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# Human hoppers compensate for simultaneous changes in surface compression and damping

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**Abstract**

On a range of elastic and damped surfaces, human hoppers and runners adjust leg mechanics to maintain similar spring-like mechanics of the leg and surface combination. In a previous study of adaptations to damped surfaces, we changed surface damping and stiffness simultaneously to maintain constant surface compression. The current study investigated whether hoppers maintain spring-like mechanics of the leg–surface combination when surface damping alone changes (elastic and 1000–4800 $\mathrm{N\,s\,m^{-1}}$). We found that hoppers adjusted leg mechanics to maintain similar spring-like mechanics of the leg–surface combination and center of mass dynamics on all surfaces. Over the range of surface damping, vertical stiffness of the leg–surface combination increased by only 12% and center of mass displacement decreased by only 6% despite up to 55% less compression of more heavily damped surfaces. In contrast, a simulation predicted a 44% decrease in vertical displacement with no adjustment to leg mechanics. To compensate for the smaller and slower compression of more heavily damped surfaces, the stance legs compressed by up to $4.1 \pm 0.2$ cm further and reached peak compression sooner. To replace energy lost by damped surfaces, hoppers performed additional leg work by extending the legs during takeoff by up to $3.1 \pm 0.2$ cm further than they compressed during landing. We conclude that humans simultaneously adjust leg compression magnitude and timing, as well as mechanical work output, to conserve center of mass dynamics on damped surfaces. Runners may use similar strategies on natural energy-dissipating surfaces such as sand, mud and snow.


*Keywords:* Biomechanics; Motor control; Running; Gait

## 1. Introduction

Quickly moving legged animals can gracefully traverse a variety of natural terrain. Specifically, hopping and running humans adjust leg mechanics to compensate for changes in surface properties and maintain similar center of mass dynamics. On elastic surfaces, humans increase the stiffness of their spring-like stance legs to compensate for softer surfaces, thereby maintaining similar bouncing center of mass dynamics regardless of surface stiffness (Ferris and Farley, 1997; Ferris et al., 1998, 1999; Kerdok et al., 2002).

Humans hopping on damped surfaces also maintain bouncing center of mass dynamics. To maintain steady hopping on a damped surface, the stance legs cannot behave like springs because they must produce mechanical work to replace the energy dissipated by the surface. We recently examined the leg mechanics of hopping on surfaces with a range of stiffness and damping combinations, but constant peak surface compression (Moritz and Farley, 2003). We found that on more heavily damped surfaces, hoppers perform more work with their stance legs to replace the energy dissipated by the surface and adjust leg compression timing to offset the slower surface compression and rebound. Because

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we maintained a constant surface compression regardless of surface damping, hoppers could maintain similar center of mass dynamics on a wide range of damped surfaces without adjusting the magnitude of leg compression.

If surface damping increases with no decrease in surface stiffness, hoppers may have to adjust the magnitude of leg compression and extension to compensate for reduced surface compression and thereby conserve similar center of mass dynamics regardless of surface damping. Indeed, a simulation of running predicts that high levels of surface damping lead to less surface compression (Nigg and Anton, 1995). Surfaces with simultaneous changes in both surface compression and damping are common in the natural world, as animals traverse sand, dirt, mud and snow.

The goal of this study was to determine whether humans adjust leg mechanics to compensate for simultaneous changes in surface compression magnitude and timing as well as energy dissipation. We hypothesized that hoppers would maintain similar center of mass dynamics regardless of surface damping by adjusting the magnitude and timing of leg compression as well as mechanical work output. 'Leg' refers to all segments between the body's center of mass and the ground. We tested this hypothesis by measuring ground reaction force and surface position while humans hopped in place on surfaces with a fixed stiffness but a range of damping. We chose to study hopping in place as it is an excellent analog to forward running (Farley et al., 1991), and it is technically more feasible to construct an adjustable damped surface for hopping in place than for running.

## 2. Materials and methods

Eight male subjects (body mass $76.2 \pm 1.7$ kg, height $176 \pm 5$ cm, age $28 \pm 2$; mean $\pm$ SD) hopped in place on a surface with adjustable stiffness and damping. All subjects gave informed consent, and the University of Colorado and California Human Research Committees approved the protocol.

The lightweight hopping surface (effective mass 3.7 kg; Fig. 1) was supported by steel springs (Century Springs, Los Angeles, CA, USA) and a bi-directional hydraulic damper (Taylor Devices, New York, NY, USA). The apparatus was mounted on a force platform (AMTI, Watertown, MA, USA), and we determined surface compression with a linear potentiometer (Omega, Stanford, CT, USA). We collected surface compression and ground reaction force data at 1000 Hz using LabView 4.1 software and a computer A/D board (National Instruments, Austin, TX, USA).

We fixed surface stiffness at 26.8 kN m$^{-1}$ and varied damping (1024–4823 N s m$^{-1}$) by adjusting the fulcrum position on a lever arm connecting the damper to the surface. We also made the surface elastic (damping ratio $<0.02$, $\sim$200 N s m$^{-1}$; Moritz and Farley, 2004) by disconnecting the damper from the surface. We initially chose a surface stiffness that would produce a 7 cm maximum surface compression during hopping on the elastic surface. We then used a computer simulation (see last paragraph of methods) to choose four levels of surface damping that resulted in maximum surface compressions during hopping of 6, 5, 4, and 3 cm, respectively (Table 1). We calibrated surface damping and stiffness for each condition as described previously (Moritz and Farley, 2003).

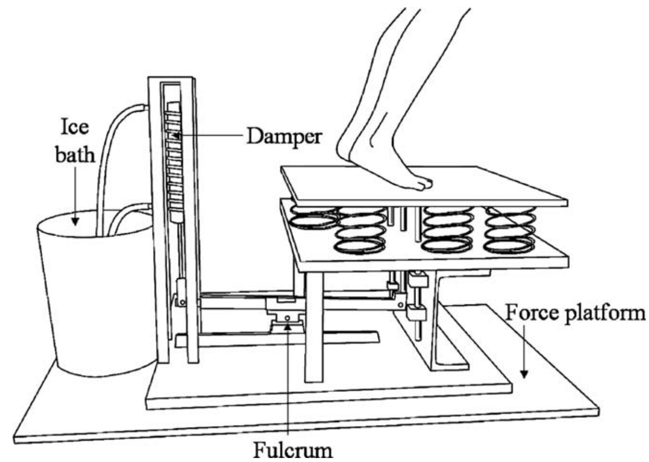


Fig. 1. The damped hopping surface mounted on a force platform. Surface damping was varied by adjusting the position of the fulcrum on the lever arm connecting the damper to the surface. The damper temperature was maintained by circulating ice water through a copper coil surrounding the damper. The surface was originally described in Moritz and Farley (2003).

Subjects hopped barefoot on two legs on an elastic surface and four damped surfaces (Table 1). Trials progressed from the least to greatest surface damping, followed by the elastic surface, and then repeated in reverse order to control for subject fatigue. There was no difference between the two trials on each surface, so both trials were averaged together. We gave subjects three instructions about how to hop: (i) follow the metronome beat at 2.2 Hz (approximately the preferred hopping frequency; Farley et al., 1991; Melville-Jones and Watt, 1971), (ii) leave the ground between hops, and (iii) clasp hands behind the back. We collected data for the final 10 s of each 40 s trial, and analyzed five consecutive hops that were within 5% of the 2.2 Hz hopping frequency.

We calculated the center of mass vertical displacement, leg compression, leg work, and surface energy dissipation after correcting for surface inertia. We subtracted the inertial force due to surface acceleration ($<4\%$ of peak vertical force in all cases) from the vertical ground reaction force to determine the net vertical force acting on the legs ('leg force'). We

Table 1
Hopping on a range of damped surfaces

| Hopping parameters | Elastic | | | | Most damped |
|---|---|---|---|---|---|
| Surface damping ($N\,s\,m^{-1}$) | NA | 1024 | 1796 | 3067 | 4823 |
| Surface stiffness ($kN\,m^{-1}$) | 26.8 | 26.8 | 26.8 | 26.8 | 26.8 |
| Surface energy dissipated per hop (J) | 2.2 (0.1) | 38.9 (2.1)* | 45.5 (2.4)* | 45.5 (2.8)* | 38.6 (2.4)* |
| Surface energy dissipated of total absorbed (%) | 3.4 (0.3) | 55.0 (0.6)* | 68.1 (0.6)* | 76.7 (0.6)* | 81.3 (0.5)* |
| Contact time (ms) | 340 (6) | 331 (9) | 319 (9)* | 307 (9)* | 303 (8)* |
| Leg length at takeoff relative to landing (cm) | 0.4 (0.1) | 2.4 (0.2)* | 3.1 (0.3)* | 3.1 (0.2)* | 2.8 (0.2)* |
| Peak vertical force (N) | 1905 (33) | 1880 (45) | 1918 (47) | 2011 (61)* | 2047 (60)* |

Subject data for an elastic surface and four damped surfaces. Values are mean (SEM) for all subjects. An asterisk (*) denotes a significant difference from the elastic surface.

determined the center of mass vertical displacement by double-integrating its vertical acceleration (calculated from leg force) with respect to time (Cavagna, 1975). We determined leg compression during stance by subtracting the surface displacement from the center of mass displacement. We calculated the negative and positive leg work during the stance phase by integrating leg force with respect to leg compression during the leg compression and extension phases, respectively. Net leg work for the entire stance phase was defined as the integral of leg force with respect to leg compression for the entire stance phase. This method is equivalent to taking the sum of the negative and positive work from the compression and extension phases, respectively. Similarly, we calculated net surface energy dissipation by integrating leg force with respect to surface displacement for the entire stance phase.

We calculated the vertical stiffness of the leg and surface combination ($k_{\mathrm{vert}}$) from the ratio of leg force ($F$) to vertical displacement of the center of mass ($\Delta y$) when the center of mass was at its lowest point (Ferris et al., 1998):

$$k_{\mathrm{vert}} = F/\Delta y. \tag{1}$$

Similarly, we calculated leg stiffness on the elastic surface by taking the ratio of leg force to leg compression at the time of peak leg compression. It is reasonable to calculate vertical stiffness and leg stiffness values in this manner because both force-displacement relations are nearly linear ($r^2 > 0.98$).

We used sagittal plane video data to quantify joint kinematics and an inverse dynamics analysis to determine joint work contributions. These methods were previously described in detail (Moritz et al., 2004). In brief, we videotaped subjects at 200 frames $s^{-1}$ (JC Labs, Mountain View, CA) and used marker positions to determine segment positions, accelerations, and joint angles (Peak Motus 6.0, Englewood, CO). We calculated the average joint angles versus time for all subjects combined by normalizing the duration of each stance phase to 100%. We used an inverse dynamics analysis to calculate the net muscle moment (Elftman, 1939; Winter, 1990) and the instantaneous net muscle power. We calculated negative and positive work at each joint from the time integral of the negative and positive portions of the instantaneous joint power over each hop cycle. Net joint work was defined as the sum of the positive and negative work at a given joint for the stance phase. We report the mechanical work that *appeared* at each joint because an inverse dynamics analysis cannot identify whether muscles crossing that joint or muscles crossing a different joint actually performed the work (Zajac et al., 2002).

We used a simulation of a linear spring-mass model to quantify how surface damping would affect hopping mechanics if subjects did not adjust leg mechanics. This simulation allowed us to quantify how adjustments to leg mechanics for surface damping affected center of mass dynamics. To simulate no leg adjustment for surface damping, we assumed that the legs behaved like springs with the leg stiffness used on the elastic surface on all of the damped surfaces. Using these leg mechanics in our simulation, we calculated the center of mass dynamics, leg compression, and surface compression that would have occurred on the damped surface if subjects did not adjust leg mechanics. We used this model to run simulations for each subject on each surface using initial conditions for the same subject on the elastic surface (The Mathworks, Natick, MA, USA, Matlab 6.1, ode 113, time step $= 0.001$ s, absolute error $= 10^{-8}$). Average initial conditions for leg stiffness and touchdown velocity were $39.4 \pm 2.0\,kN\,m^{-1}$ and $0.61 \pm 0.03\,m\,s^{-1}$, respectively. Decreasing the time step and error tolerances by an order of magnitude did not change the simulation results.

For the subject data, we tested for differences among surfaces using a one-way repeated measures ANOVA for each variable individually with an $\alpha$ of 0.05. Significant main effects were followed with Bonferroni post hoc tests (SPSS 9, Chicago, IL, USA). Similarly, to compare differences among the surfaces for the simulation, we used a one-way repeated measures ANOVA. To compare simulation and subject results, we used a two-factor (subject or simulation, surface) repeated measures

ANOVA with repeated measures on surface damping. We could perform statistical tests on the simulation outputs because separate simulations were run for each subject on each surface using initial conditions for that subject on that surface. All reported values are mean ± SEM.

## 3. Results

Hoppers maintained similar center of mass dynamics on all surfaces despite large changes in surface damping and surface compression. The elastic surface compressed by 6.7 ± 0.1 cm while the most damped surface compressed by only 3.0 ± 0.1 cm ($P<0.001$; Fig. 2A). Hoppers compensated by increasing leg compression by 4.1 ± 0.2 cm between the elastic surface and the most damped surface ($P = 0.001$; Fig. 2B). In contrast, simulation results predicted a much smaller change in leg compression than observed in the subjects ($P<0.001$; Fig. 2B). As a result of greater leg compression on more heavily damped surfaces, the center of mass downward displacement during the stance phase was similar on all surfaces ($P = 0.222$; Fig. 2C). In contrast, the simulation revealed that downward center of mass displacement would have decreased by 44% across the range of surface damping ($P<0.001$) without adjustment of leg mechanics (Fig. 2C), and this prediction differs from the subject results ($P<0.001$).

Because hoppers adjusted leg mechanics to compensate for surface damping, the leg–surface combination behaved like a single spring despite surface damping, and its vertical stiffness ($k_{vert}$, combined surface and leg stiffness) increased by only 12% from the elastic surface to most damped surface ($P = 0.043$). The simulation revealed that average vertical stiffness would have increased by 55% ($P<0.001$), and much more than actually occurred in the subjects ($P = 0.001$), if hoppers had used the same leg mechanics on the damped surfaces as they used on the elastic surface (Fig. 2D).

The legs reached peak compression earlier in the stance phase as surface damping increased and more than compensated for the slower surface compression. On the most damped surface, the surface reached peak compression up to 25 ± 5 ms later ($P = 0.009$) while the legs reached peak compression up to 40 ± 5 ms earlier in the stance phase than on the elastic surface ($P = 0.002$; Fig. 3A). Consequently, the center of mass reached its minimum height 21 ± 5 ms earlier on the most damped surface than on the elastic surface ($P = 0.010$; Fig. 3A). If subjects had used the same spring-like leg mechanics on the most damped surface as on the elastic surface, the simulation indicated that the timing of minimum center of mass height and peak leg compression would have occurred 26 and 34 ms earlier, respectively, than observed in the subjects ($P<0.001$; Fig. 3B).

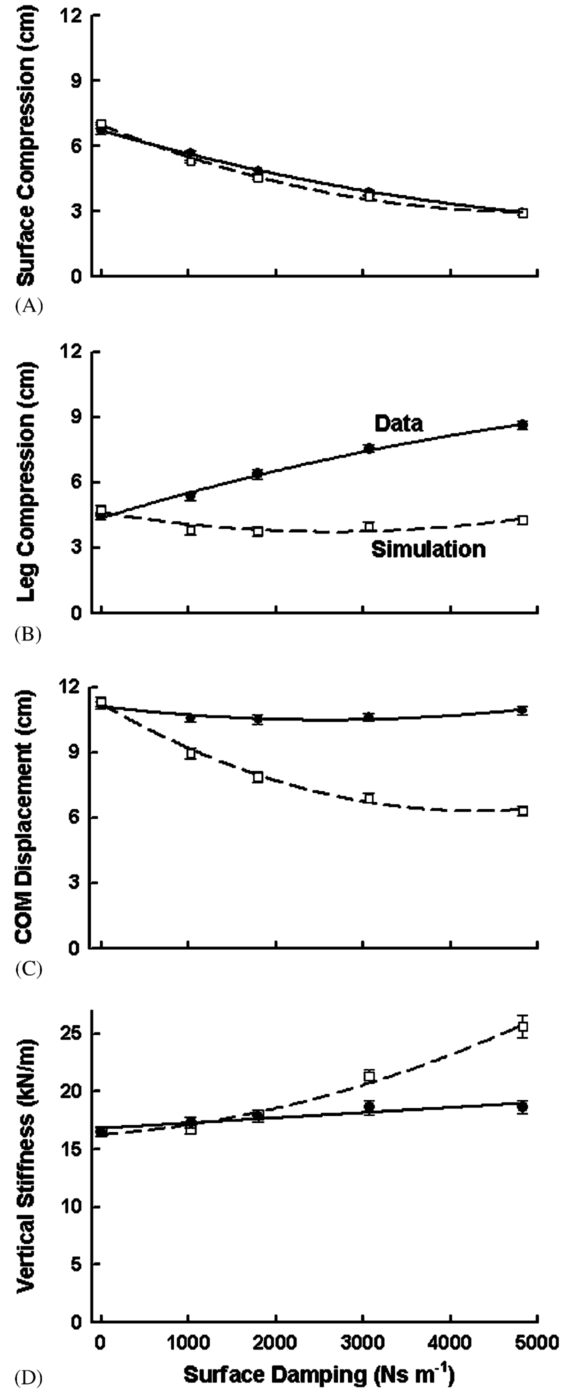


Fig. 2. (A) Peak surface compression, (B) peak leg compression, (C) peak downward center of mass displacement during stance, and (D) vertical stiffness of the leg–surface combination vs. surface damping. Solid lines and filled symbols represent subject data (mean ± SEM). On more heavily damped surfaces, larger leg compression compensated for smaller surface compression such that downward displacement of the center of mass and vertical stiffness varied only slightly. Dashed lines and open symbols represent a simulation of a spring-mass model with the leg stiffness from the elastic surface used on all surfaces. Lines are least-squares regressions, and many error bars are hidden by symbols.

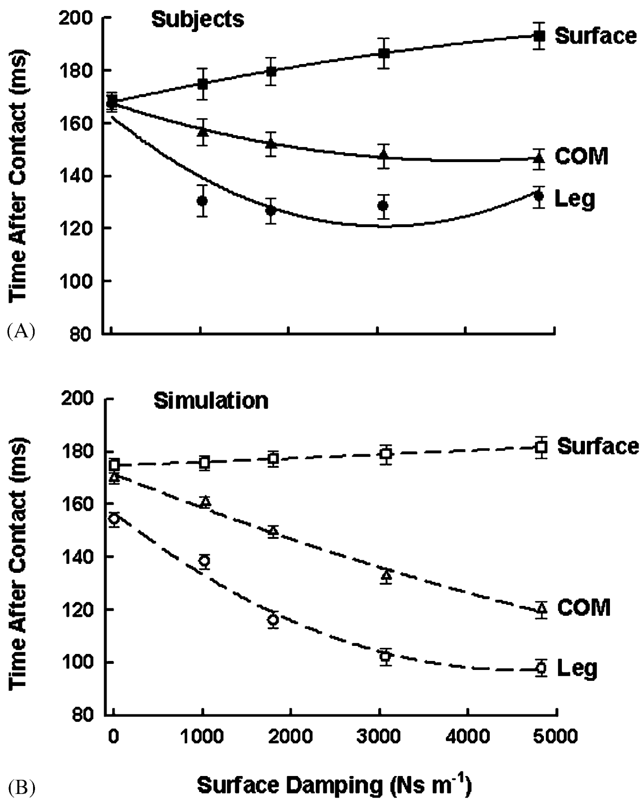


Fig. 3. Time intervals after touchdown for peak surface compression, peak downward center of mass displacement (COM), and peak leg compression vs. surface damping (mean ± SEM). Lines are least-squares regressions. (A) As surface damping increased, the stance legs reached peak compression sooner after touchdown, and this timing shift more than offset the later peak surface compression. Consequently, the center of mass displacement reached its lowest position slightly earlier. (B) For the simulation that used the same leg mechanics on the damped surfaces as on the elastic surface, peak leg compression and peak downward center of mass displacement occurred even earlier on heavily damped surfaces than in the subjects.

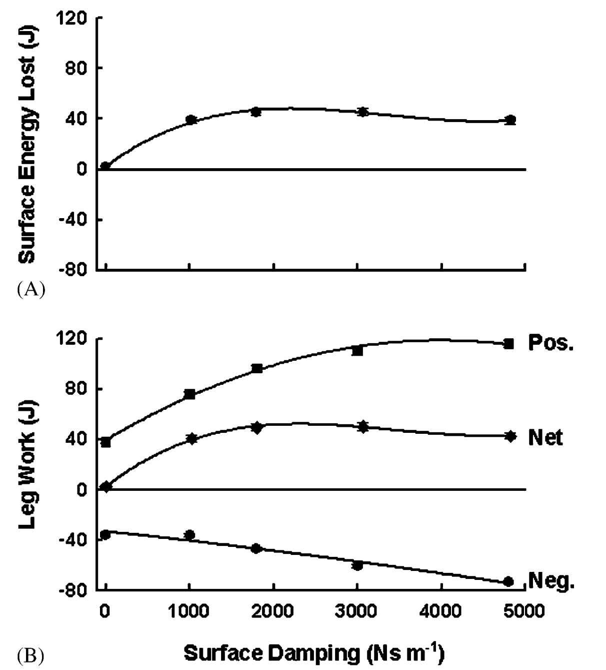


Fig. 4. (A) Surface energy dissipation and (B) negative, positive and net mechanical leg work vs. surface damping for all subjects (mean ± SEM). Lines are least-squares regressions, and many error bars are hidden by symbols. Surface energy dissipation and net leg work plateaued at intermediate damping levels and then decreased slightly on the most damped surface. Over the range of surface damping, negative leg work doubled, and positive leg work tripled so that net leg work increased sufficiently to replace the surface energy lost.

On more heavily damped surfaces, subjects performed more net mechanical leg work to replace the energy lost by the damped surfaces. Surface energy dissipation increased rapidly between the elastic surface and the least damped surface ($P<0.001$) and then reached a plateau at intermediate surface damping levels ($P = 1.000$). Energy dissipation on the most damped surface was slightly lower than on intermediate damped surfaces ($P<0.001$), and equal to the least damped surface ($P = 1.000$; Fig. 4A and Table 1). Over the entire range of surface damping, however, more heavily damped surfaces dissipated a greater percentage of the energy that they absorbed (Table 1). This change occurred primarily because more heavily damped surfaces absorbed less energy during compression while dissipating a similar amount of energy (Table 1). Net mechanical work output by the legs during the stance phase exactly compensated for surface energy dissipation (Fig. 4B) as is required for steady-state hopping.

Subjects increased net leg work on the most damped surface by performing three-fold more positive work during leg extension ($P = 0.003$) while absorbing only two-fold more energy during leg compression ($P = 0.001$) compared to the elastic surface (Fig. 4B). Negative work increased primarily because the legs compressed further to compensate for the smaller compression of heavily damped surfaces. Positive work increased more than negative work because leg extension exceeded leg compression to a greater extent on the most damped surface ($2.8 \pm 0.2$ cm) than on the elastic surface ($0.4 \pm 0.1$ cm; $P = 0.001$; Fig. 5 and Table 1).

All three leg joints contributed to the greater net leg work on more heavily damped surfaces by producing more net joint work ($P<0.001$). On the most damped surface, the majority of work appeared at the ankle joint (60.1%), while less work appeared at the knee (20.7%) and hip (19.2%; Fig. 6A). Although each joint absorbed more energy during stance on more heavily damped surfaces ($P<0.013$; Fig. 6B), it was more than offset by the large increase in positive work at each joint across the range of surfaces ($P<0.004$; Fig. 6C).

Hoppers achieved positive net joint work during stance primarily by extending the joints further during takeoff than they flexed during landing. For example,

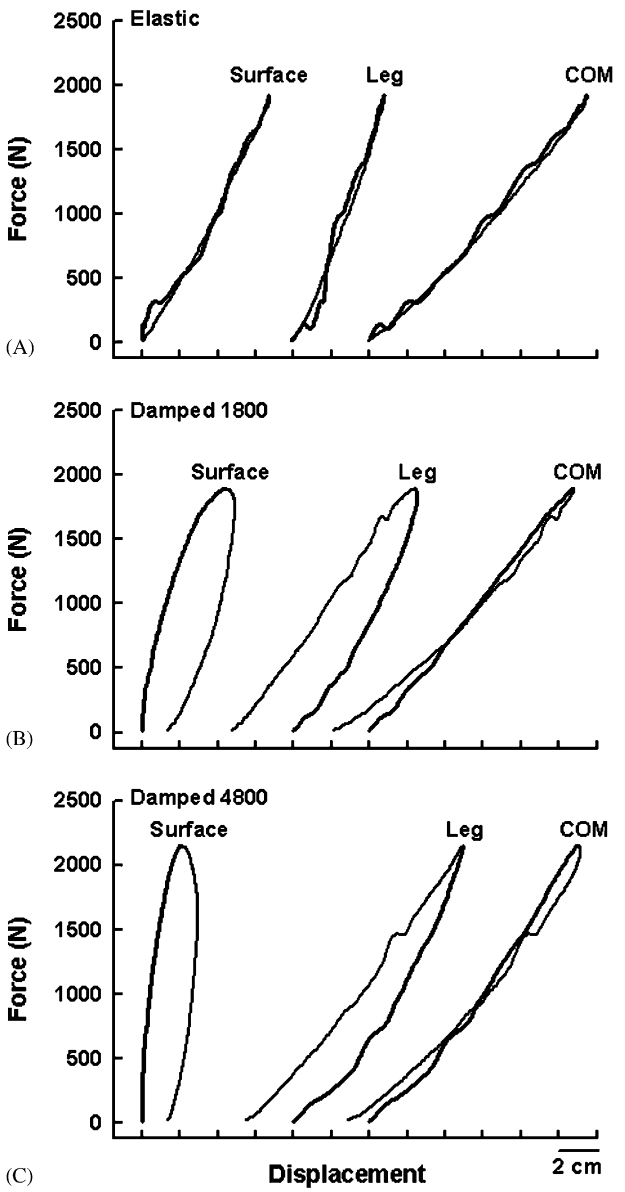


Fig. 5. Force vs. displacement for the surface, legs, and center of mass (COM) during the contact phase from representative hops on the (A) elastic surface, (B) $1800\,\mathrm{N\,s\,m^{-1}}$ damped surface, and (C) $4800\,\mathrm{N\,s\,m^{-1}}$ damped surface. During landing (thick lines), the force increased as the surface and center of mass moved downward, and the legs compressed. During takeoff (thin lines), the landing path was retraced for the elastic surface but not for the damped surfaces. On the damped surfaces, subjects extended their legs during takeoff more than they flexed their legs during landing to replace the energy lost by the surface. The COM force-displacement relationship (equivalent to the combined surface–legs force-displacement relationship) was spring-like on all surfaces.

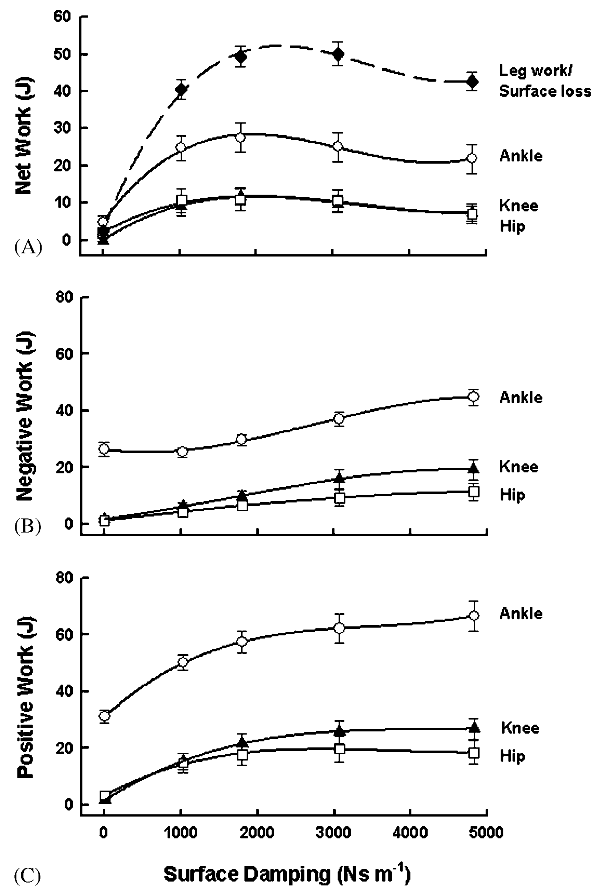


Fig. 6. (A) Net work during each stance phase vs. surface damping at the ankle, knee and hip. The dashed line represents net work per hop performed by the overall leg during the stance phase, which is equal in magnitude to the energy dissipated by the surface. The ankle contributed the most net work to overall leg work on damped surfaces. (B) Negative joint work and (C) positive joint work vs. surface damping for ankle, knee and hip. All values are means ± SEMs, and lines are least-squares regressions.

during hopping on the $1800\,\mathrm{N\,s\,m^{-1}}$ damped surface, both the ankle and knee joints were 7° more extended at takeoff than at touchdown, and the hip was 4° more extended ($P<0.006$ for all; Figs. 7 and 8A). In fact, this 'net joint extension' at all joints reached a plateau as surface damping increased that closely followed the pattern in net leg extension, net leg work, and surface energy dissipation (Figs. 4 and 8A). An additional factor in increasing net joint work on more heavily damped surfaces was that the joint moment at a given angle was greater during extension than flexion (Fig. 7A–C).

While modulating net work output at each joint to compensate for changes in surface energy dissipation, hoppers simultaneously adjusted peak flexion at each joint to compensate for changes in surface compression. More heavily damped surfaces compressed less during hopping but subjects compensated by flexing all three leg joints further during landing to produce greater leg compression ($P<0.001$; Figs. 7D–F and 8B). For example, on the most heavily damped surface, the ankle flexed $8\pm1°$ further during landing than on the elastic surface, while the knee and hip flexed $12\pm2°$ and $6\pm3°$ further, respectively. In contrast to the plateau in net joint extension and work across surface damping (Fig. 8A), hoppers increased joint flexion and leg compression continuously as surface damping increased

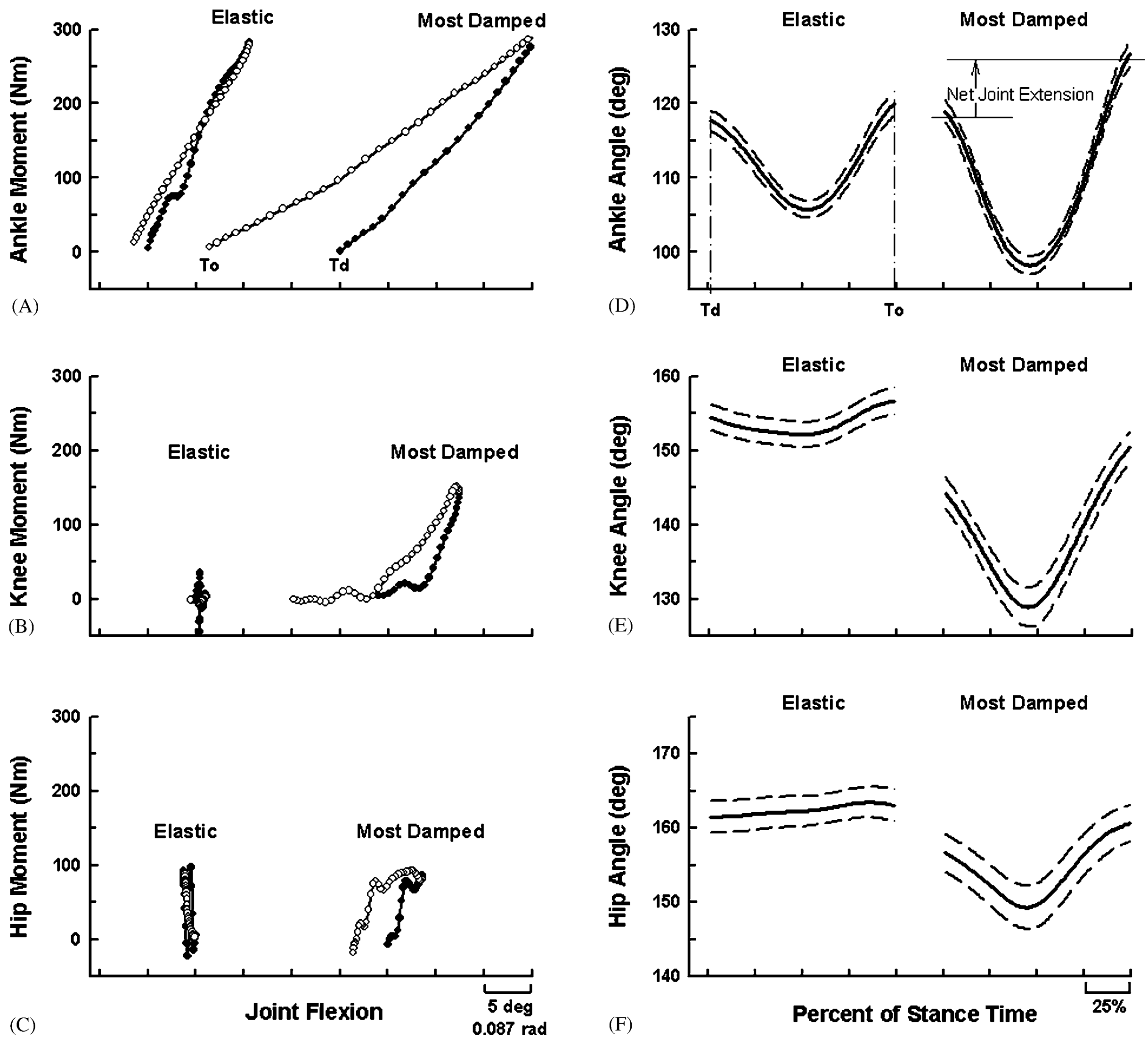


Fig. 7. (A–C) Example joint moment vs. joint angle for the ankle, knee and hip for a single hop on the elastic surface and the $4800\,\mathrm{N\,s\,m^{-1}}$ damped surface. Filled symbols represent touchdown (Td) to peak flexion, and open symbols represent peak flexion to toe-off (To). Symbols appear at 5 ms intervals. (D–F) Average joint angles vs. normalized stance time on the elastic surface and the $4800\,\mathrm{N\,s\,m^{-1}}$ damped surface for all subjects. Dashed lines indicate $\pm$SEM for each trace. All traces are from touchdown (Td) to toe-off (To). On more heavily damped surfaces, hoppers performed more net leg work by increasing net joint extension and adjusted leg compression by allowing the joints to flex further during landing.

(Fig. 8B) and thereby compensated for the smaller surface compression.

## 4. Discussion

As predicted by our hypothesis, hoppers maintain similar center of mass dynamics as surface damping increases by simultaneously changing the magnitude and timing of maximum leg compression and leg mechanical work output. By making this complex adjustment to leg mechanics, hoppers maintain spring-like center of mass dynamics despite large changes in both surface compression and energy dissipation as surface damping increases (see Fig. 5). These findings and earlier studies suggest that regulating center of mass dynamics by dramatically altering leg mechanics may be an important control strategy in locomotion. When humans hop and run on elastic surfaces, they maintain similar center of mass dynamics by adjusting leg stiffness to offset changes in surface stiffness (Ferris and Farley, 1997; Ferris et al., 1998, 1999; Kerdok et al., 2002). Similarly, in a previous study of hopping on a range of damped surfaces that compress by the same distance (Moritz and Farley, 2003), hoppers maintain center of mass dynamics by increasing net leg work without changing leg compression. In the present study, unlike the earlier studies, subjects simultaneously accommodate changes in both

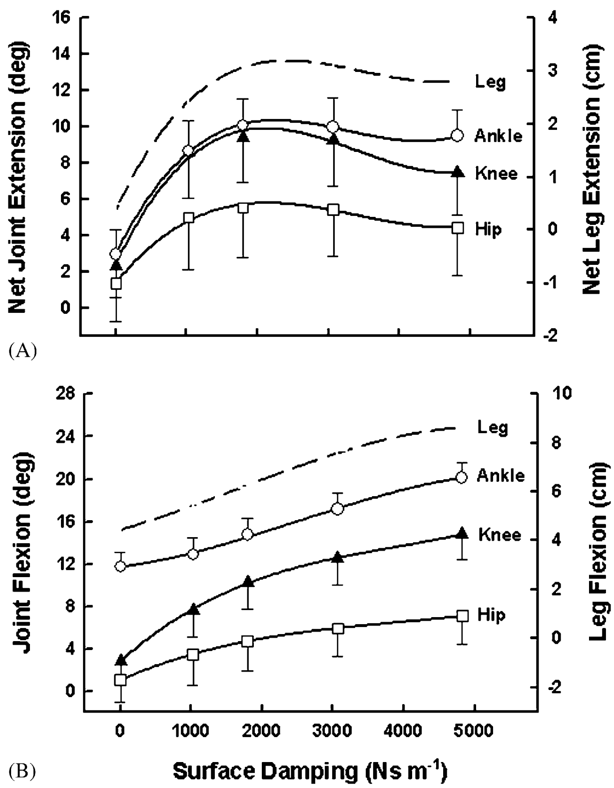


Fig. 8. (A) Net joint extension vs. surface damping for all subjects (mean ± SEM). Net joint extension increased and then reached a plateau at moderate levels of surface damping. The dashed line and right axis correspond to net leg extension, defined as the difference in leg length between touchdown and toe-off. The second data point for the knee is covered by the ankle data point. (B) Joint flexion during landing vs. surface damping for all subjects (mean ± SEM). The dashed line and right axis correspond to leg compression (i.e., peak reduction in leg length during stance). Both joint flexion and leg compression increased continuously with surface damping. For clarity, either a positive or negative error bar is shown for each joint. All lines are least-squares regressions.

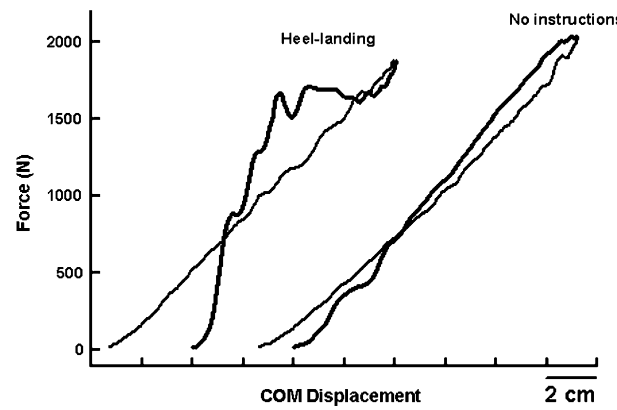


Fig. 9. Force vs. displacement for representative hops on the 1800 N s m$^{-1}$ damped surface at 2.2 Hz. The left trace is for a stance phase of hopping while landing on the heels. The right trace shows the results when the same subject was given no instructions other than to match the metronome beat, and chose to land on the forefeet. The leg–surface combination did not behave-like a spring for heel-landing as demonstrated by the nonspring-like force–displacement relationship for the center of mass ($r^2 = 0.756$ for linear regression of force vs. displacement during the landing phase), compared to spring-like force–displacement relationship for the COM ($r^2 = 0.996$) for forefoot striking.

maximum surface compression and energy dissipation by adjusting leg mechanics, thereby maintaining similar center of mass dynamics on all surfaces.

Hoppers are *not* mechanically required to use bouncing center of mass dynamics with a constant vertical stiffness of the leg–surface combination when hopping at a given frequency. For example, humans can vary the fraction of the hop cycle on the ground to alter vertical stiffness by two-fold at one hopping frequency (Farley and Morgenroth, 1999). In addition, hoppers are capable of using non-spring-like center of mass movements when instructed to hop differently. In a pilot study, we asked subjects to hop on a heavily damped surface, landing on their heels and taking off from their toes. When instructed to land on their heels, subjects used very non-spring-like center of mass movements compared to when they hopped without instructions (Fig. 9).

Humans increase net leg work to compensate for greater energy dissipation by the surface by extending their legs further during take-off than they flex their legs during landing (i.e., 'net leg extension'). Although there is a slight tendency for hoppers to have more extended legs at takeoff than at landing on elastic surfaces, this leg length difference increases by up to eight-fold when hoppers perform more net leg work to compensate for energy dissipation by heavily damped surfaces. Regardless of whether peak leg compression changes by two-fold (as in the present study) or remains nearly constant (Moritz and Farley, 2003), hoppers fine tune net leg work primarily by adjusting leg extension relative to leg compression. This strategy for modulating net leg work is used in other activities. For example, runners use net stance leg extension to perform the mechanical work needed to ascend an incline (Iversen and McMahon, 1992). Moreover, to perform the work needed to maximize drop jump height, humans extend their legs during takeoff by 10–13 cm more than they flex their legs during landing (Bobbert et al., 1987).

Hoppers simultaneously modulate net joint extension and peak joint flexion to compensate for simultaneous changes in surface energy dissipation and compression. Hoppers perform more net joint work to compensate for greater energy dissipation of damped surfaces primarily by extending all three leg joints further during takeoff than they flex during landing. Net joint extension follows a similar pattern as net leg extension, net leg work, and surface energy dissipation which initially increase and then reach plateaus on more heavily damped surfaces. In contrast, peak joint flexion increases continuously across the entire surface damping range to compensate for the continuously decreasing surface compression (see Fig. 8) and thereby maintains similar center of mass motion regardless of surface damping.

The ankle contributes more net work than either the knee or hip on damped surfaces, and it may also play the largest role in adjusting leg compression. As shown in previous studies of hopping in place (Farley et al., 1998; Farley and Morgenroth, 1999), the ankle may play the largest role in adjusting leg compression because a given flexion at the ankle leads to more leg compression than the same flexion at the knee or hip (Farley et al., 1998; Farley and Morgenroth, 1999). Leg compression is most sensitive to ankle flexion due to the horizontal orientation of the foot. Consequently, even though flexion magnitude increases to a smaller extent at the ankle than at the knee on more heavily damped surfaces, the ankle is likely to be the primary cause of the greater leg compression (see Farley et al., 1998).

In summary, hoppers compensate for changes in both peak surface compression and energy dissipation by simultaneously adjusting the magnitude and timing of leg compression, as well as leg mechanical work output. Humans perform net positive mechanical work by increasing net leg extension when hopping on damped surfaces, running up a hill (Iversen and McMahon, 1992), or performing drop jumps (Bobbert et al., 1987). By using this strategy on a range of damped surfaces, hoppers maintain similar center of mass dynamics at the expense of dramatically altering leg mechanics. This study, taken together with previous studies of hopping and running on a large range of elastic and damped surfaces, suggests strongly that controlling center of mass dynamics regardless of surface properties may be an organizing principle for the control of rapid locomotion.

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