Interaction of leg stiffness and surface stiffness during human hopping

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Ferris, Daniel P., and Claire T. Farley. Interaction of leg stiffness and surface stiffness during human hopping. *J. Appl. Physiol.* 82(1): 15–22, 1997.—When mammals run, the overall musculoskeletal system behaves as a single linear "leg spring." We used force platform and kinematic measurements to determine whether leg spring stiffness (k_{leg}) is adjusted to accommodate changes in surface stiffness (k_{surf}) when humans hop in place, a good experimental model for examining adjustments to k_{leg} in bouncing gaits. We found that k_{leg} was greatly increased to accommodate surfaces of lower stiffnesses. The series combination of k_{leg} and k_{surf} [total stiffness (k_{tot})] was independent of k_{surf} at a given hopping frequency. For example, when humans hopped at a frequency of 2 Hz, they tripled their k_{leg} on the least stiff surface (k_{surf} = 26.1 kN/m; k_{leg} = 53.3 kN/m) compared with the most stiff surface (k_{surf} = 35,000 kN/m; k_{leg} = 17.8 kN/m). Values for k_{tot} were not significantly different on the least stiff surface (16.7 kN/m) and the most stiff surface (17.8 kN/m). Because of the k_{leg} adjustment, many aspects of the hopping mechanics (e.g., ground-contact time and center of mass vertical displacement) remained remarkably similar despite a >1,000-fold change in k_{surf}. This study provides insight into how k_{leg} adjustments can allow similar locomotion mechanics on the variety of terrains encountered by runners in the natural world.

running; spring-mass model; biomechanics; motor control

WHEN HUMANS AND OTHER ANIMALS run, they literally bounce along the ground using muscles, tendons, and ligaments to store and return elastic energy (1, 8). During hopping, trotting, and running, the actions of the body's numerous musculoskeletal springs are combined so that the overall musculoskeletal system behaves as a single linear spring. As a result, the mechanics of running gaits can be described by a simple spring-mass model. This model consists of a single linear "leg spring" and a point-mass equivalent to the mass of the body (4, 20). The stiffness of the leg spring represents the stiffness of the integrated musculoskeletal system during locomotion. This stiffness governs the mechanics of the interaction between the musculoskeletal system and the external environment during the ground-contact phase of locomotion.

Experimental evidence has shown that the stiffness of the leg spring is independent of forward speed during bouncing gaits (14, 18). This constant leg spring stiffness at all forward speeds has been observed in all mammals studied to date, including running humans, hopping kangaroos, and trotting horses and dogs (14, 18). In each of these animals, the spring-mass system is adjusted for higher speeds by increasing the angle swept by the leg during the stance phase, thus reducing the vertical movements of the center of mass during the stance phase at higher speeds (14, 18).

Although leg stiffness remains nearly the same at all running speeds, it is possible for the stiffness of the leg spring to be adjusted. When humans hop in place, the stiffness of the leg can be increased by more than twofold to accommodate increases in hopping frequency or increases in hopping height at a given frequency (13). Furthermore, recent evidence reveals that the stiffness of the leg spring can be increased by more than twofold during forward running at a given speed to allow a range of stride frequencies (15). A stiffer leg spring allows humans to run with a higher stride frequency at the same forward speed.

The purpose of the present study was to determine whether leg stiffness is adjusted to accommodate surfaces with different properties. This study is part of our long-term research goal of understanding the effects of surface properties on the biomechanics of locomotion. Most locomotion biomechanics research has examined locomotion on hard smooth laboratory floors. Humans and other animals run on a wide variety of surfaces in the natural world. As a first step toward understanding the effects of surface properties on locomotion, this study examines the effects of surface stiffness on bouncing gaits.

Several studies have focused on the influence of surface stiffness on single events, such as a drop jump or a landing from a jump in humans (16, 23, 24, 28, 29). In these single events, there is less angular displacement of the ankle, knee, and hip when a subject lands on a compliant surface than on an extremely stiff surface. These results suggest that humans make their legs stiffer when they land on a compliant surface, thus decreasing the energy absorption by their musculoskeletal system and increasing the energy absorption by the surface. However, there are differences between these single-impact events and locomotion that make it difficult to predict whether the same strategy will be used for both. Locomotion is a cyclic activity that is sustained for long periods of time. As a result, minimizing metabolic energy cost is likely to be important in determining the strategy used for locomotion on surfaces of different stiffnesses. By contrast, avoidance of injury may be most important in landing from a jump, and maximizing jump height is most important in a drop jump. Because of these differences, the musculoskeletal adjustments for surfaces of different stiffnesses may be different for locomotion than for single-impact events.

Locomotion experiments have shown that surface stiffness does affect maximum running speed (21). Humans can sprint faster on a slightly compliant surface than on an extremely stiff surface like concrete (21). This observation was used to design the tuned indoor running tracks currently used at Harvard and

Yale Universities (10, 21). Although this earlier work examined the effect of surface stiffness on top speed, it did not examine the mechanics of submaximal running at a given speed (21). Various studies have examined the effect of cushioned running shoes on the mechanics of running at a given speed. These studies have shown that compliant running shoes reduce the impact force associated with lower limb deceleration immediately after the foot hits the ground during running (9, 26). However, because running shoes are much stiffer than the leg spring, running shoe elastic properties do not have a substantial effect on the kinetics of running after the initial impact with the ground.

The purpose of this study was to determine whether the stiffness of the leg spring is adjusted to accommodate changes in surface stiffness during bouncing gaits. Several aspects of the mechanics of bouncing gaits, including peak ground reaction force, stride frequency, and ground-contact time, depend on leg spring stiffness (4, 13, 15, 20). When animals run on a compliant surface, the surface acts as a second spring in series with the leg spring. In this case, the mechanics of a bouncing gait depend on the combined stiffness of the leg spring and the surface spring. We hypothesized that the leg spring stiffness would be increased to accommodate compliant surfaces, thus offsetting the effects of the compliant surface on the mechanics of locomotion. This idea is supported by the single-impact studies, in which leg stiffness appeared to increase on compliant surfaces (16, 23, 24, 28, 29). It is important to point out that it is not mechanically required for leg stiffness to be increased for bouncing gaits on compliant surfaces. An alternative strategy would be to keep the leg stiffness the same for all surfaces, thus allowing the ground-contact time to increase on less stiff surfaces. To test our hypothesis, we used hopping in place as our experimental model. Hopping in place is an ideal model because it follows the same basic mechanics and spring-mass model as forward running (13) yet has simpler kinematics. We compared the stiffness of the leg spring during hopping in place on surfaces with a wide range of stiffnesses.

METHODS

General procedures. Five healthy subjects [3 women and 2 men; body mass 63.4 ± 5.1 (SD) kg] between 19 and 26 yr of age participated in this study. Approval was obtained from the University of California Committee for the Protection of Human Subjects, and informed consent was given by all subjects. Because subjects hopped in place using both legs simultaneously for all trials, the leg spring stiffness in the model is equivalent to the combined stiffness for both legs. All subjects hopped with their hands on their hips and wore no shoes. A digital metronome was set at the designated frequency, and the subjects were instructed to match the metronome frequency while they hopped in place. Trials were acceptable if the hopping frequency was within 2% of the designated metronome frequency. During all trials, the vertical ground reaction force signal from a force platform (AMTI, Newton, MA) was sampled at 1,000 Hz. Each subject was given as much time as needed to practice matching the beat of the metronome and maintaining balance during hopping on the compliant elastic surface. For each trial in which data were collected, data were recorded after a minimum of 30 s of hopping. The average for three consecutive hops was used for analysis.

Experimental design. We used two separate experiments to test our hypothesis that the stiffness of the leg would be greater for hopping on compliant surfaces than on stiff surfaces. The first experiment examined adjustments to leg stiffness when humans hopped at a single frequency on surfaces with a range of stiffnesses. Subjects hopped at a constant frequency of 2 Hz on an extremely stiff surface [i.e., a force platform surface; surface stiffness (k_{surf}) = 35,000 kN/m; personal communication, AMTI] and on elastic surfaces with five different stiffnesses (26.1, 31.5, 37.6, 43.1, and 50.1 kN/m). We chose a hopping frequency of 2 Hz for this experiment because it is approximately the frequency at which humans invariably prefer to hop (13, 25). The elastic surface stiffnesses chosen ranged from 1.5 to 2.9 times the leg spring stiffness used for hopping at 2 Hz on an extremely stiff surface like a force platform surface (13). When people hop on a compliant elastic surface, the surface behaves as a spring in series with the leg spring. If the surface stiffness is much greater than the leg spring stiffness, the surface stiffness will not have a substantial effect on the total stiffness of the series combination of the leg spring and the surface. For example, if the surface is 10 times stiffer than the leg spring, the total stiffness will only be ~10% less than the leg spring stiffness. By contrast, if the surface is the same stiffness as the leg spring, the total stiffness will be one-half of the leg spring stiffness. We chose elastic surface stiffnesses that were 1.5–2.9 times greater than the leg spring stiffness normally used for hopping at 2 Hz on a hard surface. With these surface stiffnesses, we predicted that the total stiffness and the mechanics of hopping would be substantially affected by the surface if leg spring stiffness were not adjusted to accommodate the surface stiffness.

The second experimental design was prompted by the finding of Farley et al. (13) that leg stiffness increases when humans increase hopping frequency. In our study, subjects hopped at 2.0, 2.4, 2.8, and 3.2 Hz on an elastic surface (k_{surf} = 50.1 kN/m) and on an extremely stiff surface (i.e., the force platform surface; k_{surf} = 35,000 kN/m). By using a range of hopping frequencies on the elastic surface, the ratio of surface stiffness to the leg spring stiffness normally used for hard surfaces ranged from 1.3 to 2.9.

A repeated-measures analysis of variance was used to determine if surface stiffness had a significant effect on any of the measured variables in each of the two experimental designs. In addition, we tested whether there were significant effects due to the interaction of subject and surface stiffness for both experimental designs.

Elastic surface design. The surface comprised an aluminum honeycomb core and fiberglass sandwich panels (45 × 45 cm, Goodfellow, Berwyn, PA) supported by metal springs (Fig. 1). This surface was connected to two aluminum beams (Wicks Aircraft Supply) that attached to a hinge joint. The hinge joint prevented substantial horizontal or lateral movement of the surface when it was compressed. Because the length of the aluminum beams (1.83 m) was much greater than the maximum vertical deformation of the surface when subjects hopped on it (0.07 m), the largest angular change at the hinge joint was 2.2° during a hop. Thus the motion of the aluminum honeycomb surface was almost entirely in the vertical direction. Metal springs (Century Spring, Los Angeles, CA) were securely attached to the bottom of the aluminum honeycomb surface and to the top of a force platform in a

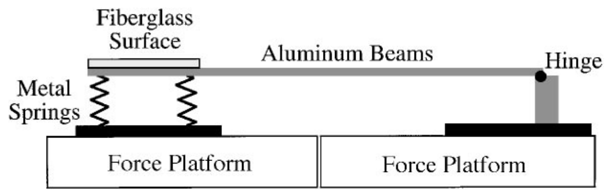

Fig. 1. Side view of compliant surface showing fiberglass hopping surface and aluminum beams connected to hinge joint. Metal springs were mounted below fiberglass. Entire surface was bolted to 2 force platforms.

symmetrical pattern. By adjustment of the number of springs, the stiffness of the surface could be adjusted from 26.1 to 50.1 kN/m.

The surface stiffness was determined by using static load tests in which weights were placed on the surface and the displacement of the surface was measured. The force-displacement curve for each surface configuration was linear to within 3% over the range of forces that occurred during hopping. Loaded free-vibration tests showed that the effective mass of the surface was 1.5 kg. This low effective mass was possible due to the use of lightweight aluminum and fiberglass construction materials. The damping characteristics of the sprung surface were measured from the logarithmic decrement of free vibration and were found to be negligible (damping ratio <0.01). The entire surface was bolted to the top of two force platforms.

Calculation of leg spring stiffness and total stiffness on hard force platform surface. The spring-mass model consists of a single point-mass equivalent to the body mass and a single linear compression spring, the leg spring (Fig. 2*A*) (4, 6, 13–15, 20). The leg spring represents the overall stiffness of the multijointed leg during locomotion. Because two legs were used for hopping, the leg spring stiffness was equal to the combined stiffness of both legs. When subjects hopped on the hard surface (i.e., the force platform surface), the maximum vertical displacement of the center of mass (COM) of the body during the ground-contact phase (Δy_{tot}) was equal to the maximum displacement of the leg spring (ΔL; Fig. 2*A*). The average stiffness of the leg spring (k_{leg}) during the ground-contact phase was calculated by taking the ratio of the peak vertical ground reaction force (F_{peak}) to the ΔL at the instant that the leg spring was maximally compressed (*Eq. 1*). Because of the springlike nature of the leg, the peak ground reaction force and the peak leg spring displacement both occurred simultaneously at the middle of the ground-contact phase

$$k_{leg} = \frac{F_{peak}}{\Delta L} \tag{1}$$

ΔL was calculated by double integration of the vertical acceleration of the COM as calculated from the vertical ground reaction force. This technique has been used extensively and is described in detail elsewhere (5, 7). When the subjects hopped on the hard surface, the leg spring stiffness was equal to the total stiffness.

Calculation of leg spring stiffness and total stiffness on the elastic surface. When subjects hopped on the elastic surface, the vertical movements of the COM during the ground-contact phase depended on the stiffness of the leg spring and the stiffness of the surface (Fig. 2*B*). The stiffness of these two springs in series will be referred to as the "total stiffness" (k_{tot}). The average k_{tot} of the system was defined as the ratio of F_{peak} to Δy_{tot} at the instant of the ground-contact phase when the COM reached its lowest point

$$k_{tot} = \frac{F_{peak}}{\Delta y_{tot}} \tag{2}$$

The value for Δy_{tot} was calculated by integrating the vertical acceleration twice (5, 7).

Δy_{tot} comprised two components, ΔL and the vertical displacement of the surface (Δy_{surf})

$$\Delta y_{tot} = \Delta y_{surf} + \Delta L \tag{3}$$

The value for Δy_{surf} was calculated from the ratio of the peak vertical ground reaction force to the surface stiffness. The value for ΔL was then calculated from Δy_{tot} and Δy_{surf} by using *Eq. 3*. Subsequently, leg spring stiffness was calculated by using *Eq. 1*.

There were two approximations used in the calculation of leg spring stiffness for hopping on the elastic surfaces. First, we approximated that the force in the leg spring was equal to the ground reaction force. This approximation is reasonable because our measurements showed that the inertial force due to surface acceleration was very small (Fig. 3). The inertial force due to surface acceleration during a hop is equal to the product of the acceleration and effective mass (1.5 kg) of the surface. To determine the surface acceleration, we videotaped

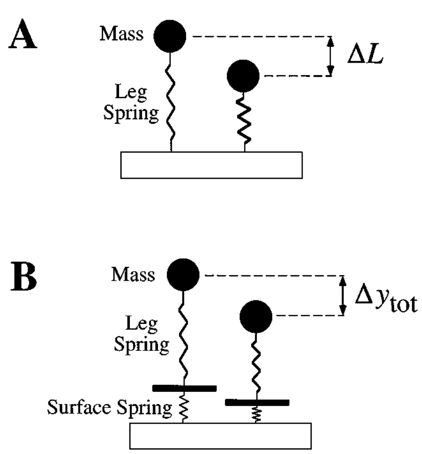

Fig. 2. *A*: spring-mass model on an extremely stiff surface shown at beginning (*left*) and middle (*right*) of the ground-contact phase. Model consists of a point mass and a single linear leg spring. Because vertical displacement of point mass is equal to maximum displacement of leg spring (ΔL), total stiffness is equal to leg stiffness. *B*: when humans hop on an elastic compliant surface, surface spring is in series with leg spring. Displacement of point mass (Δy_{tot}) is equal to sum of ΔL and surface spring displacement. Total stiffness is equal to series combination of leg stiffness and surface stiffness.

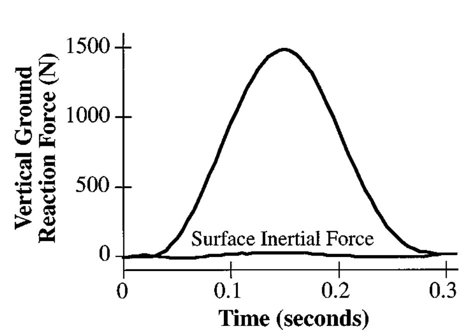

Fig. 3. Peak inertial force due to surface acceleration was <2% of vertical peak ground reaction force during hopping under all conditions. This typical graph shows surface inertial force and vertical ground reaction force during ground-contact phase of a hop.

the surface at 200 Hz (JC Labs, Mountain View, CA) while a subject hopped on the surface with the range of hopping frequencies and surface stiffnesses used in this study. The kinematic data were filtered by using a fourth-order zero-lag Butterworth low-pass filter (Peak Performance Technologies) with an optimal cutoff frequency (15 Hz) as determined by residual analysis (32). Peak surface acceleration during a hop was between 5 and 33 m/s^2, depending on surface stiffness and hopping frequency. The peak inertial force was always <2% of the peak vertical ground reaction force (Fig. 3). These experimental tests showed that the approximation that the force in the leg spring is equal to the vertical ground reaction force led to a maximum of 1.5% overestimation of the leg spring stiffness. Thus we concluded that it was reasonable to use the vertical ground reaction force as an approximation of the force in the leg spring for the calculation of leg spring stiffness.

The second approximation used was that Δy_{tot}, as calculated by integrating the vertical ground reaction force twice, was equal to the sum of ΔL and Δy_{surf} (*Eq. 3*). Integrating the vertical ground reaction force twice gives the vertical displacement of the COM of the entire system of masses that are moving on the force platform, including both the subject mass and the surface mass. Because the surface's COM and the subject's COM move relative to each other during the ground-contact phase, the leg spring displacement calculated from force platform measurements will be slightly lower than the actual leg spring displacement. The potential error due to this approximation was calculated from actual data for the surface effective mass (1.5 kg), the average mass of a subject (63.4 kg), and the distance between the two COMs (i.e., the length of the leg spring). The length of the leg spring at the instant of touchdown was estimated as the distance from the ground to the subject's greater trochanter (mean = 0.9 m). We calculated that the COM of the system, including both the subject and the surface, was 0.0225 m below the subject's COM at the instant of touchdown. Because the leg spring compressed during the first half of the ground-contact phase, the COM of the entire system moved upward relative to the COM of the subject. The maximum upward movement of the system's COM relative to the COM of the subject was 0.003 m (hopping frequency of 2 Hz, k_{surf} = 50.1 kN/m), causing a 3.8% underestimation of maximum displacement of the leg spring and a 3.7% overestimation of leg spring stiffness. Because this error is small compared with the adjustment of leg spring stiffness by as much as 3.6-fold when subjects hopped on surfaces of different stiffnesses, we concluded that it was reasonable to use this approximation in our calculation of leg spring stiffness.

RESULTS

Typical force-displacement curves for the leg spring are shown in Fig. 4 for a subject hopping at 2 Hz on the most stiff and least stiff surfaces. A single ground-contact phase is shown, including both the landing and takeoff curves. At the instant before the subject first touched the ground, the vertical ground reaction force and leg spring displacement were both zero. The force and the leg spring displacement both increased during the first half of the ground-contact phase. At the middle of the ground-contact phase, the force reached its maximum value at the same time as the leg spring was maximally compressed. During the second half of the contact phase, the force and displacement both decreased, reaching zero as the subject left the ground. During both landing and takeoff, the slope of the force-displacement curve gradually increased at low levels of force and displacement and became approximately linear at moderate and high levels of force and displacement. The average slope of the leg spring force-displacement curve during the ground-contact phase was the average leg spring stiffness. This average slope and thus the leg spring stiffness were much greater for hopping on the least stiff surface than for hopping on the most stiff surface.

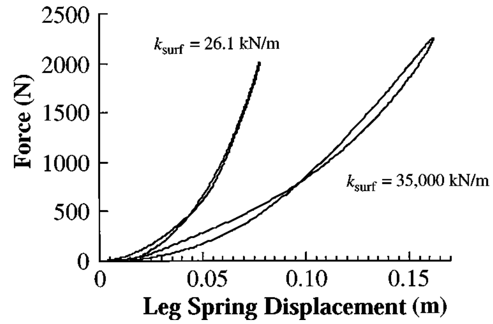

Fig. 4. Force in leg spring (vertical ground reaction force) plotted vs. leg spring displacement for ground-contact phase for 1 subject hopping at 2 Hz on most stiff and least stiff surfaces. Both landing and takeoff curves are shown for each hop. Average slopes of these force-displacement curves represent average leg stiffness. As surface stiffness (k_{surf}) decreased, this slope and thus leg stiffness increased.

When the subjects hopped at a frequency of 2 Hz on surfaces with a range of stiffnesses, the peak vertical ground reaction force decreased as surface stiffness decreased ($P < 0.0005$; Fig. 5*A*). The peak force decreased by 20% from 3.94 BW on the most stiff surface to 3.14 BW on the least stiff surface. The displacement of the leg spring also decreased as surface stiffness decreased but to a much greater extent (71%) than the peak force ($P < 0.0001$; Fig. 5*B*). The leg spring displacement was 0.138 m on the most stiff surface and 0.043 m on the least stiff surface. This decrease in displacement of the leg spring was due to a nearly threefold increase in leg spring stiffness when subjects hopped on the least stiff surface ($P < 0.005$; Fig. 5*C*). Leg spring stiffness increased from 17.8 kN/m on the most stiff surface to 53.3 kN/m on the least stiff surface. Although there were significant differences in leg spring stiffness among subjects ($P < 0.005$), all subjects increased their leg stiffness as surface stiffness decreased (subject-k_{surf} interaction, $P = 0.56$).

As a result of the adjustment to leg spring stiffness, the total stiffness and the ground-contact time remained the same regardless of surface stiffness (Fig. 6). The total stiffness was 17.8 kN/m during hopping on the most stiff surface and 16.7 kN/m during hopping on the least stiff surface ($P = 0.60$; Fig. 6*A*). The constant total stiffness allowed the subjects to use the same ground-contact time regardless of surface stiffness, ranging from 0.287 s on the least stiff surface to 0.268 s on the most stiff surface ($P = 0.17$; Fig. 6*B*).

In the second experiment, subjects hopped at a range of frequencies on an elastic compliant surface (k_{surf} = 50.1 kN/m) and on a very stiff surface (k_{surf} = 35,000 kN/m). The leg spring stiffness was significantly greater on the compliant surface than on the stiff surface at every hopping frequency ($P < 0.0001$; Fig. 7*A*). At a

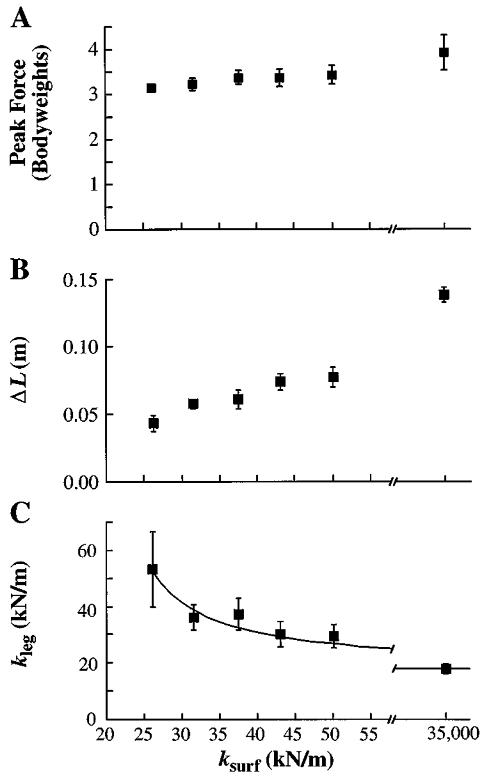

Fig. 5. *A*: when subjects hopped at 2 Hz on surfaces with different stiffnesses, peak vertical ground-reaction force decreased slightly on less stiff surfaces ($P < 0.0005$). *B*: ΔL decreased substantially on less stiff surfaces ($P < 0.0001$). *C*: leg spring stiffness (k_{leg}) was greater during hopping on less stiff surfaces ($P < 0.005$). Line, k_{leg} value required to maintain a constant total stiffness equal to value for hopping on hard surface of force platform ($k_{surf} = 35{,}000$ kN/m). ■, Means for all subjects ($n = 5$) in all parts. Error bars, SE.

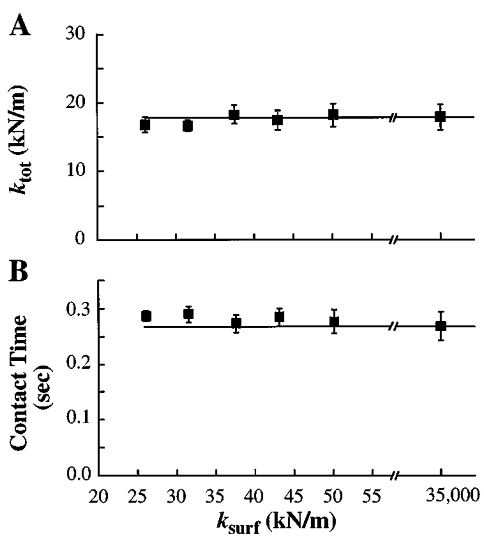

Fig. 6. *A*: when subjects hopped at 2 Hz on surfaces with a range of stiffnesses, total stiffness (k_{tot}) remained nearly the same regardless of k_{surf} ($P = 0.60$). Line, k_{tot} for hopping on most stiff surface (i.e., $k_{surf} = 35{,}000$ kN/m). *B*: ground-contact time also remained nearly the same regardless of k_{surf} ($P = 0.17$). Line, ground-contact time for hopping on most stiff surface ($k_{surf} = 35{,}000$ kN/m). Symbols and error bars are defined as in Fig. 5.

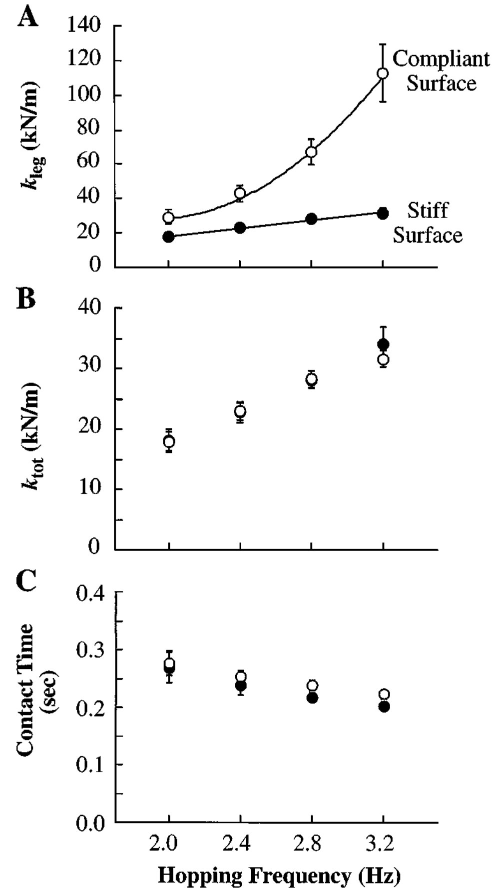

Fig. 7. *A*: when subjects hopped in place at a range of frequencies on a stiff surface (i.e., force-platform surface) and a compliant elastic surface ($k_{surf} = 50.1$ kN/m), k_{leg} at each frequency was greater on compliant surface than on stiff surface ($P < 0.0001$). Lines, least-squares regressions. *B*: k_{tot} was same on both surfaces at a given hopping frequency ($P = 0.44$). *C*: ground-contact time was slightly longer on compliant surface than on stiff surface ($P < 0.05$). However, difference was <10% even at greatest hopping frequency of 3.2 Hz. ●, Means for all subjects ($n = 5$) on stiff surface. ○, Means for all subjects on compliant surface. Errors bars, SE.

hopping frequency of 2.0 Hz, the stiffness of the leg spring was 1.65-fold greater on the compliant surface than on the stiff surface (17.8 and 29.4 kN/m, respectively). The increase in leg spring stiffness on the compliant surface was even greater at higher frequencies. At a hopping frequency of 3.2 Hz, leg spring stiffness increased by 3.6-fold from 31.6 kN/m on the stiff surface to 112.7 kN/m on the compliant surface.

Because subjects increased their leg stiffness for hopping on the compliant surface, the total stiffness was the same at each hopping frequency on both surfaces ($P = 0.44$; Fig. 7*B*). At a hopping frequency of 3.2 Hz, the total stiffness was 34.0 kN/m on the stiff surface and 31.6 kN/m on the compliant surface. As a result of the total stiffness being the same on both surfaces, the ground-contact time was <10% greater on the compliant surface than on the stiff surface at every hopping frequency ($P = 0.011$; Fig. 7*C*).

DISCUSSION

Although the actual musculoskeletal system is a complex combination of muscles, tendons, and ligaments, a simple spring-mass model accurately describes the mechanics of running, hopping, and trotting (4, 6, 13–15, 18, 20). This model represents the spring-like characteristics of the overall musculoskeletal system as a single linear spring (the leg spring). The stiffness of the leg spring remains nearly the same at all forward speeds in each of the animals studied to date, including running humans (14, 18). In addition, leg stiffness remains constant when humans run at reduced gravity levels (18). The only situations in which leg stiffness has been observed to change are when humans are asked to alter their preferred pattern for hopping in place or forward running by changing their hopping height or stride frequency (13, 15). These observations have led to speculation that the leg stiffness chosen during normal locomotion is strongly dependent on fundamental properties of the musculoskeletal system, such as tendon stiffnesses and reflex properties (18, 20).

The present study examined whether humans choose to adjust their leg spring stiffness to accommodate changes in terrain. When humans and other animals run in the natural world, they encounter a variety of terrains. However, we know very little about the biomechanics of locomotion on substrates other than hard and smooth laboratory floors. This study represents a first step toward understanding the role of musculoskeletal stiffness in the biomechanics and control of locomotion across a range of terrains.

Our findings support the hypothesis that humans adjust their leg spring stiffness to accommodate different surface stiffnesses. The stiffness of the leg spring is increased by as much as 3.6-fold to accommodate decreases in surface stiffness. As a result of the adjustment to the leg stiffness, the total stiffness of the series combination of the leg and the surface is nearly the same on all surfaces. This constant total stiffness makes it possible for the center of mass mechanics to be remarkably similar on surfaces with a wide range of stiffnesses. For example, the constant total stiffness allows the ground-contact time at a given hopping frequency to be nearly unaffected when surface stiffness is changed by as much as 1,000-fold (Fig. 6). If the leg spring stiffness had not been adjusted for different surfaces, the ground-contact time would have increased substantially on lower stiffness surfaces. For example, when the subjects hopped at 2 Hz on the least stiff surface, the ground-contact time would have been ~70% longer (0.499 vs. 0.287 s) if the leg spring stiffness had been the same as on the hard surface.

It should be emphasized that the leg stiffness adjustments and the constant total stiffness are not mechanically required to maintain a given hopping frequency. The mechanical behavior of a bouncing spring-mass system depends on its natural frequency. The natural frequency (f in *Eq. 4*) is determined by the k_{tot} of the system and the mass (m)

$$f = \frac{1}{2\pi}\sqrt{\frac{k_{tot}}{m}} \qquad (4)$$

Due to the aerial phase of hopping, there is a wide range of natural frequencies possible for a given hopping frequency. The only mechanical requirement is that the natural frequency of a subject's spring-mass system must be greater than or equal to the subject's hopping frequency. Experimental evidence has shown that humans are capable of hopping at 2.2 Hz with a natural frequency ranging from slightly >2.2 Hz up to 3.7 Hz (13). When the leg stiffness and the natural frequency used at a given hopping frequency increase, the person spends less time in contact with the ground and more time in the air (13). Thus it is both mechanically and physiologically possible for humans to hop at a given frequency while using a range of natural frequencies (13).

It would have been mechanically possible for the subjects to hop at 2 Hz on all of the surfaces when using the leg spring stiffness normally used on a hard surface (17.8 kN/m). On the least stiff surface (26.1 kN/m), this would have produced a total stiffness of 10.6 kN/m and a natural frequency of 2.06 Hz. This natural frequency is above the lowest possible natural frequency of 2 Hz. Our findings demonstrate that humans prefer to increase the stiffness of their leg spring to accommodate decreases in surface stiffness. For example, when subjects hopped at 2 Hz on the least stiff surface, they tripled the stiffness of their leg spring to 53.3 kN/m, keeping the total stiffness and the natural frequency nearly the same as on the hard surface. The constant total stiffness allowed the ground-contact time and the aerial time to remain nearly the same at a given hopping frequency regardless of surface stiffness. This strategy represents a choice and not a mechanical necessity. Additionally, related observations from our laboratory indicate that when subjects are allowed to freely choose their preferred hopping frequency on a range of surface stiffnesses, their preferred frequency is remarkably similar on surfaces with different stiffnesses. However, the leg spring stiffness at the preferred frequency increases by almost threefold when humans hop on the least stiff surface compared with the hard surface (n = 3; k_{surf} = 35,000 kN/m, preferred frequency = 2.2 Hz, k_{leg} = 18.9 kN/m; and k_{surf} = 26.1 kN/m, preferred frequency = 2.0 Hz, k_{leg} = 53.3 kN/m, respectively).

Running surfaces used by humans and other animals have a wide range of stiffnesses. Typical running tracks have much lower surface stiffnesses than the force platforms used for most locomotion biomechanics studies (track stiffnesses = 100–875 kN/m (21); force platform stiffness = 35,000 kN/m). When humans run on a very stiff surface, the most important parameter in determining the movements of the COM of the body and the ground-contact time is the vertical stiffness of their spring-mass system (14, 15, 18, 20). The vertical stiffness ranges from 20 kN/m at the lowest running speeds (18) to >100 kN/m at the highest running speeds (21). Thus the stiffness of some running tracks ranges from 1 to 8.7 times the vertical stiffness of the runner. Because the track stiffness is in the same range as the vertical stiffness during running, it may have a substantial effect on running mechanics if the vertical stiffness of the runner is not adjusted to accommodate the surface. During forward running, the vertical stiffness can be adjusted either by changing the leg spring stiffness or by changing the angle swept by the leg spring during the ground-contact phase (14, 18, 20). Our current research is examining stiffness adjustments for different surfaces in running humans.

It is interesting to note that the effect of surface stiffness on mammalian bouncing gaits is likely to vary with body size. Recent research has shown that the simple spring-mass model used to describe human hopping in place and human running also describes the biomechanics of bouncing gaits in a variety of hopping and trotting mammals. Both leg spring stiffness and vertical stiffness increase dramatically with body mass (M) in mammals ($k_{leg} \propto M^{0.67}$; vertical stiffness $\propto M^{0.61}$) (14). For example, the leg and vertical stiffnesses in a trotting horse are ~100 times greater than in a trotting rat (14). As a result, for a surface of a given stiffness, the ratio of the surface stiffness to the vertical stiffness will be 100-fold higher for the rat than for the horse. This means that a surface of a given stiffness is much less likely to affect the mechanics of locomotion in a rat than in a horse. A surface would have to be extremely compliant ($k_{surf} = <5$ kN/m) to require a substantial adjustment in the vertical stiffness of a trotting rat in order to maintain a constant total stiffness.

The increased stiffness of the leg spring on compliant elastic surfaces may lead to a lower energetic cost compared with hopping or running on hard surfaces. The metabolic energy cost of locomotion is thought to be determined by a combination of the cost of performing mechanical work and the cost of generating muscular force (2, 19). When a person hops on a compliant elastic surface, part of the mechanical work required for hopping is supplied by the musculoskeletal system and part is supplied by storage and recovery of elastic energy in the surface. By increasing leg stiffness on a compliant elastic surface, the human reduces the mechanical work done by the leg and increases the mechanical work done by the surface. The second factor important in determining the energetic cost of locomotion is the cost of generating muscular force (19). With increased leg stiffness on compliant elastic surfaces, there is reduced flexion of the leg joints during the ground-contact phase. This is likely to result in a better mechanical advantage for the locomotor muscles (3). As a result, the average muscle force required for hopping or running would also be reduced. Because both the amount of work done by the person and the amount of force generated by the muscles would be reduced, the energetic cost of hopping or running is likely to be lower on a compliant elastic surface than on a hard surface.

Although it is clear that humans adjust their leg stiffness to accommodate changes in surface stiffness during hopping, the physiological mechanisms for this adjustment are not yet known. The actual leg comprises multiple joints, with muscles, tendons, and ligaments acting about each joint. The overall stiffness of the leg undoubtedly depends on a combination of the geometry of the joints and the torsional stiffness of the joints. For example, running with flexed knees increases the moment arm of the ground reaction force about the knee and greatly decreases leg stiffness (22). Many motor control studies have shown that the stiffness of a joint is highly adjustable when it is subjected to externally driven displacements and depends on both muscle activation and the modulation of reflexes (12, 17, 27, 30, 31). However, data on human locomotion suggest that reflexes do not play a large role in the control of leg stiffness. When humans have their lower limb reflexes temporarily blocked by ischemia, they run in place with a ground-contact time that is nearly the same as with active reflexes, suggesting that leg stiffness is unchanged (11). Future research should explore the link among limb stiffness, joint stiffness, and muscle activation in locomotion.

Present studies in our laboratory are examining the mechanisms by which leg spring stiffness is adjusted and how surface stiffness affects leg stiffness during forward running. The findings from this research could aid in the construction of athletic surfaces designed to reduce locomotion-related injuries and have implications for the design of spring-based prosthetic legs and legged robots intended to traverse a wide variety of terrains. Although humans and other animals run on a huge variety of terrains in the natural world, much of the locomotion biomechanics research to date has focused on locomotion across hard and smooth laboratory floors. Our results provide important insight into how the behavior of the musculoskeletal system is controlled to accommodate different surface properties.

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