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Passive dynamics change leg mechanics for an unexpected surface during human hopping

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Moritz, Chet T., and Claire T. Farley. Passive dynamics change leg mechanics for an unexpected surface during human hopping. *J Appl Physiol* 97: 1313–1322, 2004. First published May 28, 2004; 10.1152/japplphysiol.00393.2004.—Humans running and hopping maintain similar center-of-mass motions, despite large changes in surface stiffness and damping. The goal of this study was to determine the contributions of anticipation and reaction when human hoppers encounter surprise, expected, and random changes from a soft elastic surface (27 kN/m) to a hard surface (411 kN/m). Subjects encountered the expected hard surface on every fourth hop and the random hard surface on an average of 25% of the hops in a trial. When hoppers on a soft surface were surprised by a hard surface, the ankle and knee joints were forced into greater flexion by passive interaction with the hard surface. Within 52 ms after subjects landed on the surprise hard surface, joint flexion increased, and the legs became less stiff than on the soft surface. These mechanical changes occurred before electromyography (EMG) first changed 68–188 ms after landing. Due to the fast mechanical reaction to the surprise hard surface, center-of-mass displacement and average leg stiffness were the same as on expected and random hard surfaces. This similarity is striking because subjects anticipated the expected and random hard surfaces by landing with their knees more flexed. Subjects also anticipated the expected hard surface by increasing the level of EMG by 24–76% during the 50 ms before landing. These results show that passive mechanisms alter leg stiffness for unexpected surface changes before muscle EMG changes and may be critical for adjustments to variable terrain encountered during locomotion in the natural world.

biomechanics; neural control; locomotion; running; gait

QUICKLY MOVING LEGGED ANIMALS traverse a huge variety of terrain with incredible grace and agility. This observation suggests that animals possess mechanisms that compensate for terrain changes extremely rapidly. Recent research has revealed that human hoppers and runners adjust stance leg mechanics to maintain similar center-of-mass dynamics over a large range of surface stiffness and damping (18, 20, 26, 30). Runners also conserve similar center-of-mass motions when they traverse an abrupt but expected change in surface stiffness (19). This conservation suggests that regulating center-of-mass dynamics may be a key strategy in the control of locomotion.

A combination of anticipation and reaction may help hoppers and runners to adapt seamlessly when surface properties change. The role of anticipation is clear when animals land from a jump or prepare for the stance phase of running. When monkeys and humans jump downward to land on a false surface, extensor muscle activity begins 80–200 ms before they expect to land on the false floor and is independent of the actual impact with a solid surface below (9, 11). Similarly, human runners begin to activate their leg extensor muscles 120–180 ms before touchdown (6, 8). Therefore, neural anticipation likely plays a role in adjusting to expected surface changes during locomotion across variable terrain.

Reflexive neural feedback probably augments anticipation as an animal adjusts to the new surface underfoot. Reflexes are heavily modulated during walking, hopping, and running (25, 37, 45). Specifically, cutaneous and stretch reflex excitabilities are high during the stance phase of hopping and running (3, 10, 12, 36, 40), suggesting that reflexes help produce the large burst of extensor muscle activity shortly after touchdown (12, 36). Reflex excitabilities, however, are smaller during running compared with walking (3, 44). Thus reflexes may play a smaller role as speed increases, and limb mechanics may dominate control during the short ground contact times of rapid locomotion.

Mechanical reactions to landing, caused by intrinsic muscle properties and passive dynamics of the body's linked segments, may contribute to adjustments for new surfaces more rapidly than reflexes. Intrinsic muscle properties provide a zero-delay feedback mechanism for stabilizing the joints after perturbations. Analytic models reveal that these properties, termed "preflexes" (27), stabilize human posture (43), knee bends (42), and arm flexion (1) after perturbations. For example, when a standing human is pushed forward, ankle flexion causes active ankle extensor muscles to stretch and immediately generate more force due to the force-velocity properties of muscle (22, 24). This preflex acts to extend the ankle and stabilize posture (43). Passive dynamics of the body's linked segments also help stabilize humans after perturbations. For example, passive dynamics play key roles when walking humans step over an obstacle (33) or recover from a trip (13). In these cases, active knee flexion results in passive hip flexion due to the mechanical interaction of adjacent segments. Muscle preflexes and passive dynamics likely play a key role in fast adjustments to surface changes during rapid locomotion.

The goal of the present study was to gain insight into the relative contributions of anticipation and reaction to the control of center-of-mass dynamics during rapid locomotion over changing surfaces. Mechanical reactions (i.e., preflexes and passive dynamics) may be critical in rapid locomotion because ground contact time is too short for reflexive neural feedback to change muscle force and center-of-mass dynamics before midstance. Therefore, we hypothesized that mechanical reactions change leg stiffness soon after landing on a surprise

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surface and before neural feedback contributes. It is known from previous studies that runners change leg stiffness for expected surface changes (19). This led to our second hypothesis that humans alter kinematics and/or muscle activation before contact when expecting a surface stiffness change. We tested these hypotheses by collecting ground reaction force, kinematics, and leg muscle electromyography (EMG) while subjects hopped in place on a sprung surface as we introduced surprise, expected, and random changes in surface stiffness.

METHODS

Ten healthy female subjects (body mass 57 ± 5 kg, height 167 ± 6 cm, age 22 ± 4 yr, means ± SD) hopped in place on a consistently hard surface and a consistently soft surface. Subjects also encountered surprise, expected, and random transitions from a soft surface to a hard surface. All subjects gave informed consent, and the University of Colorado Human Research Committee approved the protocol.

We chose to study hopping in place for several reasons. First, hopping in place is mechanically similar to forward running and thus serves as an excellent analog to forward running (15). Second, we could induce larger changes in surface stiffness during hopping compared with running without the risk of a fall or the need for a safety harness. Finally, it was more feasible to introduce a long series of random changes to surface stiffness during hopping than running.

Surface control. Subjects hopped in place on a custom-built surface mounted on a force platform (Fig. 1*A*). The surface stiffness could be abruptly changed from 27 kN/m (~6-cm peak compression) to 411 kN/m (~0.6 cm peak compression). The surface deck was a lightweight (3.7 kg), 60 × 60-cm fiberglass and aluminum honeycomb sandwich panel (Goodfellow, Berwyn, PA) supported by steel springs (Century Springs, Los Angeles, CA). We calculated surface stiffness from the linear force-displacement relations ($r^2 > 0.99$) determined from static tests. Surface damping was negligible at the compression velocities observed during hopping (damping ratio < 0.02).

The surface deck was constrained to only move vertically by a linear bearing assembly (INA, Fort Mill, SC) with the bearing races attached to the moving deck. To abruptly increase surface stiffness, we used two solenoid-activated locking mechanisms that blocked the linear bearing races, thereby limiting surface compression to 0.6 cm (Fig. 1*B*). The hard surface was not perfectly rigid (surface stiffness = 411 kN/m) due to rubber pads on the locking mechanisms. We wrote control software (Matlab 6.1, The Mathworks, Natick, MA) to monitor the ground reaction force and activate and deactivate the locking mechanisms during the aerial phase of a hop in surprise, expected, and random patterns. We surrounded the surface with soft foam rubber at the level of the surface deck for safety and to visually hide the locking mechanisms.

Hopping trials. For all trials, we instructed subjects to match the beat of a metronome, clasp their hands behind their backs, and leave the surface between each hop. Subjects wore full-coverage wireless stereo headphones (Amphony, Berlin, Germany), which played a metronome beat and white noise. We set the metronome at 2.2 Hz, which is approximately the preferred hopping frequency, regardless of surface stiffness (15, 18, 29). The white noise completely masked the clicks of the surface locking mechanisms. We collected data for 10 s after 30 s of hopping at the correct frequency for each trial and gave 2-min rests between trials.

We first collected data for subjects hopping on the sprung surface set to 27 kN/m ("consistently soft surface"). The consistently soft surface compressed by 6.1 ± 0.2 cm during hopping. At the beginning of the experiment, subjects were unaware that the surface stiffness could abruptly increase. During the second trial, the surface stiffness increased without warning ("surprise hard surface"; 411 kN/m; 0.6 ± 0.1 cm peak compression) for a single hop and then returned to the soft surface. Because the subjects might have changed hopping strategy if they knew that the surface stiffness could change, we surprised the subjects on only one hop.

Next, we told subjects that the surface would become stiff on every fourth hop ("expected hard surface"). The same surface stiffness values (27 and 411 kN/m) were used as in the previous trials. We also played a metronome with a corresponding different pitch every fourth beat. Subjects practiced this condition for 30 s before each data collection and performed four of these trials.

Subsequently, we told subjects that the surface stiffness would change randomly ("random hard surface"). For all subjects, we used the same computer-generated random sequence that increased surface stiffness on an average of 25% of the hops over an entire trial. Subjects again practiced this condition for 30 s before each data collection and performed four of these trials.

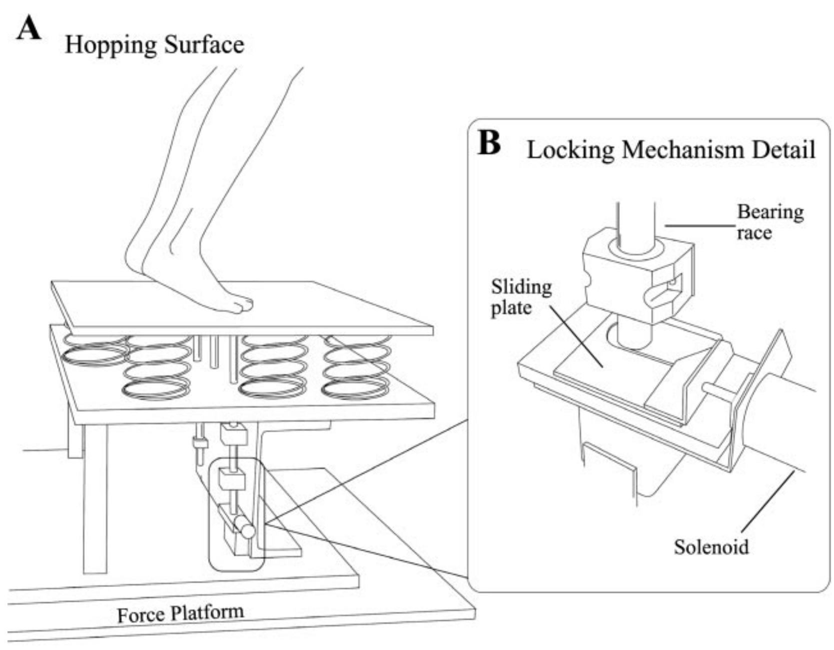

Fig. 1. *A*: diagram of the hopping surface. *B*: detail of the surface-locking mechanism. When the solenoid was activated, the sliding plate prevented the linear bearing races (mounting to the surface deck) from moving downward and increased surface stiffness from 27 to 411 kN/m. The locked surface was not perfectly rigid due to compression of hard rubber pads on the sliding plate.

At the conclusion of the session, we collected trials on the consistently hard surface (with the locking mechanism engaged continuously) and on the consistently soft surface. To convince subjects that there would be no further surprise surface changes during these final trials, we disconnected the cable between the control computer and the locking mechanisms, and we installed clamps under the hopping surface to hold the mechanisms either open or closed. Despite all efforts to reassure the subjects that there would be no further surprises, it is possible that the initial surprise trial affected the results of subsequent conditions. Nonetheless, no aspect of hopping dynamics changed between the consistently soft surface trials at the beginning and end of the experiment, suggesting that our results were not affected by experience with the surface changes during the experiment.

Data collection. To evaluate kinetic and kinematic evidence of anticipation and reaction, we recorded ground reaction force, surface deck position, and video kinematic data. We measured vertical and horizontal ground reaction force using a force platform (AMTI, Watertown, MA) under the hopping surface. In addition, we measured surface deck displacement using a linear potentiometer (Omega, Stamford, CT). We sampled force and surface position at 1,000 Hz using Labview 4.1 software (National Instruments, Austin, TX). We also collected sagittal plane kinematics (200 fields/s; JC Labs, Mountain View, CA) after placing reflective markers on seven anatomical landmarks (tip of first toe, fifth metatarsophalangeal joint, lateral malleolus, femur lateral epicondyle, greater trochanter, lateral iliac crest, and acromion scapulae).

To examine neural anticipation and reaction, we measured EMG activity from eight left leg muscles. We placed bipolar silver-silver-chloride electrodes (interelectrode distance, 2 cm) over the tibialis anterior, soleus, medial and lateral gastrocnemius, vastus medialis and lateralis, rectus femoris, and semitendinosus, according to guidelines (21). Electrodes and lead wires were secured to the leg with tape and elastic stockings and remained attached for all trials. We measured EMG using a Telemyo system (Noraxon, Phoenix, AZ) sampled at 1,000 Hz, concurrent with the force data.

Data analysis. We analyzed the single hop on the surprise hard surface for each subject. We also analyzed four hops from each of the two trials on the consistently soft surface and consistently hard surface. This yielded a total of eight hops on the consistently soft and hard surfaces. To obtain a matching number of hops from the expected and random conditions, we analyzed two hops from each of the four expected and random hard surface trials. Specifically, we analyzed the same two hops on the hard surface in each sequence from the expected and random trials. For the random condition, we selected hops on the hard surface for analysis where the preceding hop was on a soft surface. This allowed us to compare the soft-to-hard surface transition among the random, expected, and surprise conditions.

For each hop, we used the ground reaction force and surface position data to determine contact time, center-of-mass vertical movements, leg compression, and surface loading rate. We determined the first contact with the surface, as well as the stance and aerial times, using vertical force. We subtracted the inertial force due to surface acceleration (<4% of peak vertical force) and body weight from the ground reaction force to determine center-of-mass vertical acceleration. We then calculated the vertical displacement of the center of mass relative to the force platform by twice integrating the vertical acceleration with respect to time (4). We determined leg compression (i.e., reduction in distance between center of mass and surface in first half of stance) by subtracting the surface displacement from the center-of-mass vertical displacement. Finally, we calculated the average surface loading rate by dividing the magnitude of the peak vertical force by the time to reach that peak.

We determined average leg stiffness, instantaneous leg stiffness, the combined vertical stiffness of the leg and surface, and joint angles for each hop analyzed. We calculated average leg stiffness as the ratio of leg force (i.e., vertical ground reaction force) to compression when the leg was shortest. To determine when leg stiffness changed after touchdown on a new surface, we determined the instantaneous leg stiffness as the slope of the leg force-compression relationship over time. We calculated the combined vertical stiffness of the leg and surface as the ratio of force to downward center-of-mass displacement when the center of mass was lowest. We digitized and low-pass filtered marker positions at 7 Hz (Peak Motus 6.0, Englewood, CO) and determined the acute joint angles for the ankle, knee, and hip.

We determined the mean EMG for each muscle for the interval just before touchdown to evaluate anticipation. We band-pass filtered each EMG signal 20–500 Hz and then rectified it (Matlab 6.1, The Mathwork). We subsequently determined the mean activation during the 50 ms preceding each touchdown on each surface and expressed the values as a percentage of the mean activation for this time period on the consistently soft surface. Note that for the figures only, EMG was normalized to the entire hop cycle on the consistently soft surface.

Onset times. We determined the times when the kinematic and muscle activation data for hopping on each surface first differed from the consistently soft surface data. For the surprise, expected, and random hard surfaces, we compared the EMG and kinematic data for each hop to that subject's ensemble average profile for all hops on the consistently soft surface (28). Because the hops before landing on each hard surface were on a soft surface, this approach revealed whether subjects anticipated the hard surface by preparing during the preceding aerial phase or reacted to it after touchdown. We determined each subject's ensemble-average profile for each parameter by taking the average of eight hops on the consistently soft surface, with all hops aligned at touchdown. We defined the onset time as the first time when the kinematic or EMG profile differed by >2 SDs from the ensemble average for the consistently soft surface (28). For each muscle, we performed this analysis after low-pass filtering the rectified signal at 10 Hz.

We used this technique to calculate onset times for the EMG signals, leg joint angles, center-of-mass vertical displacement, and instantaneous leg stiffness. To assess reaction on the surprise hard surface, we searched for an onset from touchdown until toe-off. To assess both anticipation and reaction on the expected and random trials, we searched for an onset time from the preceding toe-off to the toe-off following the end of the stance phase on the hard surface.

The purpose of the onset analysis was to determine the time of reaction or anticipation if subjects exhibited a difference from the consistently soft surface. Therefore, we included a subject's onset time for a given parameter in the overall mean only if that subject had an onset in more than one-half of the hops on a given surface. We reported the number of subjects who contributed to each mean onset time value in Figs. 5 and 6. An onset was detected in 91 ± 1% of the hops analyzed on the surprise, expected, and random hard surfaces.

Statistics. We tested for differences among conditions using a one-way repeated-measures ANOVA and Bonferroni post hoc tests with an α of 0.05 for each variable individually (SPSS 9, Chicago, IL). All reported values are means ± SE.

RESULTS

Surprise hard surface. When subjects landed on the surprise hard surface in the midst of hopping on a consistently soft surface, joint flexion and leg stiffness began to change before any change in muscle activation. On the surprise hard surface, the ankle and knee joints began to flex more than on the consistently soft surface very soon after landing. The ankle began to flex more 47 ± 13 ms after landing, and the knee began to flex more 52 ± 11 ms after landing (Fig. 2*B*, see Fig. 5*A*, Table 1). Instantaneous leg stiffness became lower than on the consistently soft surface 52 ± 20 ms after landing (see Fig. 5*A*). EMG began to change later than the kinematics and

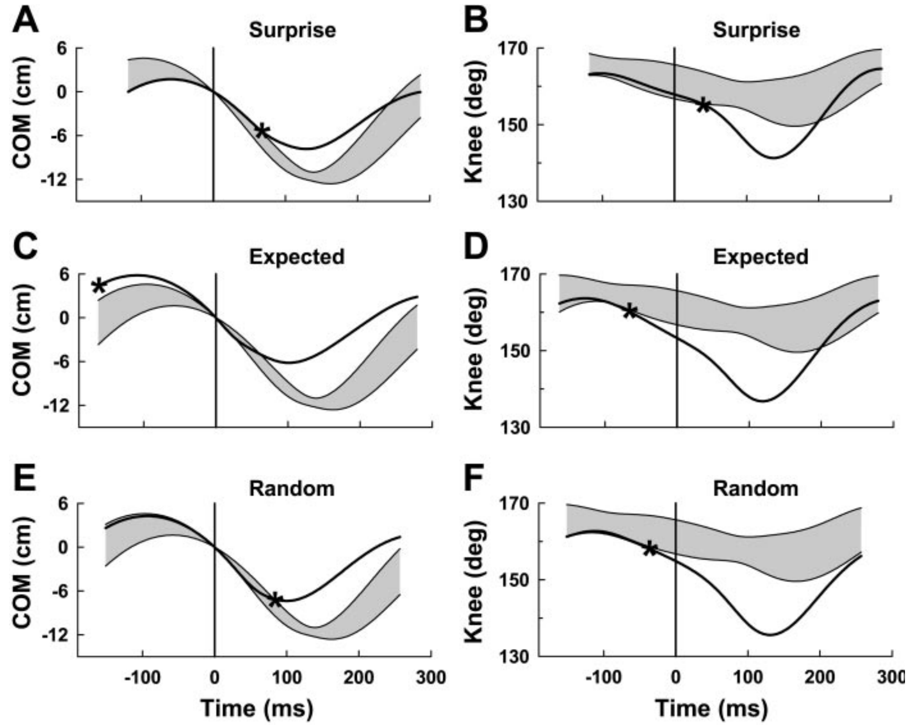

Fig. 2. Examples of center-of-mass (COM) vertical displacement and knee angle vs. time on surprise (*A* and *B*), expected (*C* and *D*), and random (*E* and *F*) hard surfaces. A complete hop cycle from toe-off to toe-off is shown, and the vertical line at *time 0* indicates touchdown on the surface. The shaded region bounded by thin lines is ±2 SD from the ensemble-average data for this subject on the consistently soft surface. Each asterisk (*) indicates the onset time of a difference from the consistently soft surface data (summarized in Figs. 5 and 6). COM displacement at touchdown is defined as zero. On the surprise hard surface, COM displacement (*A*) and knee angle (*B*) became different from the consistently soft surface data shortly after landing. When expecting a surface change, subjects hopped higher in the air (*C*) and increased knee flexion (*D*) before contact with the surface.

mechanics. In muscles crossing the ankle, EMG began to increase above values on the consistently soft surface 108–160 ms after landing, and upper leg muscle EMG began to increase 68–188 ms after landing (Figs. 3, *A* and *B*, 4, and 5*B*). The early joint flexion was likely caused by the 77% faster rise in the ground reaction force on the surprise hard surface than on the consistently soft surface (Table 1). On the surprise hard surface, kinematics, leg stiffness and EMG deviated from their profiles on the consistently soft surface in 92 ± 3% of the hops analyzed.

Expected hard surface. In contrast to their adjustments after landing on the surprise hard surface, subjects began to change kinematics and muscle activation 3–76 ms before landing on the expected hard surface (Fig. 5). Compared with the consistently soft surface, subjects hopped 50% higher in the aerial phase before the expected hard surface and landed with more knee flexion (Fig. 2, *C* and *D*, and Table 1). Similarly, subjects increased muscle activation 24–76% during the 50 ms before landing on the expected hard surface than on the consistently soft surface (Figs. 3, *C* and *D*, and 4; Table 2). Finally, leg stiffness was lower on the expected hard surface than on the consistently soft surface immediately after touchdown (Fig. 5*A*). Note that leg stiffness can be determined only after landing.

Random hard surface. When the surface randomly changed from soft to hard, subjects used a similar kinematic strategy but a different muscle activation strategy than for the expected hard surface. Compared with the consistently soft surface, subjects landed with more flexed knees when they knew that the surface might randomly become hard (Fig. 2*F* and Table 1). This change in knee angle began 54–77 ms before landing (Figs. 2*F* and 6*A*). Thus subjects flexed their knees more before landing on random or expected hard surfaces. Unlike the expected hard surface, however, EMG in most muscles did not increase before landing in the random trials (Fig. 3, *E* and *F*). Rather, muscle

Table 1. *Hopping dynamics for the consistently soft, surprise, expected, random, and consistently hard surfaces*

Condition	Consistently Soft	Surprise Hard	Expected Hard	Random Hard	Consistently Hard
Aerial time, ms	135±6	124±6	157±6*	150±6	135±6
Contact time, ms	319±6	310±17	277±7*	285±6*	320±6
Downward COM displacement-contact, cm	11.9±0.1	8.0±0.5*	9.3±0.3*	9.2±0.4*	11.7±0.2
Upward COM displacement-aerial, cm	2.2±0.2	2.1±0.5	3.3±0.4*	2.6±0.5	3.2±0.4
Maximum leg compression, cm	5.8±0.2	7.4±0.5	8.8±0.3*	8.6±0.4*	11.0±0.3*
Landing loading rate, kN/s	10.3±0.6	18.2±1.4*	21.4±2.6*	21.5±2.2*	12.9±1.3
Ankle angle at touchdown, degrees	123±2	124±2	125±2	124±2	129±2*
Ankle flexion; landing to peak flexion, degrees	17±2	21±2	21±2	20±2	31±2*
Knee angle at touchdown, degrees	157±1	157±1	153±1*	154±1*	152±1*
Knee flexion; landing to peak flexion, degrees	6±2	14±1*	14±2*	15±2*	21±1*
Hip angle at touchdown, degrees	167±2	167±2	165±2	166±3	165±2
Hip flexion; landing to peak flexion, degrees	3±2	6±2	7±2*	8±3*	11±2*

Values are means ± SE for all subjects. COM, center of mass. Upward COM displacement–aerial data are for the aerial phase before landing on each surface. *Significant difference from the consistently soft surface, $P < 0.05$.

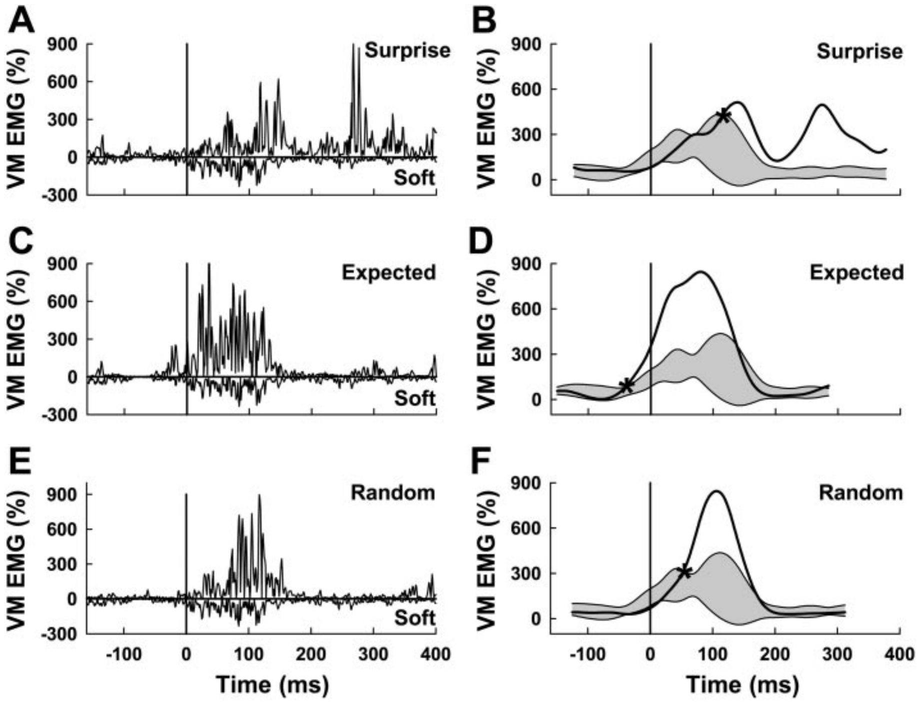

Fig. 3. Vastus medialis (VM) electromyography (EMG) vs. time for surprise (*A* and *B*), expected (*C* and *D*), and random (*E* and *F*) hard surfaces. *A*, *C*, and *E*: rectified VM EMG for an example hop is shown for the surprise, expected, and random hard surface and for the consistently soft surface (inverted). *B*, *D*, and *F*: example data from *A*, *C*, and *E* after low-pass filtering at 10 Hz. The shaded region bounded by thin lines is ±2 SD from this subject's ensemble average on the consistently soft surface. Each asterisk (*) indicates onset time of a difference from the consistently soft surface data (summarized in Figs. 5 and 6). Contact with the surface begins at *time 0* (vertical line). A full hop is shown from one toe-off to the next. EMG is expressed as a percentage of mean activation over the hop cycle on the consistently soft surface. Hoppers began to change muscle activation well after touchdown when surprised by a surface change but before touchdown when expecting a surface change.

activation generally became greater than on the soft surface 17–77 ms after touchdown (Figs. 3, *E* and *F*, 4, and 6*B*).

Comparison among surfaces: center-of-mass dynamics and average leg stiffness. Despite the lack of anticipation of the surprise hard surface, hoppers used similar average leg stiffness values for the surprise hard surface as on the expected and random hard surfaces. Because average leg stiffness was similar, downward center-of-mass displacement during stance and leg compression varied by <1.4 cm among the surprise, expected, and random surface changes (Figs. 7 and 8, Table 1).

On the expected, random, and surprise hard surface changes, subjects used different leg stiffness values than on the consistently hard surface (Fig. 7). Subjects reduced leg stiffness by 47% on the consistently hard surface to maintain the same downward center-of-mass displacement during stance and the same vertical stiffness as on the consistently soft surface (Fig. 8). Although leg stiffness was similar on the surprise, expected, and random hard surfaces, it was too low to maintain the same vertical stiffness as on the consistently soft surface (Figs. 7 and 8). As a result, on the surprise, expected, and random hard surfaces, the center of mass moved downward by 22–33% less during stance, and the combined vertical stiffness of the leg and surface was 28–36% greater than on the consistently soft or hard surfaces (Figs. 8, *B* and *C*). Without any change to leg stiffness from the value used on the consistently soft surface, center-of-mass displacement would have decreased by 50%, and vertical stiffness would have increased by 109%.

DISCUSSION

Our finding that leg stiffness decreases before muscle EMG changes supports the first hypothesis that passive mechanical reactions rapidly decrease leg stiffness when humans are surprised by an increase in surface stiffness. These passive mech-

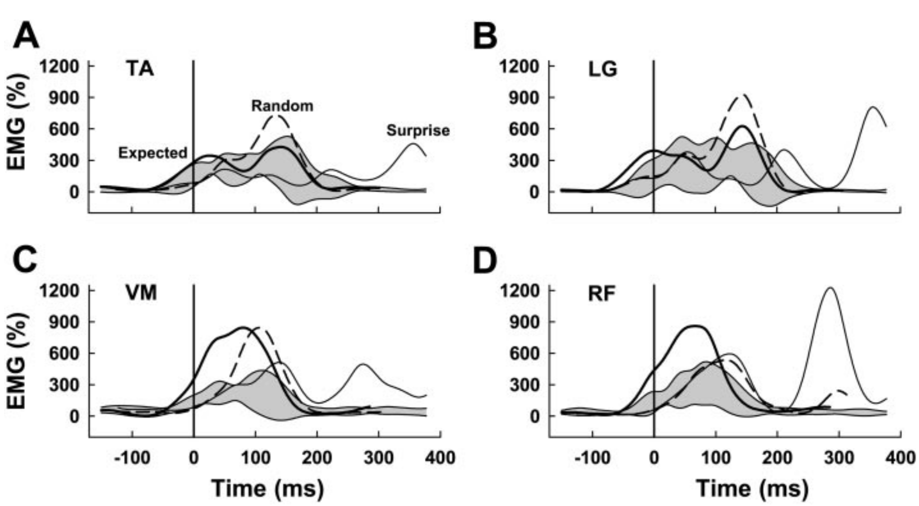

Fig. 4. Example of rectified and low-pass filtered EMG for tibialis anterior (TA; *A*), lateral gastrocnemius (LG; *B*), vastus lateralis (VL; *C*), and rectus femoris (RF; *D*) vs. time for a single hop from one toe-off to the next. Contact with the surface began at *time 0* (vertical line). Thin lines represent the surprise hard surface, thick lines represent the expected hard surface, and dashed lines represent the random hard surface. The shaded region bounded by thin lines is ±2 SD from the ensemble average on the consistently soft surface. Data are expressed as a percentage of the mean activation over the hop cycle on the consistently soft surface. Generally, muscle activation first exceeded levels on the consistently soft surface (shaded region) before touchdown on the expected surface, shortly after touchdown on the random surface, and later in the contact phase on the surprise surface. The dashed line for the random hard surface data is often overlaid by other lines early in the hop.

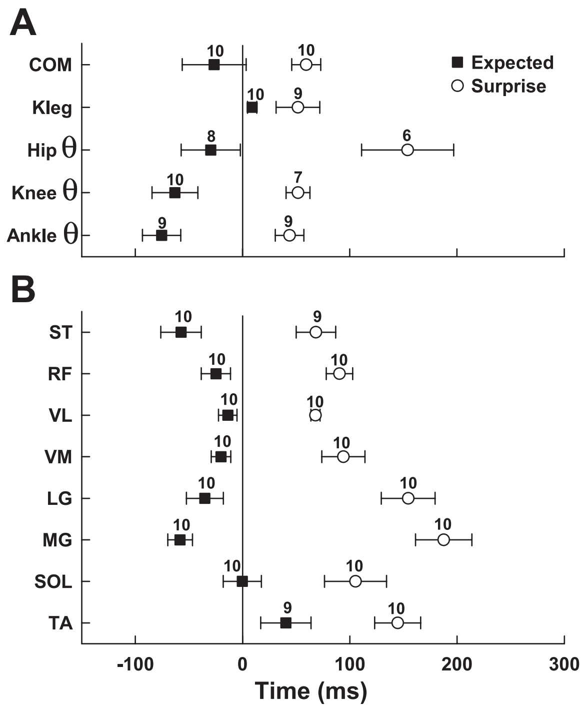

Fig. 5. Time relative to touchdown of first difference from the consistently soft surface data in kinematics (*A*) and muscle activation (*B*) for the expected and surprise hard surfaces. Values are means ± SE; n = 10. Touchdown occurred at *time 0* (vertical line). Values above data points are the no. of subjects (out of 10) whose data deviated from their consistently soft surface data (see METHODS for criteria). k_{leg}, Instantaneous slope of leg force vs. displacement; θ, joint angles; ST, semitendinosus; MG, medial gastrocnemius; SOL, soleus. When hoppers were surprised by a surface change, kinematics changed a short time before muscle activation changed. Both kinematics and muscle activation changed later when hoppers were surprised than when they expected a surface change ($P < 0.05$).

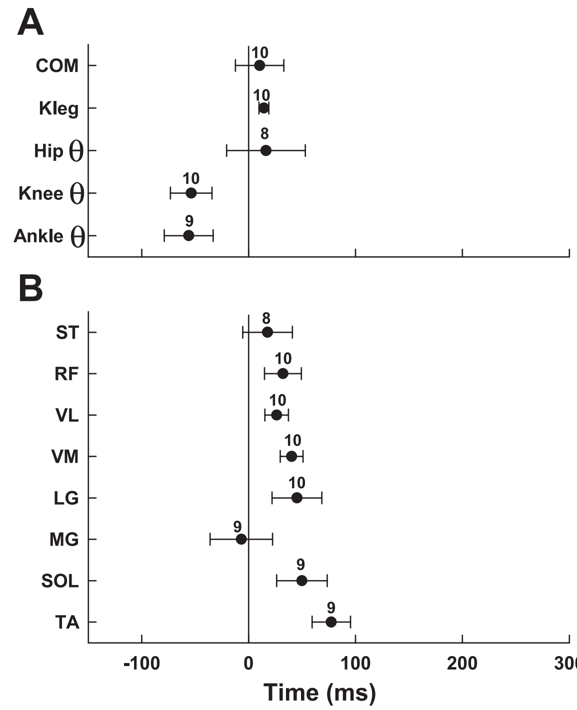

Fig. 6. Time relative to touchdown of first difference from the consistently soft surface in kinematics (*A*) and muscle activation (*B*) for the random hard surface. Values are means ± SE; n = 10. Touchdown occurred at *time 0* (vertical line). Values above data points are the no. of subjects (out of 10) whose data deviated from their consistently soft surface data. On the random hard surface, the ankle and knee angle became more flexed before landing, and muscle activation generally increased shortly after landing.

anisms begin to change leg stiffness before any change in neural control. Although anticipation is not evident when hoppers are surprised by a change in surface stiffness, it does play a role when hoppers expect a surface stiffness change. We find that when humans expect an increase in surface stiffness for the next stance phase, they hop higher, flex their knees more, and increase leg muscle activation before contact with the surface, as predicted by our second hypothesis. Despite the complete lack of these anticipatory changes for a surprise hard surface, hoppers have the same stance-phase peak joint flexion, leg compression, and downward center-of-mass movement as on an expected hard surface. Although we find no evidence of EMG changes preceding the kinematic changes on the surprise hard surface, it is possible that muscles whose EMG we did not measure contribute to the kinematic change. Nonetheless, our findings strongly suggest that passive mechanical reactions play a critical role in changing leg stiffness for surprise surface transitions.

Mechanical reactions. Passive mechanical reactions likely cause the leg and joint changes that occur before muscle activation changes after touchdown on a surprise hard surface. When hoppers land on a surprise hard surface, the ankle and knee become more flexed than on a consistently soft surface before muscle activation changes. Passive interaction between a surprise hard surface and legs likely causes early joint flexion, which, in turn, helps decrease leg stiffness (Fig. 9). These mechanical reactions are not due to muscle force-

Table 2. *Mean EMG for the final 50 ms of the aerial phase*

Condition	Consistently Soft	Surprise Hard	Expected Hard	Random Hard	Consistently Hard
Tibialis	100±13	104±8	129±14	96±11	150±15*
Soleus	100±8	93±14	124±12	105±11	119±17
Medial gastrocnemius	100±17	136±27	151±28	110±20	147±30
Lateral gastrocnemius	100±9	116±17	157±19*	117±12	138±10
Vastus medialis	100±4	70±8	149±15*	105±12	81±14
Vastus lateralis	100±4	98±22	162±15*	109±9	86±16
Rectus femoris	100±3	82±15	176±20*	119±15	101±14
Semitendinosus	100±12	91±18	138±27	83±8	142±37

Values are means ± SE in percent for all subjects. Shown is the mean aerial-phase EMG, expressed as a percentage of value on the consistently soft surface, for the surprise, expected, random, and consistently hard surfaces. All EMG values are for the final 50 ms of the aerial phase before contact. *Significant difference from the consistently soft surface, $P < 0.05$.

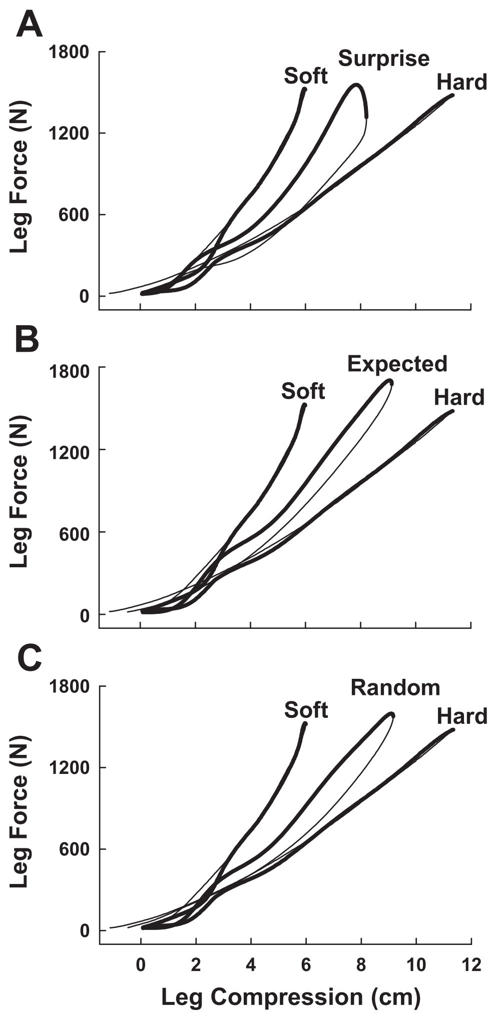

Fig. 7. Example of leg force vs. leg compression for a contact phase on surprise (*A*), expected (*B*), and random (*C*) hard surfaces. Positive compression represents shortening of the leg. Thick lines represent the landing phase when the force rises and the legs compress. Thin lines represent the takeoff phase when the force decreases and the legs extend. Each panel contains the same example data from consistently "soft" and "hard" surfaces. The average slope of each landing curve is defined as leg stiffness. Hoppers used similar leg stiffness values on the expected (19.0 kN/m), random (17.3 kN/m), and surprise (18.1 kN/m) hard surfaces (P = 1.0). These values were between the values on the consistently hard surface (14.6 kN/m) and consistently soft surface (27.6 kN/m).

velocity properties but rather to the orientation of the leg segments. Specifically, when the feet hit a surprise hard surface, it does not compress substantially, and thus the ground reaction force rises sharply. This impact causes the foot and shank to decelerate rapidly. Because the hoppers expect a soft surface before landing, they do not activate their muscles sufficiently to prevent the hard surface from driving the joints into greater flexion. Consequently, both the ankle and knee flex more rapidly than on a soft surface.

Greater joint flexion leads to a less stiff leg because leg stiffness is very sensitive to changes in the ground reaction force moment arm about the joints (16, 17). Specifically, the longer moment arms associated with a flexed leg dramatically decrease leg stiffness for two reasons. First, when the ground reaction force moment arms about the joints are greater, a given ground reaction force is associated with larger joint moments and thus more joint flexion for a given level of extensor muscle activation. Second, due to the longer moment arms, a given joint angular displacement leads to a greater change in leg length. For these reasons, even a small change in joint flexion and the moment arm of the ground reaction force can lead to a large change in leg stiffness. For example, a previous study showed that 11° more knee flexion at touch-down increases the ground reaction force moment arm about the knee by 4 cm and thereby reduces leg stiffness by 30% to compensate for a stiffer surface during hopping (16). Although we did quantify the change in joint flexion on the surprise hard surface, we could not quantify the ground reaction force moment arm about the joints because the impact of the bearing races against the locking mechanisms resulted in vibrations that made the center of pressure calculations unreliable.

The preceding explanation of passive mechanical reactions is based on a simplified model of a very complex situation. Our explanation does not account for the changes in the moment arm of the muscles about the joints with increased flexion. Preliminary simulations with a forward-dynamic musculoskeletal model, however, reveal that very similar passive reactions occur when these internal moment arms and muscle properties

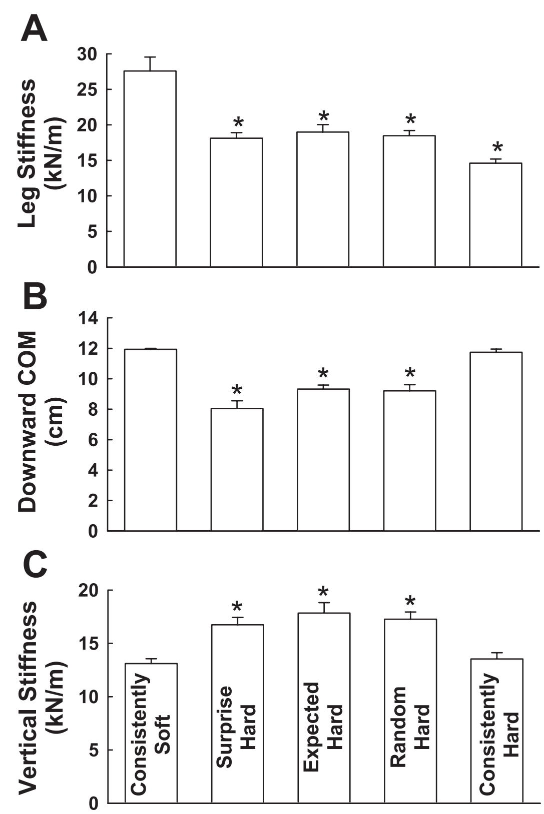

Fig. 8. Leg stiffness (*A*), downward COM displacement during stance (*B*), and combined vertical stiffness (*C*) of the leg and surface. Values are means + SE; n = 10. *Significant difference from the consistently soft surface. Compared with the consistently soft surface, hoppers decreased leg stiffness by an average of 33% on the surprise, expected, and random hard surfaces and by 47% on the consistently hard surface. This leg stiffness adjustment was sufficient to maintain a similar vertical stiffness and COM displacement as on the consistently soft surface when they were on the consistently hard surface, but it was not quite sufficient on the expected, random, and surprise hard surfaces. Without any change to leg stiffness from the value used on the consistently soft surface, vertical stiffness would have been 27.4 kN/m on the hard surfaces.

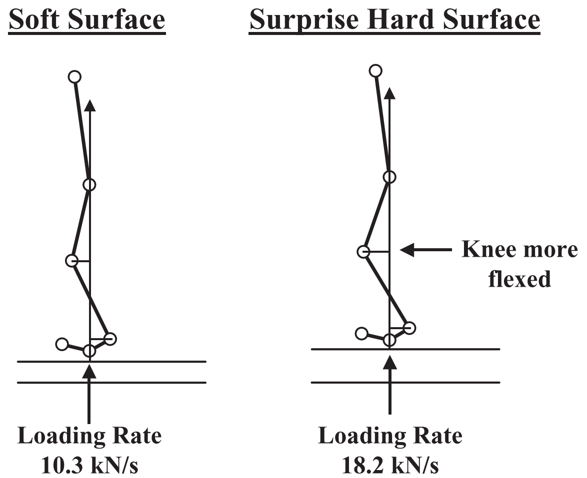

Fig. 9. Passive mechanical reactions change leg stiffness for the surprise hard surface. Representative joint kinematics are shown at midstance on the consistently soft surface and the surprise hard surface. When hoppers land on the surprise hard surface, the surface loading rate is 70% greater than on the soft surface due to a rapid deceleration of the feet and shanks. This high loading rate forces the joints into greater flexion on the surprise surface because the muscles are not sufficiently activated to resist this force. Greater joint flexion increases the moment arm of the ground reaction force and thus decreases leg stiffness rapidly on the surprise hard surface.

are included. Further work is needed to identify the precise mechanisms responsible for passive mechanical reactions.

Passive mechanical reactions, similar to the reactions that occur on a surprise hard surface, play critical roles in response to other perturbations during locomotion. Intersegment dynamics of the leg cause passive hip flexion as a result of active knee flexion when walking humans recover from a trip (13). Similarly, when running cockroaches are laterally perturbed, recovery from the perturbation occurs before reflexes could have affected body dynamics, suggesting that the body's linked segment mechanics or intrinsic muscle properties may cause this early recovery (23). Finally, a simple spring-mass model can converge on stable running due to passive mechanical reactions to changes in speed and aerial phase height (35).

Preflexes, such as muscle force-velocity properties, may also act to stabilize the legs when hoppers land on a surprise hard surface. Because the joints flex more rapidly during landing, active extensor muscles will be stretched more quickly than on a consistently soft surface. Faster muscle lengthening will allow muscles to generate higher forces and joint moments for a given level of activation (22, 24). Higher joint moments could help prevent the more flexed legs from collapsing at midstance on a surprise hard surface. Higher joint moments do not necessarily increase leg stiffness because leg stiffness depends on both joint stiffness and ground reaction force moment arm, with the latter increasing with joint flexion. Modeling studies have revealed that muscle force-velocity properties also help stabilize posture (43), knee bends (42), and elbow flexion (1).

Neural reactions. The slow changes in EMG after landing on a surprise hard surface suggest a mix of reflexive feedback sources. Leg muscle EMG begins to increase 68–188 ms after touchdown on a surprise hard surface. A similar delay (60–140 ms) occurs when walkers trip during the swing phase (14). In the present study, the long delay suggests that the increased muscle activation is not caused by short-latency, monosynaptic stretch reflexes that have delays of only 35–45 ms between muscle stretch and EMG rise (7, 8, 12, 37, 39, 44). The longer delays in the present study fall between middle- and long-latency responses. Cutaneous reflexes in the foot could cause the earliest EMG changes after impact with a surprise hard surface. They have a 50- to 80-ms onset latency and affect muscle activation strongly in running (2, 10). The latest increases in muscle activity (150–188 ms; e.g., medial and lateral gastrocnemius) after landing on a surprise hard surface might be caused by long-latency, polysynaptic reflexes, such as those acting at 146–199 ms after walking humans slip (28). Finally, muscle activation increases slightly earlier after hoppers land on a random hard surface than on a surprise hard surface, suggesting that reflex excitability may have been higher when hoppers know that surface stiffness might change on any hop (see Figs. 5 and 6).

Anticipation. The present study, combined with recent work of others, provides clear evidence of mechanical adjustments in anticipation of surface properties during human locomotion. We find that hoppers anticipate a predictable or random increase in surface stiffness by landing with greater knee flexion. Similarly, when humans run on an uneven surface, they land with 1.5° more stance leg knee flexion than on a smooth surface (38). When subjects walk across a surface that may be slippery, they anticipate a possible slip by decreasing the angle between the foot and ground at contact (5, 28).

To complement mechanical anticipation, hoppers use neural anticipation of an expected surface change that is similar to neural anticipation of landing from a jump. We find that when hoppers expect an increase in surface stiffness, they begin to change the EMG of most muscles 14–58 ms before landing. Similarly, when humans or monkeys jump downward to land on solid or false floors, extensor EMG begins 60–120 ms before the expected landing (9, 11, 34). Hoppers and jumpers likely alter muscle activation in anticipation of landing to permit muscles to develop force in time for contact with the surface, despite electromechanical delay (31, 32, 41, 46).

Leg adjustments. Although hoppers adjust leg stiffness to produce nearly identical vertical stiffness and center-of-mass dynamics for consistently soft and hard surfaces in the present study and earlier studies (16, 18), they do not change leg stiffness as much for the expected, random, and surprise surface changes. When hoppers encounter an expected, random, or surprise change from a soft to a hard surface, they decrease leg stiffness by ~33%. In contrast, leg stiffness is 47% lower on a consistently hard surface than on a consistently soft surface. Due to the smaller reduction in leg stiffness for an abrupt surface stiffness increase, hoppers have somewhat different center-of-mass dynamics than on a consistently hard surface. For example, after an expected, random, or surprise increase in surface stiffness, the center of mass moves downward by a smaller distance during the stance phase, and vertical stiffness is higher than on consistently hard and soft surfaces.

The change in vertical stiffness after a change in surface stiffness in this study contrasts with a previous study of expected surface changes during running. When human runners traverse a single expected change in surface stiffness, they adjust leg stiffness for their first step on the new surface so that vertical stiffness and center-of-mass dynamics change very little (19). In the present study, it is possible that hoppers do not adjust leg stiffness sufficiently to conserve vertical stiffness because they hop only once on the expected hard surface before the surface becomes soft again. In contrast, previous running studies maintained a consistent surface stiffness after the expected transition (19). It is not surprising that a different strategy is used for a transient surface change than for a single transition to a new surface.

Summary. When hoppers land on a surprise hard surface, passive mechanics begin to change leg stiffness to compensate for the new surface soon after landing and before any change in EMG. In contrast, hoppers anticipate predictable changes in surface stiffness in the preceding aerial phase by hopping higher, increasing EMG, and changing leg geometry. Similarly, hoppers anticipate random changes in surface stiffness before landing by changing leg geometry but not EMG. Despite the lack of these anticipatory changes when they are surprised by a new surface, hoppers use nearly the same leg stiffness and center-of-mass dynamics as for an expected surface change. Impacting a surprise hard surface rapidly changes leg geometry and thereby causes an almost immediate change in leg stiffness. These results show that passive mechanics adjust leg stiffness for surprise surface changes with shorter delays than neural reflexes and may be critical for producing stable locomotion over variable terrain.

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