1 (1.8)	∗	16.6 (0.8)	NS	17.9 (0.8)

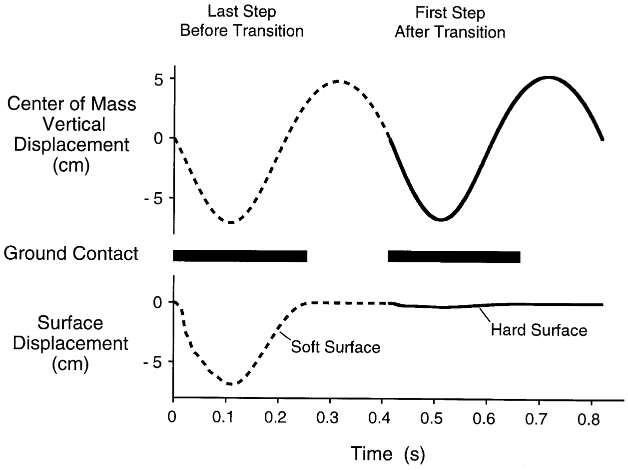

Fig. 5. Center-of-mass displacement and surface displacement during a transition from soft to hard surfaces. Because the runner decreased leg stiffness to offset the increase in surface stiffness, the trajectory of the center of mass was the same despite a change in surface compression from 6.9 to 0.3 cm.

running pattern. Ground contact time, peak ground reaction force, angle swept by the leg spring, and center of mass vertical displacement were all similar for the last step before transition (SH0) and the first step after transition (SH1) despite a 25-fold change in surface stiffness (Table 2). Surface compression decreased from 5.9 to 0.23 cm, but the adjustment to leg stiffness caused an increase in vertical displacement of the center of mass relative to the surface from 0.87 to 5.8 cm. Thus, the path of the center of mass was nearly the same before and after the surface transition (Fig. 5). Tracking the movement of a runner's head and trunk would provide very little indication that the runner had made the surface transition. Further evidence that the runners made a smooth transition between surfaces was that the net change in horizontal speed during stance was very small. Runners maintained a constant net speed during the step before and the step after the transition. Changes in the mean horizontal speeds were less than 1% (SH0: 0.9 ± 0.6% and SH1: − 0.2 ± 0.5%).

3.4. Transition from the hard surface to the soft surface

Runners completely adjusted to the change in surface stiffness by the first step on the soft surface. Comparing the first step on the soft surface (HS1) to a step on the continuous soft surface (S) showed that all running parameters were the same (Table 2). Runners used a leg stiffness of 10.0 kN m^{-1} for the first step on the soft surface after transition and 10.7 kN m^{-1} for the step on the continuous soft surface ($p > 0.05$).

Subjects tended to increase leg stiffness before the transition, but the increase was not statistically significant (Table 2). Leg stiffness was 7.1 kN m^{-1} for a step on the continuous hard surface (H) and 8.3 kN m^{-1} for the last step before the transition (HS0). Most other running parameters were similar (Table 2).

Runners used a leg stiffness during the first step on the soft surface after transition (HS1) that was 41% greater than the leg stiffness used for the continuous hard surface (H) ($p < 0.05$). However, because subjects tended to preadjust leg stiffness for the last step on the hard surface, leg stiffness did not change significantly between the last step on the hard surface (HS0) and the first step on the soft surface (HS1) (Table 2). These observations suggest that runners used multiple steps to adjust leg stiffness when making the transition from the hard surface to the soft surface. Runners had no net change in horizontal velocity in the steps before and after the transition (HS0: − 0.1 ± 0.8% and HS1: 0.6 ± 0.5%).

4. Discussion

Humans and other animals run from one surface to another with amazing grace and agility in the natural world. Our past research has shown that runners maintain similar center of mass movements on surfaces with different stiffnesses by adjusting leg stiffness to accommodate the surface stiffness (Ferris et al., 1998). In most real-life situations, runners see changes in the terrain ahead of them and have knowledge of the mechanical properties of the surfaces from previous experience. Thus, runners in the real world are likely to anticipate surface changes as the subjects did in the present study.

The results from this study demonstrate that runners adjust leg stiffness for their first step on a new surface. Furthermore, the computer simulations reveal that rapid leg stiffness adjustments prevent disruptions to a runner's movement. By quickly adjusting leg stiffness, runners make a very smooth transition between surfaces. In spite of a 25-fold change in surface compression, the center of mass follows nearly the same path before and after the transition with no discontinuity at the transition.

Because the biomechanical mechanism for adjusting leg stiffness during running has not been determined, it is difficult to predict which neural pathways are involved in leg stiffness adjustments. One way to adjust leg stiffness is to adjust the torsional stiffness of the leg joints (Farley et al., 1998). If the stretch reflex contributes substantially to extensor muscle activation during running (Dietz et al., 1979), then runners may use pre-synaptic inhibition or fusimotor action (Prochazka, 1989; Stein and Capaday, 1988; Stein et al., 1995) to modulate stretch reflex response and adjust joint stiffness for different surface stiffnesses. However, when humans run in place with stretch reflexes temporarily blocked by ischemia, ground contact time is nearly the same as with active reflexes (Dietz et al., 1979). This finding suggests that leg stiffness is unchanged by the loss of stretch reflexes. Further study is required to identify the biomechanical mechanism for adjusting leg stiffness during running before specific neural pathways can be implicated.

Our findings provide insight into how runners might respond to an unexpected change in surface stiffness. To limit the scope of our study, we examined only situations where runners knew about the change in surface stiffness and had practiced making the transition. However, the computer simulations suggest that an unexpected change in surface stiffness without any adjustment by a runner would substantially disrupt the runner's movements. For an unexpected increase in surface stiffness, a runner's leg would be too stiff and the horizontal velocity of their center of mass would decrease (Table 1). In addition, the higher ground reaction force (Table 1) might lead to a greater stretch of the leg muscles and increase muscle activity via the stretch reflex (Dietz, 1981), causing an even greater disruption to running mechanics. Conversely, for an unexpected decrease in surface stiffness, a runner's leg would not be stiff enough and the horizontal speed of their center of mass would increase (Table 1). The vertical takeoff velocity of the center of mass would decrease, resulting in a shorter aerial time to swing the opposite leg forward and prepare for ground contact. Both types of unexpected transitions could lead to disruptions that might cause a runner to lose balance. The finding that runners tended to make a pre-adjustment to leg stiffness when running from the hard surface to the soft surface suggests that the runners may have been more concerned about maintaining dynamic stability during this transition than during the transition from the soft surface to the hard surface.

The central nervous system could rely on polysynaptic reflexes to guard against unexpected changes in surface stiffness during running. Complex phase dependent reflexes prevent stumbling during walking (Berger et al., 1984; Forssberg, 1979), but it is not known if similar reflex responses operate during running. The shorter ground contact times and faster velocities of running provide less time for long reflex loops to function. Future research should examine reflex reactions and running mechanics for unexpected changes in surface stiffness. These studies could determine whether reflex responses can override the passive dynamics of the spring-mass system during the first step after an unexpected transition in surface stiffness. In addition, comparing results for different running speeds would also provide further insight. We limited our study to a single running speed (i.e., $3\ \mathrm{m\ s^{-1}}$), but future studies should examine a range of speeds for both expected and unexpected transitions in surface stiffness.

The main finding of our study suggests that controlling the center of mass trajectory may be a general control principle for running. Runners rapidly adjust leg stiffness to offset changes in surface compression on compliant elastic surfaces. This adjustment allows runners to maintain stability as they move from one surface to another. It would be interesting to monitor the path of a runner's center of mass on energy dissipating natural terrains such as snow or sand. Offsetting increased surface compression on these terrains would require added muscular work because the surface does not store and return energy as the surfaces in our study do (Lejeune et al., 1998). Nevertheless, kinetic data from humans running on sand suggest that the center-of-mass may follow a similar trajectory on sand and hard surfaces (Lejeune et al., 1998). The time of ground contact is slightly longer on sand, but running is still a bouncing motion with the same stride frequency as on hard surfaces (Lejeune et al., 1998; Zamparo et al., 1992). Thus, the basic conclusions of this study may apply to a wide range of surfaces in the natural world.

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