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Human hopping on very soft elastic surfaces: implications for muscle pre-stretch and elastic energy storage in locomotion

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Summary

During hopping in place and running, humans maintain similar center of mass dynamics by precisely adjusting leg mechanics to compensate for moderate changes in surface stiffness. We investigated the limits of this precise control by asking humans to hop in place on extremely soft elastic surfaces. We found that hoppers drastically altered leg mechanics and maintained similar center of mass dynamics despite a sevenfold change in surface stiffness (11–81 kN m^{-1}). On the stiffest surfaces, the legs compressed in early stance and then extended in late stance in the pattern that is typical for normal bouncing gaits. On the softest surfaces, however, subjects reversed this pattern so that the legs extended up to 8 cm in early stance and then compressed by a similar distance in late stance. Consequently, the center of mass moved downward during stance by 5–7 cm less than the surface compressed and by a similar distance as on the stiffest surfaces. This unique leg action probably reduced extensor muscle pre-stretch because the joints first extended and then flexed during stance. This interpretation is supported by the observation that hoppers increased muscle activation by 50% on the softest surface despite similar joint moments and mechanical leg work as on the stiffest surface. Thus, the extreme adjustment to leg mechanics for very soft surfaces helps maintain normal center of mass dynamics but requires high muscle activation levels due to the loss of the normal extensor muscle stretch–shorten cycle.

Key words: running, biomechanics, spring-mass model, gait.

Introduction

Running animals traverse an astounding variety of terrain while gracefully maintaining bouncing gaits. Recent studies have examined how human hoppers and runners precisely adapt to changing surface properties. When surface stiffness varies over a moderate range, hoppers and runners use spring-like leg behavior and adjust leg stiffness to maintain similar center of mass dynamics (Farley et al., 1998; Ferris and Farley, 1997; Ferris et al., 1998, 1999; Kerdok et al., 2002). Moreover, on heavily damped surfaces, humans abandon spring-like leg behavior to replace the energy lost by the surface and prevent changes to center of mass dynamics during hopping in place (Moritz and Farley, 2003). On all surfaces, hoppers and runners maintain the same combined stiffness of the surface and leg (i.e. 'preferred vertical stiffness') regardless of surface stiffness or damping. Furthermore, on moderately stiff elastic surfaces, damped surfaces and hard surfaces, the legs first compress in early stance and then extend in late stance.

While previous studies have examined locomotion on a range of surfaces, none have examined hopping or running on extremely soft elastic surfaces. On extremely soft surfaces, hoppers and runners would need to adjust leg mechanics drastically to prevent the surface from dictating center of mass dynamics. It is obvious that when a person bounces on a trampoline, the extremely low stiffness of the surface dictates the dynamics of the bouncing movement. In fact, McMahon and Greene's (1979) model predicts that below an optimal track stiffness the track will dictate a longer contact time and a slower top speed.

The goal of the present study is to examine whether humans can compensate for extremely soft elastic surfaces to prevent the surface from dictating center of mass dynamics. On extremely soft surfaces, it is mechanically impossible to prevent the surface from dictating center of mass dynamics without abandoning spring-like leg mechanics. In earlier studies, surface stiffness has always exceeded the preferred vertical stiffness for hopping or running (Farley et al., 1998; Ferris and Farley, 1997; Ferris et al., 1998, 1999; Kerdok et al., 2002). Therefore, the legs behaved like springs regardless of surface stiffness and subjects maintained a constant vertical stiffness of the leg–surface combination (i.e. 'preferred vertical stiffness') by adjusting leg stiffness to offset changes in surface stiffness. This study extends the surface stiffness range below the preferred vertical stiffness for hopping. Consequently, if hoppers maintain normal spring-like leg mechanics, they cannot achieve the preferred vertical stiffness of the leg–surface combination. On these extremely soft elastic surfaces, hoppers may allow the surface stiffness to dictate the vertical stiffness or they may abandon spring-like leg mechanics to achieve the preferred vertical stiffness.

We first hypothesized that hoppers abandon spring-like leg mechanics on very soft elastic surfaces to prevent large reductions in vertical stiffness. Based on this hypothesis, we predicted that on very soft elastic surfaces, hoppers would extend their legs as the surface moves downward in early stance and then retract their legs as the surface moves upward in late stance. Furthermore, when surface stiffness equals the preferred vertical stiffness, hoppers may simply ride the surface and perform very little leg work. Therefore, we also hypothesized that extensor muscle activation would be minimized when hopping on surfaces with stiffness equal to the preferred vertical stiffness. We tested our hypotheses by measuring ground reaction force, kinematics and muscle activity while subjects hopped on a large range of elastic surfaces.

Materials and methods

Eight male subjects (body mass 76±3 kg, height 177±7 cm, age 29±6, mean ± S.D.) volunteered for this study. All subjects gave informed consent and the University of Colorado Human Research Committee approved the protocol.

Subjects hopped in place on a custom-built elastic surface mounted on a force platform (AMTI, Watertown, MA, USA). We systematically reduced the number of steel springs supporting the surface (Century Springs, Los Angeles, CA, USA) to achieve eight surface stiffness values between 81 and 11 kN m^{-1} (Table 1). The effective mass of the surface was 4.3 kg. The surface damping was minimal (damping ratio <0.02) when calculated with a loaded free vibration test. When subjects hopped on progressively softer surfaces, however, active movement of the legs resulted in much greater surface displacements than during free vibration. The surface therefore dissipated a greater fraction of the subjects' center of mass energy on the softest (10%) compared with the stiffest (3%) surface. Greater detail on the surface construction and calibration was previously published (Moritz and Farley, 2003).

Hopping protocol

For all trials, we instructed subjects to clasp their hands behind their backs, leave the ground during each hop and match the beat of a metronome. We set the metronome beat to the preferred hopping frequency of 2.2 Hz (Ferris and Farley, 1997; Melville-Jones and Watt, 1971) and also to 3.0 Hz. We collected data at both hopping frequencies because the vertical displacement of the center of mass during stance is smaller and preferred vertical stiffness is greater at 3.0 Hz than at 2.2 Hz. As a result, the compression of the softest surface exceeded the center of mass displacement to a larger extent during hopping at 3.0 Hz than at 2.2 Hz.

Table 1. *Hopping at 2.2 Hz on a range of elastic surfaces*

Parameters	Stiffest							Softest	Simulation
Surface stiffness (kN m^{-1})	81	40	27	22	17	15	13	11	11 – Sim
Vertical stiffness (kN m^{-1})	19.5 (0.4)	17.5 (0.5)*	16.3 (0.3)*	16.0 (0.3)*	15.3 (0.2)*	14.8 (0.3)*	14.9 (0.3)*	15.3 (0.2)*	7.8 (0.1)*
Surface compression (cm)	2.9 (0.1)	5.6 (0.1)*	7.2 (0.1)*	8.6 (0.2)*	10.6 (0.3)*	11.7 (0.4)*	12.7 (0.3)*	14.7 (0.3)*	17.7 (0.2)*
Downward COM displacement (cm)	11.9 (0.1)	12.0 (0.1)	11.8 (0.1)	11.5 (0.1)*	11.4 (0.1)	11.6 (0.3)	11.2 (0.2)	10.7 (0.2)	23.7 (0.2)*
Contact time (ms)	297 (6)	323 (7)	348 (5)*	357 (5)*	358 (5)*	370 (8)*	371 (5)*	375 (4)*	505 (6)*
Aerial time (ms)	159 (6)	133 (7)	109 (5)*	97 (5)*	98 (5)*	90 (7)*	88 (4)*	81 (4)*	169 (7)
Peak vertical force (N)	2314 (51)	2104 (62)*	1916 (38)*	1836 (38)*	1740 (41)*	1705 (49)*	1659 (34)*	1622 (43)*	1861 (24)*
Landing leg length (cm) relative to standing	–8.2 (1.8)	–7.1 (1.3)	–10.8 (2.2)	–7.7 (0.5)	–13.0 (1.6)*	–14.7 (1.0)*	–20.7 (1.4)*	–21.9 (1.1)*	NA
Peak ankle moment (Nm)	300 (21)	251 (15)	235 (19)	207 (13)*	169 (19)*	171 (15)*	188 (11)*	168 (13)*	NA
Peak knee moment (Nm)	103 (20)	43 (14)	–3 (26)	28 (8)	65 (11)	77 (9)	50 (14)	72 (12)	NA
Peak hip moment (Nm)	27 (19)	41 (12)	59 (15)	38 (6)	63 (12)	60 (10)	93 (10)	98 (7)	NA
Δ Ankle θ – landing (deg.)	–21 (2)	–16 (2)	–10 (3)	–5 (2)*	–2 (3)*	–4 (3)*	–3 (2)*	–3 (2)*	NA
Δ Ankle θ – takeoff (deg.)	28 (2)	20 (2)	13 (3)	7 (2)*	2 (3)*	2 (3)*	1 (2)*	1 (2)*	NA
Δ Knee θ – landing (deg.)	–12 (1)	–6 (2)*	–2 (2)*	4 (2)*	11 (1)*	15 (1)*	20 (2)*	24 (2)*	NA
Δ Knee θ – takeoff (deg.)	16 (1)	8 (2)*	4 (2)*	–1 (2)*	–8 (2)*	–11 (1)*	–16 (2)*	–20 (2)*	NA
Δ Hip θ – landing (deg.)	–5 (1)	–2 (1)	1 (2)	5 (2)	14 (2)*	18 (2)*	24 (2)*	28 (3)*	NA
Δ Hip θ – takeoff (deg.)	7 (1)	3 (1)	1 (2)	–3 (2)	–11 (2)*	–15 (2)*	–20 (2)*	–25 (3)*	NA

Values are means (S.E.M.) for all subjects. *Denotes a significant difference from the 81 kN m^{-1} surface. COM, center of mass. Negative values for landing leg length indicate the legs are shorter at landing than when standing with knees extended and feet flat on the floor. Extension is positive for all changes (Δ) in joint angle (θ). Simulation values are from a spring–mass model with leg stiffness from experimental data on the 81 kN m^{-1} surface but landing on the 11 kN m^{-1} surface. They predict COM dynamics that would have occurred if subjects had not altered leg mechanics between the stiffest and softest surfaces.

Each subject performed 15 trials on the range of surface stiffness values with 2 min rest between trials. During each trial, the subject hopped for 40 s after matching the metronome beat and we collected data for the final 10 s. We randomized the order of the surfaces and the order of hopping frequencies on each surface. We did not collect data for hopping at 3.0 Hz on the softest surface because subjects could not leave the ground consistently. At the beginning and end of each session, we collected a trial at 2.2 Hz on the 27 kN m^{-1} surface to test for fatigue and found no significant change.

For each condition, we selected ten consecutive hops closest to the metronome frequency for analysis (2.19±0.01 Hz and 2.97±0.02 Hz) We tested for differences among conditions with a repeated measures ANOVA and Bonferroni *post-hoc* test (SPSS 9, Chicago, IL, USA). All reported values are means and S.E.M.S.

Kinetic and kinematic data collection and analysis

We collected ground reaction force and surface position data (linear potentiometer, Omega, Stamford, CT, USA) at 1000 Hz. From these data, we calculated center of mass position, leg length and instantaneous power. First, we subtracted the force due to surface acceleration from the vertical ground reaction force (<4% of peak force in all cases). Next, we calculated center of mass vertical displacement by twice integrating the vertical acceleration (obtained from the vertical force) with respect to time (Cavagna, 1975). We defined leg compression as the reduction in the distance between the center of mass and the surface. Finally, we calculated the instantaneous power of the center of mass, leg and surface by multiplying the vertical force by the respective velocity.

We calculated the combined vertical stiffness of the leg and surface (K_{vert}) by dividing the vertical force by center of mass displacement when the center of mass was at its lowest point. For an inverse dynamics analysis, we also calculated the sagittal plane center of pressure using the standard procedure for the AMTI force platform except that we accounted for surface position to determine the vertical distance from the plane of force application to the force platform axis (Moritz et al., 2003). Applying forces at known locations on the hopping surface demonstrated that this method was accurate to within 0.5 cm.

We analyzed sagittal plane kinematics to calculate touchdown leg length and joint angles, as well as to calculate net muscle moments from an inverse dynamics analysis (Elftman, 1939). We placed reflective markers on the tip of first toe, fifth metatarsophalangeal joint (MP5), lateral malleolus, femur lateral epicondyle, greater trochanter, lateral iliac crest (IC) and acromion scapulae. We videotaped subjects at 200 fields s^{-1} (JC Labs, Mountain View, CA, USA). We digitized marker positions and then low-pass filtered the data with a 7 Hz cutoff frequency (Peak Motus 6.0, Englewood, CO, USA). Finally, we determined acute joint angles and estimated leg length at touchdown as the distance between the MP5 and IC markers. We used the IC marker because it approximated the vertical position of the center of mass.

EMG data collection and analysis

We sampled the electromyographic activity of eight left leg muscles (Telemyo, Noraxon, Phoenix, AZ, USA) at 1000 Hz concurrent with the force and kinematic data. We placed bipolar silver silver-chloride electrodes (inter-electrode distance 2 cm) over the tibialis anterior (TA), soleus (SOL), medial and lateral gastrocnemius (MG and LG), vastus medialis (VM), vastus lateralis (VL), rectus femoris (RF) and semitendinosus (ST) according to guidelines (Freriks et al., 1999). Electrodes and lead wires were secured with tape and elastic stockings and remained attached for all trials.

We filtered (bandpass 20–500 Hz) and rectified each EMG signal before computing the mean activation of each muscle during the stance phase (Matlab 6.1, The Mathworks, Natick, MA, USA). We then calculated the combined mean EMG for all leg extensor muscles (SOL, MG, LG, VM, VL, RF and ST) during the stance phase. These combined mean values are expressed as a percent of the mean EMG of the extensor group during the stance phase on the 81 kN m^{-1} surface during 2.2 Hz hopping. Based on their actions during hopping, biarticular muscles RF and ST were classified as extensor muscles of the knee and hip, respectively. Specifically, we used observed joint angular excursions and published values for internal muscle moment arms (van Soest et al., 1993) to estimate muscle–tendon length changes. This method revealed that RF shortened when the knee extended and ST shortened when the hip extended on all surfaces.

Simulation

We used a computer simulation of a spring–mass model on an elastic surface to predict the center of mass dynamics that would have occurred if hoppers had used the same spring-like leg mechanics on the softest surface as on the stiffest surface. We used initial conditions from each subject's data for hopping at each frequency on the stiffest surface (81 kN m^{-1}). In the simulation, we set the surface stiffness to its lowest values, 11 kN m^{-1} and 13 kN m^{-1}, for hopping at 2.2 Hz and 3.0 Hz, respectively. Specifically, we used values from the 81 kN m^{-1} surface for leg stiffness (average 25.7 kN m^{-1} at 2.2 Hz and 54.5 kN m^{-1} at 3.0 Hz) and touchdown velocity (0.83 m s^{-1} at 2.2 Hz and 0.49 m s^{-1} at 3.0 Hz). We determined leg stiffness for each hopping trial by the ratio of force to leg compression at the time of maximum leg compression. We ran the simulation ten times for each subject using initial conditions from each of ten hops at each frequency (ode113, time step: 0.001s, absolute error: 10^{-8}, Matlab 6.1, The Mathworks, Natick, MA, USA). Reducing the time step or error tolerances by an order of magnitude changed all parameters by <1%. A numerical approach was needed to calculate contact and aerial times for each condition because hopping involves alternating contact times governed by spring properties and aerial times governed by projectile motion.

Results

Hoppers adjusted leg mechanics so dramatically for the range of surfaces that the downward center of mass displacement during stance varied by less than 10% despite a fivefold increase in surface compression. On the softest surfaces, the vertical displacement of the hopper during stance was less than the surface compression (Fig. 1A,B; Tables 1 and 2). For example, the softest surface compressed by 15 cm but the center of mass moved downward by only 11 cm during hopping at 2.2 Hz. To accomplish this, hoppers made the combined vertical stiffness of the leg and surface (K_{vert}) 40% greater than the stiffness of the softest surface and consequently, it was within 24% of the value on the stiffest surface (Fig. 1C; Table 1). If hoppers had not adjusted leg mechanics between the stiffest surface and the softest surface during hopping at 2.2 Hz, simulation results indicated that the vertical stiffness of the leg–surface combination would have decreased by 60% and the center of mass would have moved downward twice as far during stance (Table 1). Even larger changes would have occurred if hoppers had not adjusted leg mechanics for reductions in surface stiffness during hopping at 3.0 Hz (Table 2).

On stiff surfaces, hoppers conserved spring-like leg mechanics and adjusted the leg force–displacement relation to maintain the 'preferred' vertical displacement of the center of mass and the 'preferred' vertical stiffness. As normally occurs on stiff surfaces, the legs compressed as the center of mass moved downward in early stance and then extended as the center of mass moved upward in late stance (Fig. 2A). As surface stiffness decreased, hoppers maintained this pattern but their legs compressed less to compensate for the greater surface compression. This compression–extension cycle by the legs on the stiff surfaces produced the familiar spring-like leg force–displacement relationship with a slope that became steeper as surface stiffness decreased (Fig. 3). On these surfaces, the center of mass displacement during stance exceeded surface displacement due to leg compression in early stance. When hopping at 2.2 and 3.0 Hz on the stiffest surface ($81\ \mathrm{kN\ m^{-1}}$), stance phase center of mass displacements were 11.9 cm and 6.4 cm and vertical stiffness values were $19.5\ \mathrm{kN\ m^{-1}}$ and $32.1\ \mathrm{kN\ m^{-1}}$, respectively (Fig. 1; Tables 1 and 2). We will refer to these center of mass displacements and vertical stiffness values as 'preferred' for each frequency.

When surface stiffness was approximately equal to the preferred vertical stiffness and peak surface compression was approximately equal to the preferred center of mass displacement, the legs changed length only slightly during stance. Consequently, the center of mass movements followed surface movements in timing and magnitude (Fig. 2B). In this case, the leg force–displacement curve had a nearly infinite slope (Fig. 3). Because the preferred vertical stiffness was greater during hopping at 3.0 Hz than at 2.2 Hz, the legs became almost infinitely stiff on a stiffer surface during hopping at 3.0 Hz than 2.2 Hz (Fig. 3; 27 *vs* $17\ \mathrm{kN\ m^{-1}}$).

When surface stiffness fell below the preferred vertical stiffness and surface compression exceeded the preferred center of mass displacement for each frequency, hoppers reversed the pattern of leg action such that they first extended their legs and then retracted them during stance (Fig. 2C). Thus, as hoppers extended their legs in early stance, the surface

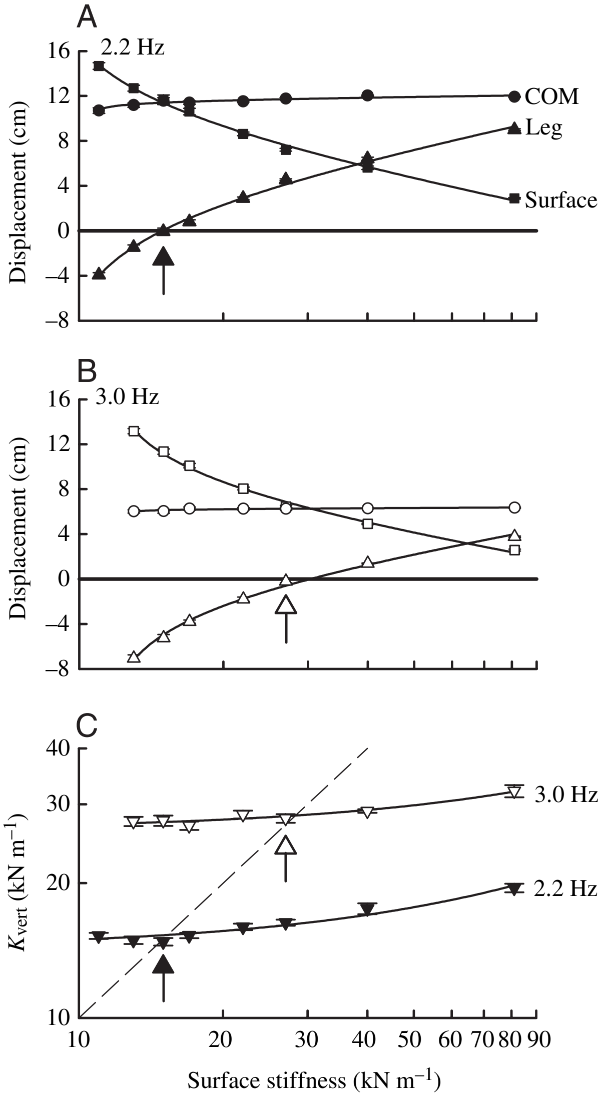

Fig. 1. (A,B) Peak downward center of mass displacement during stance (COM), peak 'leg' compression and peak 'surface' compression *vs* surface stiffness for hopping at (A) 2.2 Hz and (B) 3.0 Hz. Positive leg compression values indicate shorter legs at midstance than at landing, and positive values for COM displacement and surface compression indicate downward movement. (C) Combined vertical stiffness of the leg and surface (K_{vert}) *vs* surface stiffness during hopping at 2.2 and 3.0 Hz. Values are means and S.E.M.s for all subjects, lines are least squares regressions and many error bars are hidden by symbols. The arrows indicate when the surface stiffness equals the preferred vertical stiffness at 2.2 Hz (filled arrows) and 3.0 Hz (open arrows). At this surface stiffness, center of mass displacement equals surface displacement. The dashed line in (C) indicates equal vertical stiffness and surface stiffness over the entire range. Vertical stiffness exceeded surface stiffness on the softest surfaces because the legs extended while the surface simultaneously compressed in the first half of stance.

Table 2. *Hopping at 3.0 Hz on a range of elastic surfaces*

Parameters	Stiffest							Softest	Simulation
Surface stiffness (kN m^{-1})	81	40	27	22	17	15	13	11	13 – Sim
Surface compression (cm)	2.6 (0.1)	4.9 (0.1)*	6.5 (0.1)*	8.1 (0.1)*	10.1 (0.2)*	11.3 (0.2)*	13.2 (0.2)*	NA	13.4 (0.2)*
Contact time (ms)	240 (5)	261 (2)	276 (4)*	271 (3)	282 (4)*	280 (4)*	281 (4)*	NA	453 (7)*
Aerial time (ms)	94 (5)	74 (2)	61 (2)*	67 (3)	58 (2)*	58 (3)*	60 (3)*	NA	107 (6)
Downward COM displacement (cm)	6.4 (0.1)	6.3 (0.1)	6.3 (0.1)	6.2 (0.1)	6.3 (0.1)	6.0 (0.2)	6.0 (0.1)	NA	16.2 (0.1)*
Peak vertical force (N)	2035 (73)	1815 (21)	1729 (33)	1751 (23)	1657 (33)*	1636 (30)*	1628 (24)*	NA	1711 (21)
Vertical stiffness (kN m^{-1})	32.1 (1.0)	29.0 (0.3)	27.9 (0.6)*	28.5 (0.6)	26.9 (0.6)*	27.6 (0.8)*	27.5 (0.7)*	NA	10.4 (0.1)*
Landing leg length (cm) relative to standing	–6.9 (0.7)	–11.9 (2.1)	–17.4 (2.4)*	–17.2 (1.0)*	–21.1 (0.8)*	–24.1 (1.9)*	–25.9 (1.0)*	NA	NA
Peak Ankle moment (Nm)	252 (13)	213 (22)	218 (21)	194 (18)	163 (22)	156 (21)	174 (15)	NA	NA
Peak knee moment (Nm)	6 (13)	11 (19)	–2 (17)	41 (19)	62 (17)	43 (22)	31 (24)	NA	NA
Peak hip moment (Nm)	54 (12)	100 (30)	122 (19)	133 (10)	132 (13)	156 (15)*	159 (15)*	NA	NA
Δ Ankle θ – landing (deg.)	–8 (2)	–4 (3)	–3 (2)	–5 (3)	–2 (3)	–2 (3)*	–2 (3)*	NA	NA
Δ Ankle θ – takeoff (deg.)	10 (2)	5 (3)	3 (2)	4 (3)	1 (3)	1 (3)*	1 (3)*	NA	NA
Δ Knee θ – landing (deg.)	1 (3)	10 (2)	15 (3)*	18 (2)*	23 (3)*	25 (3)*	30 (3)*	NA	NA
Δ Knee θ – takeoff (deg.)	0 (3)	–7 (2)	–12 (3)*	–15 (2)*	–18 (3)*	–22 (3)*	–26 (2)*	NA	NA
Δ Hip θ – landing (deg.)	3 (2)	11 (3)*	16 (4)*	21 (2)*	25 (4)*	28 (3)*	33 (3)*	NA	NA
Δ Hip θ – takeoff (deg.)	–2 (2)	–9 (3)*	–14 (4)*	–18 (3)*	–20 (4)*	–24 (4)*	–30 (3)*	NA	NA

Values are means (S.E.M.) for all subjects. *Denotes a significant difference from the 81 kN m^{-1} surface. COM, center of mass. Negative values for landing leg length indicate the legs are shorter at landing than when subjects stand with knees extended and feet flat on the floor. Extension is positive for all changes (Δ) in joint angle (θ). Simulation values are from a spring–mass model with leg stiffness from experimental data on the 81 kN m^{-1} surface but landing on the 13 kN m^{-1} surface. They predict center of mass dynamics that would have occurred if subjects had not altered leg mechanics between the stiffest and softest surfaces.

and center of mass moved downward. Subsequently, as hoppers retracted their legs in late stance, the surface and center of mass moved upward. Due to the out-of-phase motions of the legs and surface, the center of mass moved vertically during stance by a smaller distance than the surface. Hoppers compensated for further reductions in surface stiffness by increasing the magnitude of the leg extension–compression cycle (Fig. 1A,B) and by making the slope of the leg force–displacement more negative (Fig. 3). This strategy prevented large changes to center of mass displacement and vertical stiffness over the large range of surface stiffness (Fig. 1; Tables 1 and 2).

As surface stiffness decreased below the preferred vertical stiffness, hoppers landed with progressively shorter legs to permit immediate leg extension. On the softest surfaces, subjects landed with their legs 14–19 cm more compressed than on the stiffest surface (Tables 1 and 2) due to greater joint flexion (Fig. 2G–I). After landing, hoppers immediately extended their legs by 4–7 cm (Fig. 1A,B) primarily by extending their knees and hips in the first half of stance (Fig. 2). This extreme action resulted in more extended legs at midstance than at landing on the softest surfaces. When hopping at 3.0 Hz on the softest surfaces, the legs were even shorter at landing than when hopping at 2.2 Hz to allow more extension after landing (Fig. 1A,B; Table 2). This extra extension maintained a smaller center of mass displacement than at 2.2 Hz even on very soft surfaces.

The reversal of the usual leg compression–extension timing on the softest surfaces caused a reversal of negative and positive leg work timing. On the stiffest surfaces, the legs absorbed mechanical energy from the center of mass as they compressed during landing and then performed positive mechanical work on the center of mass as they extended during takeoff (Fig. 2D,F; Fig. 4). This pattern is typical of the spring-like leg mechanics normally used by hoppers and runners on hard surfaces. When the surface stiffness was close to the preferred vertical stiffness, the legs did almost no work as they barely changed length (Fig. 2D,F; Fig. 4). Finally, when surface stiffness fell below the preferred vertical stiffness, the legs performed positive work on the surface springs as they extended during landing and then absorbed mechanical energy from the surface springs as they compressed during takeoff (Fig. 2D,F; Fig. 4). This absorption of part of the energy released by the surface springs prevented the center of mass from moving too high in the subsequent aerial phase and thereby prevented a slowing of hopping frequency. By contrast, when surface stiffness was greater than preferred vertical stiffness, the legs performed work directly on the center of mass and not on the surface.

Hoppers activated their extensor muscles least on a surface stiffness that was substantially greater than the preferred vertical stiffness. Hoppers increased mean extensor EMG 1.5- to 2-fold during stance as surface stiffness decreased from the stiffest to softest surface (Figs 5, 6; $P<0.05$ for 3.0 Hz). This trend was not continuous for hopping at 2.2 Hz, as extensor muscle EMG reached a minimum of 32% less on a moderately

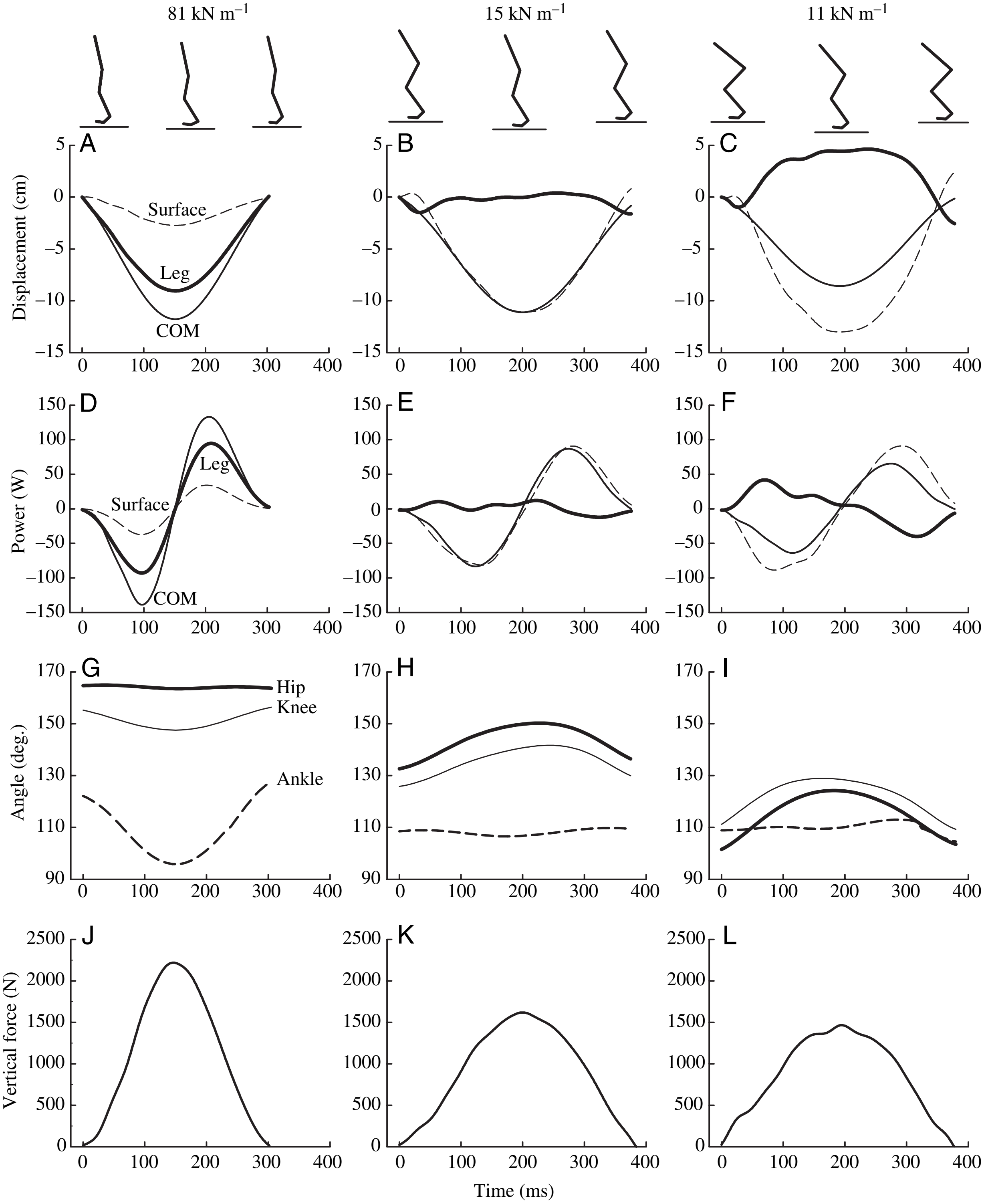

Fig. 2. Examples of displacements, powers, joint angles and vertical ground reaction force *vs* time for hopping at 2.2 Hz on the 81, 15 and 11 kN m^{-1} surfaces. All traces begin at landing and end at takeoff. Stick figures show body posture and surface position at instants of landing, peak force and takeoff on each surface. On the stiffest surface (81 kN m^{-1}), the legs first compressed and then extended, leading to in-phase kinematics and power of the leg, center of mass (COM) and surface. Also, the joints flexed and then extended. On the 15 kN m^{-1} surface, the legs barely changed length and the center of mass followed the surface motion and power. On the softest surface (11 kN m^{-1}), the legs first extended and then compressed, resulting in out-of-phase leg and surface power. The transient changes in leg length on the 15 and 11 kN m^{-1} surfaces are likely due to the fact that small changes in muscle force result in large changes in surface compression and thus leg length, on the softest surfaces.

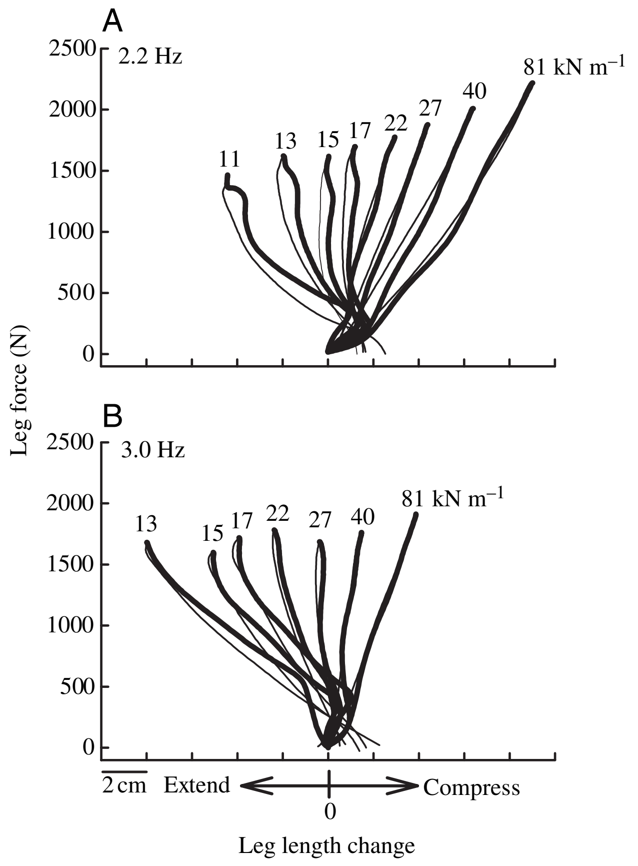

Fig. 3. Example leg force *vs* leg length change for the same subject as in Fig. 2 hopping at (A) 2.2 Hz and (B) 3.0 Hz on a range of surfaces. Surface stiffness values are above each curve. Thick lines represent early stance and thin lines represent late stance. On the stiffest surface, the spring-like legs compressed as force rose to its peak at midstance (thick line) and then extended as force fell until takeoff (thin line). In contrast, on the softest surface, legs extended as force rose to its peak and then compressed as force fell to zero at takeoff. The slight increase in area of the leg force–displacement work loops on softer surfaces offset the slightly greater energy dissipated by the surface when it compressed further. The increase in stiffness at peak force on the softest surfaces in A was observed in four of the eight subjects.

stiff surface (27 kN m^{-1}) than on the stiffest surface (Figs 5 and 6; $P<0.05$). Counter to our hypothesis, this minimum EMG did not occur on the surface stiffness nearly equal to the preferred vertical stiffness or on the surface stiffness with the lowest absolute leg work. Rather, it occurred on a stiffer surface where the legs first compressed and then extended. When hopping at 3.0 Hz, extensor EMG was lowest on the stiffest surface and increased continuously as surface stiffness decreased over the entire range (Fig. 6B). Thus, at both hopping frequencies, mean EMG was lower on stiff surfaces where the legs first compressed and then extended than on the surface where the legs remained nearly isometric. Finally, muscles extending the same joint had similar trends in EMG across the range of surface stiffness and muscles extending different joints had minimum EMG on slightly different surfaces (Fig. 7).

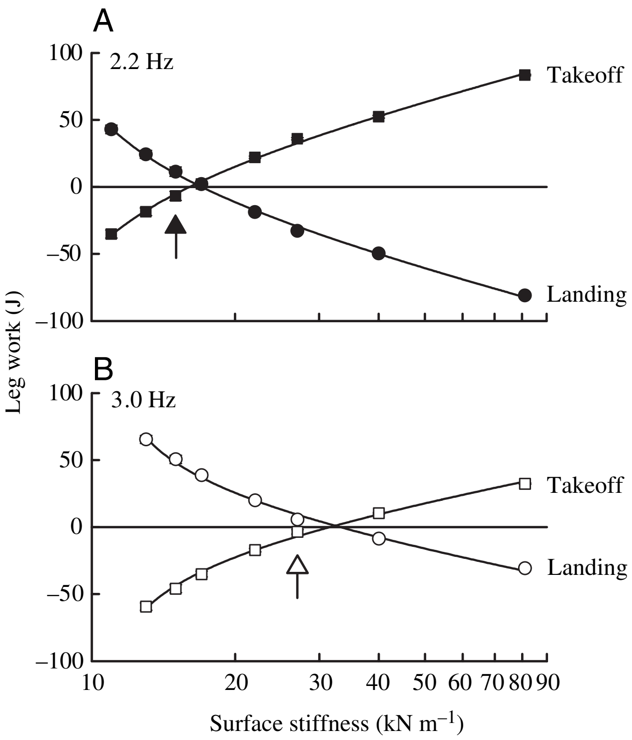

Fig. 4. Mechanical work by the legs during the landing (circles) and takeoff (squares) parts of the stance phase *vs* surface stiffness for hopping at (A) 2.2 Hz and (B) 3.0 Hz. Values are means and S.E.M.S for all subjects, lines are least squares regressions and error bars are hidden by symbols. Arrows indicate when the surface stiffness equals the preferred vertical stiffness at 2.2 Hz (filled arrow) and 3.0 Hz (open arrow). On all surfaces, the magnitudes of the positive and negative work were equal because the surfaces dissipated negligible energy. On stiffer surfaces, the legs absorbed mechanical energy (i.e. performed negative work) during landing and then performed positive mechanical work during takeoff. In contrast, on softer surfaces, this sequence was reversed. The legs performed positive work during landing and then absorbed mechanical energy during takeoff. Leg work was not minimized when surface stiffness and vertical stiffness were equal due to small transient changes in leg length in early and late stance (see Fig. 2B) that were not reflected in the values for leg compression between touchdown and midstance in Fig. 1.

Discussion

The results support our first hypothesis that hoppers abandon spring-like leg mechanics on very soft surfaces so that the legs first extend and then compress exactly out of phase with surface compression and rebound. This strategy prevents the large reduction in vertical stiffness (up to 60%; see Tables 1, 2) that would occur if hoppers were to maintain spring-like leg mechanics when surface stiffness falls below the preferred vertical stiffness. By extending their legs in the first half of stance, hoppers partly compensate for the large compression of a very soft surface. Consequently, the center of mass moves downward during stance by less than the surface and the vertical stiffness of the leg–surface combination exceeds the surface stiffness. Moreover, the center of mass moves

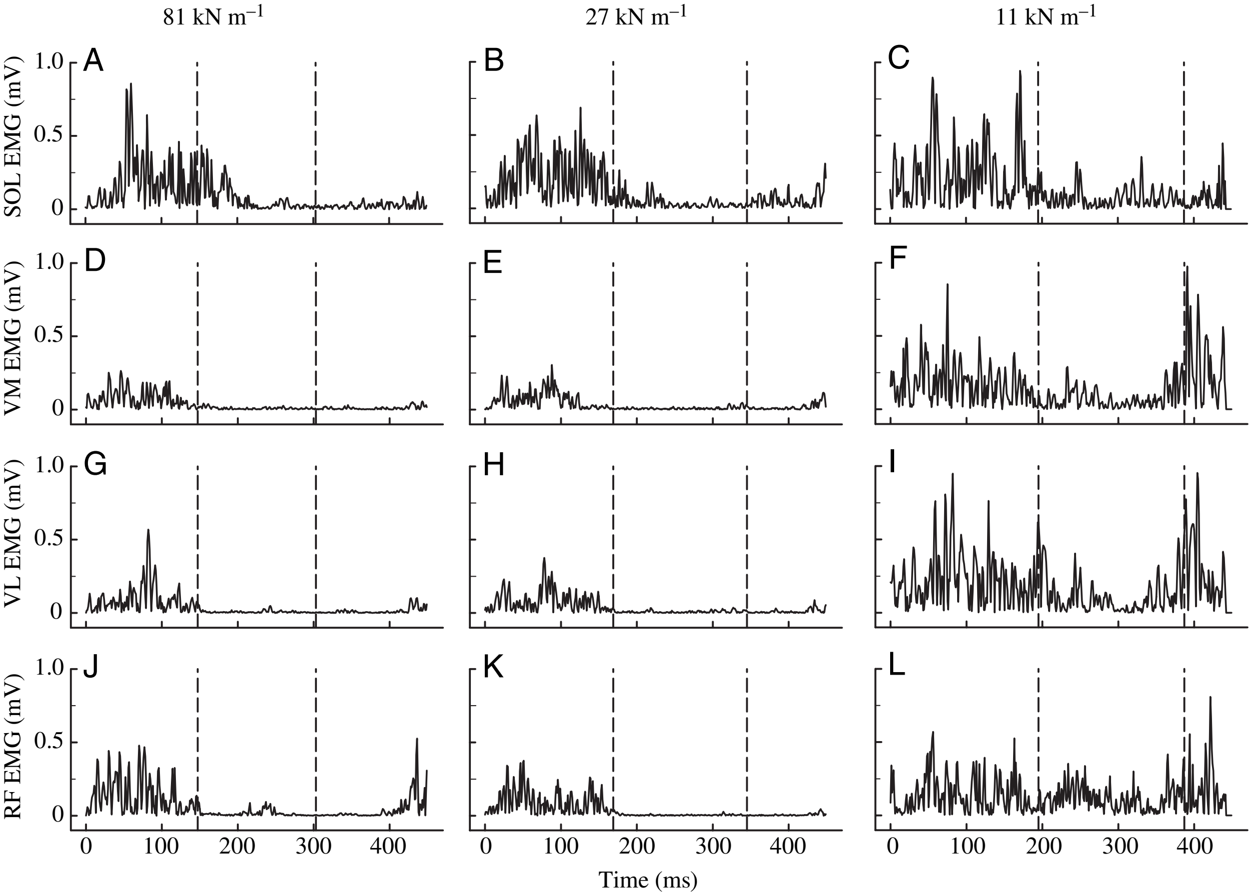

Fig. 5. Example rectified EMG *vs* time during hopping at 2.2 Hz on the 81, 27 and 11 kN m^{-1} surfaces for the (A–C) soleus (SOL), (D–F) vastus medialis (VM), (G–I) vastus lateralis (VL) and (J–L) rectus femoris (RF). All traces begin at touchdown and end at the following touchdown. First and second dashed lines indicate the times of peak force and takeoff, respectively. Hoppers had the least extensor muscle activity on a moderately stiff surface (27 kN m^{-1}) and more activity on the softer and stiffer surfaces.

downward during stance by a similar distance on all surfaces despite a 400% increase in peak surface compression.

This study extends previous work showing that hoppers and runners increase leg stiffness to offset moderate decreases in surface stiffness and thereby maintain similar center of mass dynamics on a range of elastic surfaces (Farley et al., 1998; Ferris and Farley, 1997; Ferris et al., 1998; Kerdok et al., 2002). Hoppers in the present study maintain a similar preferred vertical stiffness on all surfaces as previously reported for hopping on hard surfaces at ~2 Hz (14-18 kN m^{-1}; Farley et al., 1998; Ferris and Farley, 1997; Moritz and Farley, 2003). As surface stiffness decreases to lower values than previously studied for hopping, we find that hoppers maintain the normal spring-like leg action but leg compression gradually decreases to zero as surface stiffness approaches the preferred vertical stiffness. Similarly, McMahon and Greene (1979) found that the legs do not compress in the first half of stance when running on a ‘pillow track’ composed of very soft foam rubber with some energy loss. Finally, when we reduce surfaces stiffness even further, hoppers reverse the sequence of leg action so that the legs extend and then retract during stance. At each hopping frequency, this reversal occurs when surface stiffness falls below the preferred vertical stiffness for that frequency. This drastic adjustment allows hoppers to maintain similar center of mass dynamics at each frequency despite a sevenfold change in surface stiffness.

Hoppers are not mechanically required to conserve center of mass dynamics and vertical stiffness at a given frequency. Because hoppers can vary the fraction of the hop period spent in the air, they can use a large range of vertical stiffness values at a given hopping frequency. For example, hoppers can double vertical stiffness when instructed to hop higher at 2.2 Hz (Farley and Morgenroth, 1999). Thus, conserving vertical stiffness is one strategy among many and is not driven by a mechanical constraint.

In this study as well as a previous study of hopping on damped surfaces (Moritz and Farley, 2003), hoppers choose to abandon spring-like leg mechanics to maintain very similar center of mass dynamics as on a hard surface. On damped surfaces, hoppers perform work partly by landing with more flexed legs and taking off with more extended legs than on a hard surface. On very soft surfaces, hoppers land with very

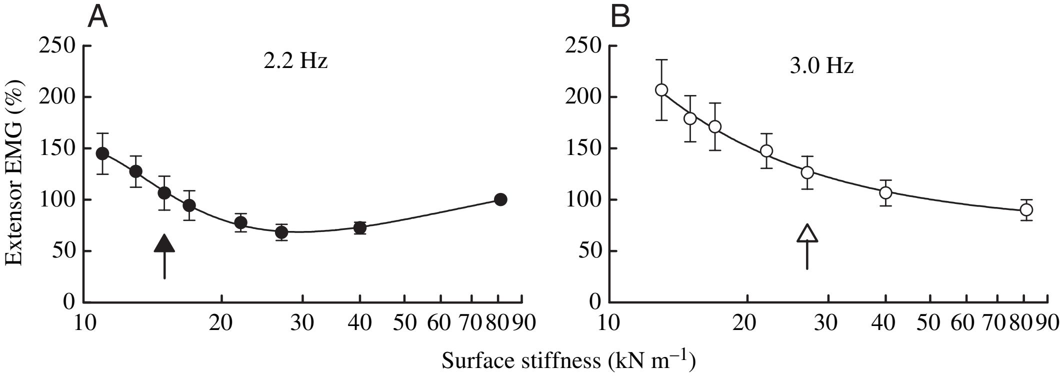

Fig. 6. Extensor muscle mean EMG during the stance phase (mean ± S.E.M.) *vs* surface stiffness for hopping at (A) 2.2 Hz and (B) 3.0 Hz. Extensor muscles are SOL, MG, LG, VM, VL, RF and ST. Mean EMG values are expressed as a percent of the mean EMG during stance phase on the 81 kN m^{-1} surface during 2.2 Hz hopping. Solid lines are least squared regressions. Arrows indicate when the surface stiffness equals the preferred vertical stiffness at 2.2 Hz (filled arrows) and 3.0 Hz (open arrows). Extensor muscle activation was minimized on the 27 kN m^{-1} surface when hopping at 2.2 Hz, whereas absolute leg work was minimized on the 17 kN m^{-1} surface (see Fig. 4).

flexed legs before extending them as the surface compresses. In addition, the phase of leg compression–extension is somewhat out of phase with surface movements on damped surfaces while it is in counter phase with surface movements on very soft surfaces. Taken together, the two studies show that hoppers vary leg length at landing, the relative timing of leg and surface compression and the amount of work performed on the surface to compensate for surface properties. In both cases, the leg–surface combination always behaves like a spring with a nearly constant vertical stiffness (K_{vert}). However, hoppers produce this spring-like behavior by using active non-spring-like leg mechanics to compensate for surface properties. Overall, these findings suggest that the center of mass movements are tightly controlled by adjusting leg mechanics to offset surface properties.

Contrary to our second hypothesis, leg muscle activation reaches a minimum on surfaces where the legs compress and then extend rather than on softer surfaces where the legs perform almost no work. Further study is needed to ascertain whether there is a moderately stiff surface where EMG is minimized during hopping at 3.0 Hz. We can, however, reject this hypothesis for both hopping frequencies because extensor muscle activation was lower on stiffer surfaces than on the surface stiffness equal to the preferred vertical stiffness for each frequency (see Fig. 6).

It is counterintuitive that extensor muscle activation during stance is not lowest on surfaces where the legs remain nearly isometric. On these surfaces, the surface springs store and return elastic energy and the legs perform very little work. The minimum extensor activation, however, occurs on stiffer surfaces where the legs first compress and then extend, and extensor muscle–tendon units stretch and then shorten during contact. During hopping at 2.2 Hz, muscle activation is minimized on a moderately stiff surface where leg work is low but muscles still undergo a stretch–shorten cycle. To determine whether an optimum surface stiffness exists for hopping at 3.0 Hz, future studies should include stiffer surfaces. It is possible that the stiffest surface used in this study is the optimum for 3.0 Hz because the legs absorb a similar amount of energy at 3 Hz on the stiffest surface as they do at 2.2 Hz on the optimum surface (Fig. 4).

Muscle activation may be lowest when hopping on moderately stiff surfaces where the extensor muscles undergo a stretch–shorten cycle for two reasons. First, when muscle fibers are pre-stretched, they generate greater force and have better efficiency during the subsequent concentric contraction (Bobbert et al., 1986; Bosco et al., 1987; Finni et al., 2001; Heglund and Cavagna, 1985). Even if muscle fibers perform no work, as a nearly constant leg length suggests, they still must generate force to support body weight. Because pre-stretch enhances muscle force, it reduces the cross-sectional area of muscle that must be recruited to support body weight. The second reason is that a stretch–shorten cycle allows storage and recovery of elastic energy in tendons and thus reduces muscle work (Alexander, 1991; Alexander and Bennet-Clark, 1977; Biewener et al., 1998; Biewener and Roberts, 2000; Cavagna, 1977; Ker et al., 1987; Lindstedt et al., 2001). In the present study, hoppers may have very high muscle activation levels on the softest surfaces due to reduced muscle pre-stretch and elastic energy storage when the legs do not compress prior to extending. This idea is supported by the observation that despite elevated muscle activation on the softest surfaces, hoppers do not generate greater ankle and knee muscle moments, peak ground reaction forces, or more positive leg work than on the stiffest surface.

The optimum stiffness surface for minimal EMG may be one where muscle contractile elements undergo a small stretch–shorten cycle. If the overall leg does not change length, as is the case when no leg work is performed, force is still generated and tendons are stretched. To maintain the same leg length, contractile elements must shorten to compensate for the stretching elastic elements. On slightly stiffer surfaces, it is possible that tendons stretch and recoil while the contractile fibers remain isometric. On stiffer surfaces still, both

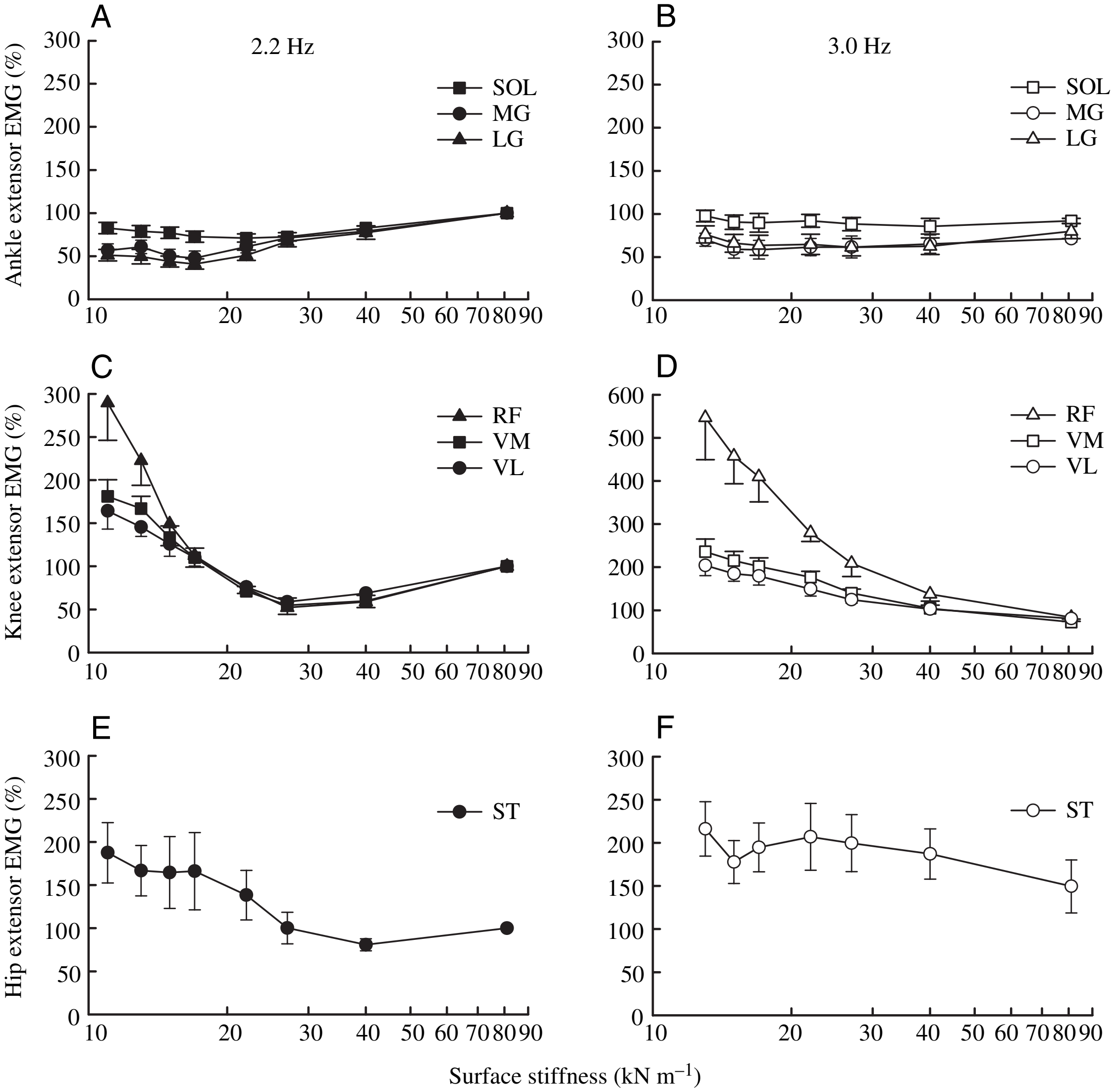

Fig. 7. Individual extensor muscle mean EMG during the stance phase (mean ± s.e.m.) *vs* surface stiffness for hopping at (A, C and E) 2.2 Hz and (B, D and F) 3.0 Hz. Muscles are grouped by those that extend the angle (A and B), knee (C and D) and hip (E and F). All values are expressed as a percent of the mean EMG for that particular muscle during stance phase on the 81 kN m^{-1} surface during 2.2 Hz hopping. Notice that vertical axis scale differs to accommodate the large increase in RF EMG during hopping at 3.0 Hz. Muscles extending the same joint exhibit similar trends in EMG across the range of surface stiffness, possibly as a result of series elastic stiffness of the shared distal tendons.

contractile elements and tendons may undergo a stretch–shorten cycle while the leg compresses and extends slightly, taking full advantage of both muscle pre-stretch and tendon elastic energy storage. An extension of this prediction is that each muscle may exhibit minimal EMG on a different surface stiffness, based on its tendon stiffness, and its internal and external moment arms. This prediction is supported by Fig. 7, where knee extensor muscles have minimal EMG on a stiffer surface than ankle extensor muscles. In addition, muscles sharing a common tendon have minimal EMG on a similar surface stiffness (e.g. MG and LG; all knee extensors).

Previous studies have also shown that it is easier to hop and run on moderately stiff surfaces than on very stiff surfaces and a theoretical model predicts that runners will consume the least metabolic energy on a moderately stiff surface. An earlier study revealed that muscle activation is lower during hopping on moderately stiff surfaces than on a hard surface, but did not include very soft elastic surfaces (Farley et al., 1998). Similarly, runners consume less metabolic energy as surface stiffness decreases over a moderate range (Kerdok et al., 2002) but no data exist for very soft elastic surfaces. In the present study, extensor muscle activation is lowest during hopping on the 27 kN m^{-1} surface at 2.2 Hz (Fig. 6A). As surface stiffness continues to decrease, muscle activation increases dramatically after the legs reverse their pattern of length change. This study is the first to show empirical data supporting the prediction by McMahon and Greene (1979) that muscle activation, and likely metabolic cost, do not continue to decrease on progressively softer elastic surfaces. McMahon and Greene (1979) used a model to predict that there is a moderate running track stiffness that maximizes running performance and that performance deteriorates on softer elastic surfaces. Unfortunately, we could not test this prediction directly by measuring metabolic cost because hopping continuously on the softest surfaces was too fatiguing to sustain for more than three minutes.

In summary, human hoppers drastically alter leg mechanics to maintain similar center of mass dynamics on a large range of elastic surfaces. When the surface compresses by more than the preferred center of mass displacement, hoppers extend their legs in early stance and then retract their legs in late stance. Although this strategy prevents the surface from dictating the vertical stiffness and center of mass dynamics, it also may reduce or eliminate muscle pre-stretch. Consequently, this leg phase reversal may be responsible for the 1.5- to 2-fold higher muscle activation on very soft surfaces than on stiff surfaces. Contrary to intuition, the minimum muscle activation occurs on a surface where the legs compress and extend, and the extensor muscles probably stretch and shorten, rather than on a surface where the legs remain a nearly constant length and perform almost no work. The reduced muscle activation associated with the stretch–shorten cycle in human hopping suggests that the bouncing gaits used by virtually all legged animals may be particularly economical for rapid locomotion because the dynamics are ideal for muscle stretch–shorten cycles.

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