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HIGHLIGHTED TOPIC | *Neural Control of Movement*

Neuromuscular changes for hopping on a range of damped surfaces

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Moritz, Chet T., Spencer M. Greene, and Claire T. Farley. Neuromuscular changes for hopping on a range of damped surfaces. *J Appl Physiol* 96: 1996–2004, 2004. First published December 19, 2003; 10.1152/japplphysiol.00983.2003.—Humans hopping and running on elastic and damped surfaces maintain similar center-of-mass dynamics by adjusting stance leg mechanics. We tested the hypothesis that the leg transitions from acting like an energy-conserving spring on elastic surfaces to a power-producing actuator on damped surfaces during hopping due to changes in ankle mechanics. To test this hypothesis, we collected surface electromyography, video kinematics, and ground reaction force while eight male subjects (body mass: 76.2 ± 1.7 kg) hopped in place on a range of damped surfaces. On the most damped surface, most of the mechanical work done by the leg appeared at the ankle (52%), whereas 23 and 25% appeared at the knee and hip, respectively. Hoppers extended all three joints during takeoff further than they flexed during landing and thereby did more net positive work on more heavily damped surfaces. Also, all three joints reached peak flexion sooner after touchdown on more heavily damped surfaces. Consequently, peak moment occurred during joint extension rather than at peak flexion as on elastic surfaces. These strategies caused the positive work during extension to exceed the negative work during flexion to a greater extent on more heavily damped surfaces. At the muscle level, surface EMG increased by 50–440% in ankle and knee extensors as surface damping increased to compensate for greater surface energy dissipation. Our findings, and those of previous studies of hopping on elastic surfaces, show that the ankle joint is the key determinant of both springlike and actuator-like leg mechanics during hopping in place.

biomechanics; locomotion; running; gait

HUMANS AND OTHER ANIMALS MUST perform work on their environment when moving up a hill or over terrain that dissipates energy. On hard and level surfaces, hopping and running animals bounce along the ground with center-of-mass dynamics predicted by a spring-mass model (1, 4, 9). In that model, stance leg mechanics are represented by a linear spring that supports a point mass at the animal's center of mass (3, 22). Humans hopping or running on a range of elastic surfaces adjust the stiffness of their springlike stance legs to maintain similar center-of-mass dynamics (10, 12–14, 20). On a range of damped surfaces, human hoppers use non-springlike leg mechanics but adjust their legs to maintain similar springlike behavior of the leg-surface combination and center-of-mass dynamics as on elastic surfaces (25). On sand, a natural energy-dissipating surface, runners also use a bouncing gait generally similar to the gait used on a hard surface (21).

On a range of damped surfaces, humans adjust leg mechanical work output as well as leg compression magnitude and timing to maintain normal center-of-mass dynamics during hopping (25). The legs do not behave like energy-conserving springs during steady hopping on damped surfaces because they replace the energy dissipated by the surface. To increase work output, the legs extend more than they compress, and thus they are longer at takeoff than at touchdown. Despite similar ground contact times on elastic and damped surfaces, the legs reach maximum compression (i.e., peak reduction in leg length due to joint flexion) earlier in the stance phase to compensate for the slower compression and rebound of more heavily damped surfaces. Surprisingly, these adjustments cause the leg-surface combination to behave like a linear spring with the same stiffness on all damped surfaces (25). Because most natural surfaces are viscoelastic, understanding the mechanisms for adjusting leg mechanics may inspire new designs for prostheses (5) and legged robots (26) that can adapt to a variety of terrain.

The goal of the present study was to examine how joint dynamics and EMG change with surface damping. From purely elastic surfaces to damped surfaces, the legs transition from acting like energy-conserving springs to work-producing actuators. Previous studies found that human hoppers almost exclusively rely on adjusting ankle stiffness to change leg stiffness (10, 11). Thus we hypothesized that hoppers compensate for surface damping primarily by adjusting ankle dynamics to increase mechanical work output and to change leg compression-extension timing. Based on this hypothesis, we predicted that the EMG of muscles that extend the ankle would increase to allow them to perform more mechanical work. To test our hypothesis, we analyzed joint moments, joint work, and surface EMG data for humans hopping in place on a range of damped surfaces.

MATERIALS AND METHODS

Overview. Eight healthy male subjects (body mass 76.2 ± 1.7 kg, height 176 ± 5 cm, age 28 ± 2 yr; means ± SD) hopped in place on a surface with adjustable damping and stiffness. All subjects gave informed consent, and the protocol was approved by the University of Colorado Human Research Committee. The overall leg mechanics for these subjects were reported in a previous study (25). The present study examined joint kinematics and electromyography (EMG). This multilevel analysis allows us to evaluate how joints and muscles are coordinated to produce overall the leg mechanics on damped surfaces observed in the previous study.

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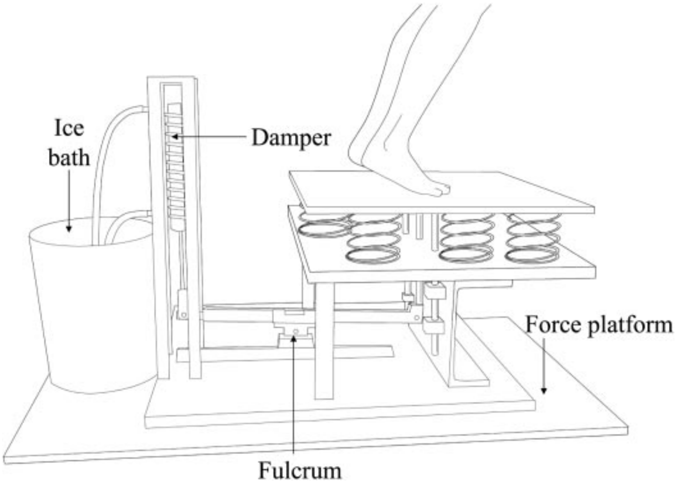


Fig. 1. The damped hopping surface mounted on a force platform. Surface damping was varied by adjusting the position of the fulcrum on the lever arm connecting the damper to the surface. The damper temperature was maintained by circulating ice water through a copper coil. The surface was originally described in Moritz and Farley (25).

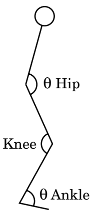
Subjects hopped in place on a custom-built hopping surface (Fig. 1) supported by steel springs (Century Springs, Los Angeles, CA) and a linear hydraulic damper (Taylor Devices, New York, NY). The linear damper produced a force directly proportional to the surface velocity magnitude ($r^2 = 0.98$) but in the opposite direction. We report surface damping (in N·s·m^{-1}), and a larger damping coefficient indicates a greater force resisting a given surface velocity. We adjusted surface stiffness by changing the number of springs, and surface damping by changing the position of the fulcrum on a 50-cm lever arm connecting the damper to the surface. We calculated surface stiffness from the linear force-displacement relations ($r^2 > 0.99$) determined from static tests and surface damping from linear force-velocity relations determined from constant-velocity ramp tests (Instron, Canton, MA). The surface deck was a lightweight (effective mass = 3.7 kg), 60 × 60-cm fiberglass and aluminum honeycomb sandwich panel (Goodfellow, Berwyn, PA). Linear bearings constrained the surface to move only vertically. Because the damping coefficient was sensitive to the temperature of the damping fluid, we maintained the damper temperature between 21 and 22°C by using a surface thermocouple (Omega, Stamford, CT) and a water pump to circulate ice water through a copper coil surrounding the damper (Fig. 1). A detailed description of the hopping surface was published previously (25).

Subjects hopped on an elastic surface with no damping and on surfaces with four levels of damping. We selected damping and stiffness combinations (Table 1) to maintain maximum surface compression between 6.0 and 6.5 cm for all surfaces. We chose this surface compression to permit the maximum surface energy dissipation while still permitting the damped surfaces to rebound completely before each hop. Subjects matched the beat of a metronome at 2.2 Hz (approximately the preferred hopping frequency; Refs. 8, 23) while hopping barefoot on two legs with hands clasped behind their backs. Subjects hopped on each surface for 40 s, and data were collected for the final 10 s. Trial order progressed from the least to most damped surface and then the elastic surface. Trials were then repeated in reverse order, and data from pairs of trials on each surface were averaged. Subjects rested for 2 min between trials and between the first and second sets of trials. From each trial, we selected five consecutive hops for analysis that were within 5% of the 2.2-Hz hopping frequency. We used a repeated-measures ANOVA and Tukey's post hoc test to determine differences among the surfaces ($P < 0.05$; Statview 5, SAS Institute, Cary, NC). All values are means ± SE.

Kinematics and kinetics collection and analysis. The hopping surface was mounted on a force platform (AMTI, Watertown, MA) and incorporated a linear potentiometer (Omega, Stamford, CT) to measure surface compression. We sampled ground reaction force and surface position at 1,000 Hz with an analog-to-digital board using Labview 4.1 software (National Instruments, Austin, TX). We calculated center of pressure under the feet in the sagittal plane by using surface compression data to determine the vertical distance to the force platform origin. Applying forces at known locations on the hopping surface demonstrated that this method was accurate to within 0.5 cm.

We collected and analyzed sagittal plane video data to quantify joint kinematics. We videotaped subjects at 200 frames/s (JC Labs, Mountain View, CA) after placing reflective markers on seven anatomic landmarks (tip of first toe, fifth metatarsophalangeal joint, lateral malleolus, femur lateral epicondyle, greater trochanter, lateral iliac crest, acromion scapulae). From marker positions, we determined segment positions, accelerations, and joint angles (Peak Motus 6.0, Englewood, CO). We calculated the average joint angle profile vs. time by normalizing the duration of each stance phase to 100% and then taking the mean of the average profiles for all subjects on each surface. We defined the change in leg length (i.e., "leg compression")

Table 1. *Joint kinematics during hopping on an elastic surface and four damped surfaces*



	Elastic				Most Damped
Surface damping, N·s·m^{-1}		582	1,145	1,634	2,073
Surface stiffness, kN/m	30.3	27.8	22.0	16.2	13.3
Ankle angle-touchdown, °	118±2	115±2*	114±1*	113±2*	114±2*
Ankle angle-minimum, °	104±2	102±1	102±1	101±2*	102±2
Ankle angle-takeoff, °	120±2	121±2	123±2*	125±2*	126±2*
Knee angle-touchdown, °	153±2	146±3*	140±3*	138±3*	138±2*
Knee angle-minimum, °	149±2	139±3*	133±3*	130±2*	128±2*
Knee angle-takeoff, °	156±2	153±2*	151±3*	151±2*	150±2*
Hip angle-touchdown, °	162±2	156±2*	150±3*	149±3*	148±3*
Hip angle-minimum, °	161±2	154±3*	148±3*	145±3*	144±3*
Hip angle-takeoff, °	164±2	161±2	158±3*	157±3*	156±2*
Ankle mean extension velocity, °/s	62±6	67±5	74±5	81±6*	81±6*
Knee mean extension velocity, °/s	42±13	64±12	82±12*	91±10*	101±10*
Hip mean extension velocity, °/s	29±18	42±14	59±17	59±15	61±13*
Ankle mean acceleration during flexion, $°/s^2$	348±62	556±95	698±106	840±118*	882±126*
Knee mean acceleration during flexion, $°/s^2$	337±120	716±149	1,044±176*	1,162±139*	1,134±106*
Hip mean acceleration during flexion, $°/s^2$	128±71	310±87	553±156*	605±126*	571±102*

Values are means ± SE for all 8 subjects. *Significant difference from the elastic surface, $P < 0.05$.

as the change in the distance between the center of mass and surface. We used the vertical displacement of the center of mass and surface compression to calculate leg compression throughout stance (25). We synchronized the force and video data by illuminating a light-emitting diode in the video field and simultaneously signaling the analog-to-digital hardware.

We used an inverse dynamics analysis to calculate the net muscle moment and work at each leg joint. We combined the ground reaction force, center of pressure, and segment kinematic data to calculate the net muscle moment at the ankle, knee, and hip (7, 31). Next, we calculated the instantaneous net muscle power (P) at each joint as the product of the net muscle moment (M) and the joint angular velocity in the sagittal plane (ω)

$$P = M \cdot \omega \qquad (1)$$

We calculated negative and positive work at each joint from the time integral of the negative and positive portions of the joint power over each stance phase. Net joint work was defined as the sum of the positive and negative work at a given joint. We report the mechanical work that appeared at each joint, because an inverse dynamics analysis cannot account for work performed by muscles not crossing the joint that is transferred and appears at a given joint (32).

EMG collection and analysis. We measured EMG of seven leg muscles using surface electrodes to gain insight into how muscle activity changes as surface damping increases. The skin over each muscle (tibialis anterior, medial gastrocnemius, soleus, vastus medialis, vastus lateralis, rectus femoris, and semitendinosus) was shaved and prepared with sandpaper and alcohol. We positioned bipolar silver-chloride electrodes (interelectrode distance: 2 cm) according to published guidelines (15), and they remained attached for all trials. We sampled the EMG signals from a Telemyo system (Noraxon, Phoenix, AZ) at 1,000 Hz, concurrent with the force data.

We processed the EMG signals before computing the mean EMG during two phases of the hop cycle. EMG signals were band-pass filtered at 20–500 Hz by using a fourth-order zero-lag Butterworth digital filter and then rectified (Matlab 6.1, The Mathworks, Natick, MA). We calculated the mean rectified EMG during the stance and aerial phases of each hop by averaging over the duration of each phase. We expressed mean EMG values as a percentage of the mean EMG from the respective phase for the elastic surface trial. It is important to note that, due to electromechanical delay and relatively long muscle relaxation times, muscle force generation is not exactly synchronized with EMG activity. For example, EMG activity late in the aerial phase likely represents force generation in the following stance phase.

RESULTS

Hoppers adjusted joint mechanics dramatically as their legs transitioned from acting like energy-conserving springs on the elastic surface to power-producing actuators on the damped surfaces. On the elastic surface, each joint had a net work output of approximately zero and behaved like a torsional spring. On the most damped surface, the increase in net mechanical work at each joint was clearly seen from the greater moment during extension than during flexion and the resulting area inside the joint moment vs. angular displacement relationships (Fig. 2). The ankle contributed twice as much net work as the knee or hip to replace the energy lost by the damped surfaces. On the most damped surface, 52% of the net leg work appeared at the ankle, whereas 23 and 25% appeared at the knee and hip, respectively (Fig. 3*A*).

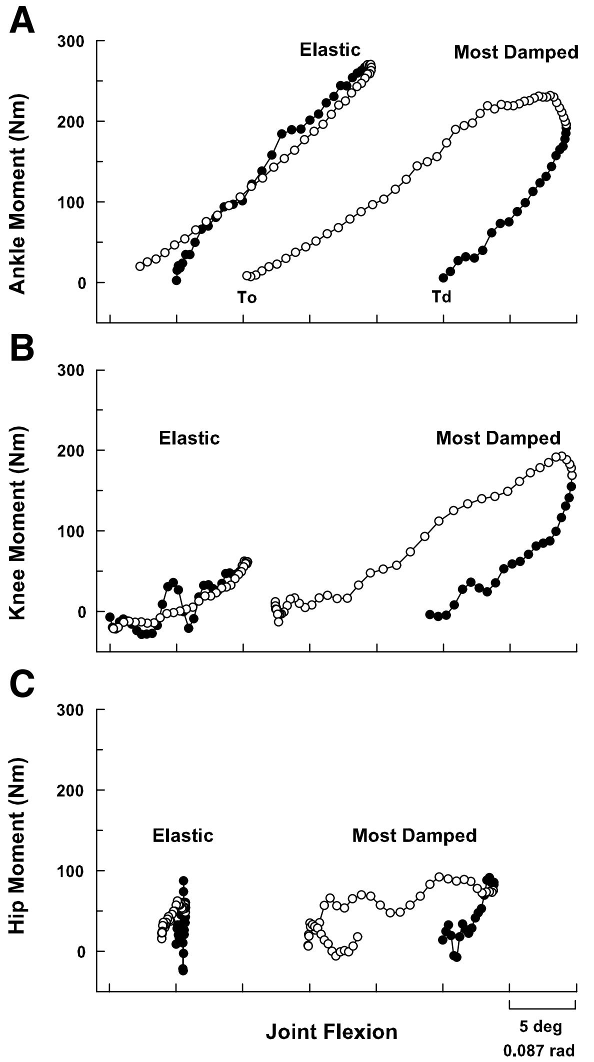


Fig. 2. Net muscle moment vs. joint flexion for a representative contact phase on the elastic surface and most damped surface for ankle (*A*), knee (*B*), and hip (*C*). From touchdown (Td) until peak leg compression (●), moments increase as joints flex. Subsequently, moments fall as joints extend (○). Symbols appear at 5-ms intervals. On the most damped surface, all 3 joints performed net mechanical work, as demonstrated by the greater net muscle moment generated during extension than flexion. On the elastic surface, the moment was similar for extension and flexion, and thus net joint work was ~0. A small amount of negative work often appeared as the hip flexed shortly before toe-off (To) as subjects lifted their feet off the heavily damped surfaces.

Hoppers increased net work output at the joints primarily by producing more positive work. As surface damping increased, the ankle produced up to 27 ± 5 J more positive work during extension and absorbed up to 10 ± 2 J less energy during flexion (Fig. 3, *B* and *C*). Thus decreased energy absorption at the ankle contributed about one-fourth of the increase in net ankle work. The knee and hip performed up to 23 ± 3 and 20 ± 5 J more positive work during extension as surface damping increased, respectively, but that increase was partially offset by slightly more energy absorption during flexion at both joints (Fig. 3, *B* and *C*).

Hoppers performed positive net work primarily by extending the joints during takeoff much further than they flexed during landing. For example, the ankle and knee extended 12 ± 1° further during takeoff than they flexed during landing on the most damped surface (Fig. 4). In contrast, both joints extended only 2–3° further than they flexed on the elastic surface (Fig. 4). As surface damping increased, hoppers achieved net joint extension partly by landing with their joints more flexed. The ankle was 4 ± 1° more flexed at touchdown on the most damped surface than on the elastic surface, whereas the knee and hip were 14–15° more flexed (Fig. 4, *A–C*; Table 1). Net joint extension on damped surfaces resulted in longer legs at takeoff than at touchdown (Fig. 4*D*), partly compensating for the incomplete rebound of heavily damped surfaces by the instant of takeoff.

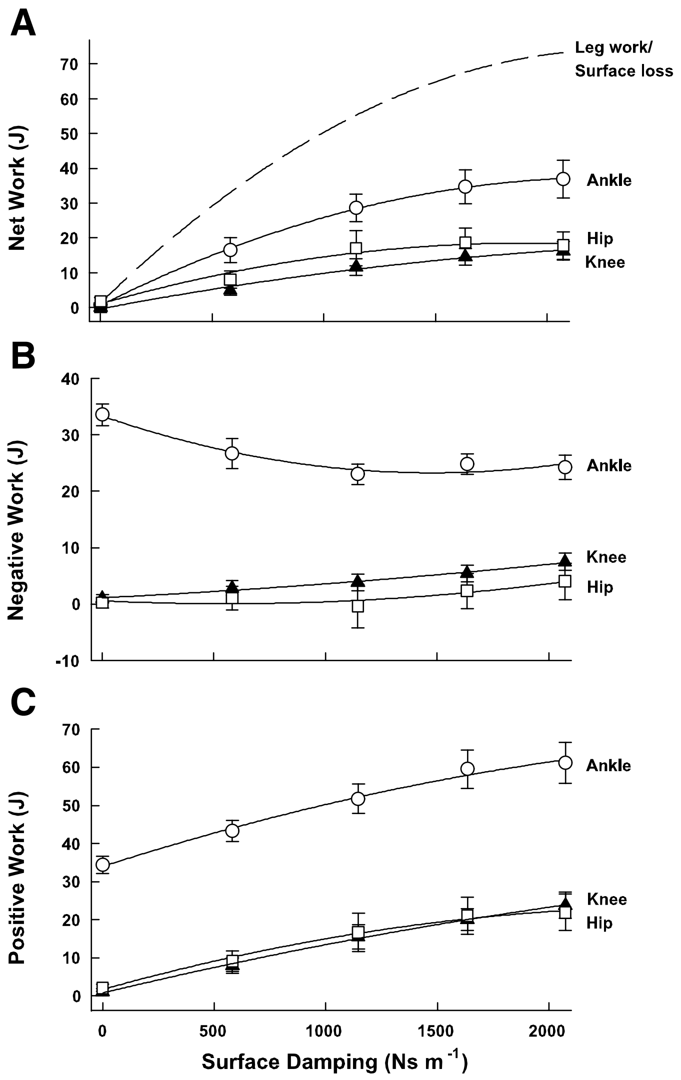


Fig. 3. *A*: net joint work per hop vs. surface damping at the ankle, knee, and hip. Dashed line corresponds to net work per hop performed by the overall leg, which is equal to the energy dissipated by the surface (25). The ankle contributed the most net work to overall leg work on damped surfaces ($P < 0.05$). Negative joint work during leg compression (*B*) and positive joint work during leg extension (*C*) are shown vs. surface damping for ankle, knee, and hip. Values are means ± SE for all subjects, and lines are least squares regressions.

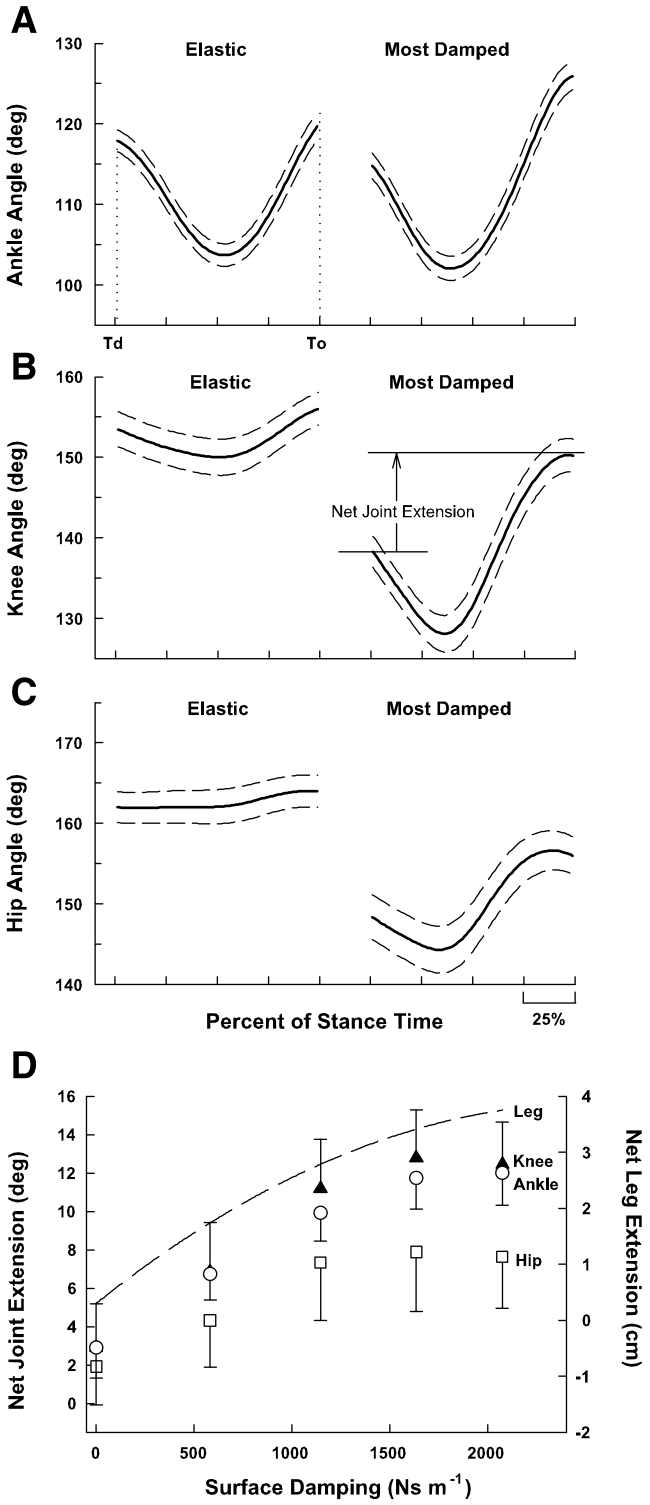


Fig. 4. Average joint angles vs. normalized stance time on the elastic and most damped surface for all subjects are shown for ankle (*A*), knee (*B*), and hip (*C*). Dashed lines indicate ± SE for each trace. All traces are from touchdown to toe-off. On the most damped surface, all 3 joints were more flexed at touchdown than on the elastic surface. Subsequently, all 3 joints were more extended at take-off than at touchdown (net joint extension). Average contact time was 319 ms on the elastic surface and 334 ms on the most damped surface. *D*: net joint extension vs. surface damping for all subjects (means ± SE). Net joint extension increased at all joints with surface damping ($P < 0.05$). Dashed line and right axis correspond to net leg extension (25). Net leg extension is the difference between leg length at takeoff and touchdown. The first 2 data points for the knee are covered by the ankle data. For clarity, either a positive or negative error bar is shown for each joint. Due to the horizontal orientation of the foot, the small increase in net ankle extension between surface damping of 1,600 and 2,100 N·s·m^{-1} was sufficient to produce more net leg extension (10, 11).

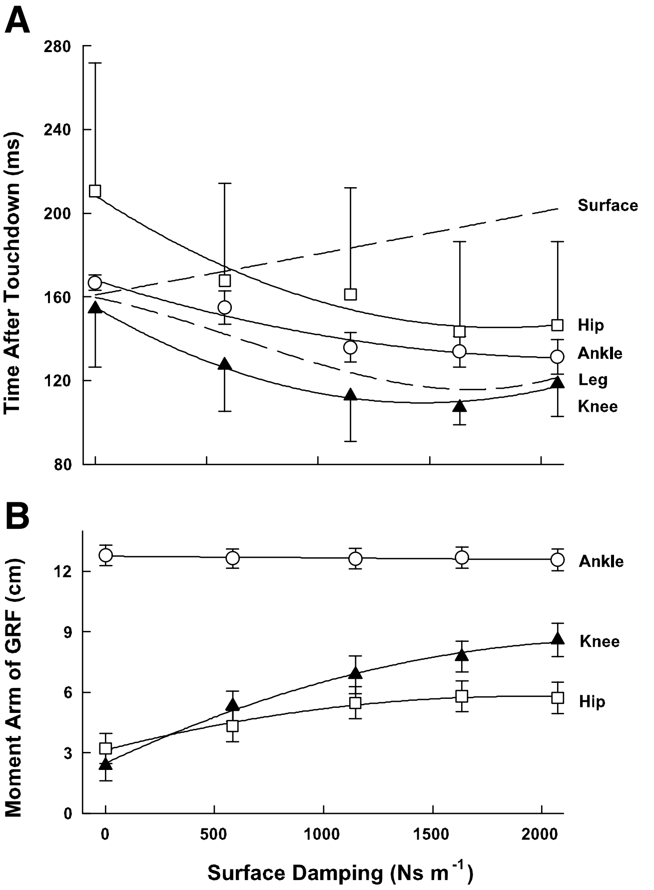


Fig. 5. *A*: time from touchdown until minimum joint angle vs. surface damping. All lines are least squares regressions, and some error bars are shown in 1 direction for clarity. *Top* dashed line represents the time interval after touchdown until the surface reached peak compression; *bottom* dashed line represents the time interval until peak leg compression (25). All 3 joints reached peak flexion earlier as surface damping increased ($P < 0.05$), but the ankle and knee most closely followed the timing of peak leg compression. *B*: midstance moment arm of the ground reaction force (GRF) about the ankle, knee, and hip vs. surface damping. The moment arms about the knee and hip increased 4- and 2-fold, respectively, with increased surface damping ($P < 0.05$). Values are means ± SE, and lines are least squares regressions.

All three joints reached peak flexion earlier in the stance phase and began to extend sooner after touchdown as surface damping increased (Fig. 5*A*). This earlier peak flexion permitted more time to perform positive work during joint extension and also compensated for slower compression of more heavily damped surfaces. Earlier peak flexion of the ankle and knee also caused peak joint moment to occur during joint extension on more heavily damped surfaces (Table 2). This timing shift caused the average moment to be greater during extension than during flexion (Fig. 2 and Table 2) and thus caused higher net mechanical work output during stance. In addition to spending more time extending on more heavily damped surfaces, the joints also extended 31–140% faster and thereby increased net joint extension and mechanical work over the stance time (Table 1). On all surfaces, the ankle and knee reached peak flexion at nearly the same time as the leg reached peak compression (dashed line in Fig. 5*A*).

Because hoppers landed with more flexed knees and hips on more heavily damped surfaces, the ground reaction force had a longer moment arm about these joints. For example, the moment arm of the ground reaction force about the knee at midstance increased by 6 ± 1 cm (260%) between the elastic surface and most damped surface (Fig. 5*B*). This longer moment arm led to a 2.8-fold increase in the peak knee extensor muscle moment on the most damped surface compared with the elastic surface (Fig. 2*B* and Table 2). The moment arm about the hip was moderately longer (81%) on more heavily damped surfaces, but, due to the effect of thigh inertia, the peak moment increased much less (22%; $P > 0.05$; Fig. 2*C* and Table 2). In contrast, the moment arm of the ground reaction force about the ankle (Fig. 5*B*), as well as the peak net muscle moment at the ankle (Table 2), changed little with surface damping because the ankle angle at touchdown changed only slightly (Table 1). On all surfaces, however, the ground reaction force moment arms and net muscle moments were greater at the ankle than at the knee or hip (Figs. 2 and 5*B*; Table 2).

Hoppers increased leg muscle EMG substantially on more heavily damped surfaces, and this factor likely contributed to the greater positive mechanical work at all leg joints. Mean EMG of the lower leg muscles increased similarly during stance (69–92%) and aerial phases (56–79%; Figs. 6 and 7).

Table 2. *Joint moments during hopping on an elastic surface and four damped surfaces*

	Elastic				Most Damped
Surface damping, N·s·m^{-1}		582	1,145	1,634	2,073
Surface stiffness, kN/m	30.3	27.8	22.0	16.2	13.3
Peak ankle moment, N·m	269±12	254±10	249±11	245±10*	241±12*
Peak knee moment, N·m	73±16	116±17*	160±22*	186±22*	204±21*
Peak hip moment, N·m	139±27	143±26	165±21	165±27	169±28
Time of peak ankle moment after minimum angle, ms	−10±5	17±8*	28±9*	28±9*	35±10*
Time of peak knee moment after minimum angle, ms	−49±25	−1±17	9±15	17±7*	17±8*
Time of peak hip moment after minimum angle, ms	−100±39	−29±31	−44±32	−19±29*	−37±29
Ankle mean moment during flexion, N·m	148±7	136±7	131±6	129±5	127±7
Ankle mean moment during extension, N·m	146±7	146±5	151±6	149±6	147±6
Knee mean moment during flexion, N·m	34±9	53±9	68±12	76±11	83±9
Knee mean moment during extension, N·m	30±7	57±7	82±12*	97±13*	106±13*
Hip mean moment during flexion, N·m	52±12	60±11	74±13	80±14	84±13
Hip mean moment during extension, N·m	57±9	70±11	79±12	83±11	83±11
Mean ground reaction force-leg compression, N	991±21	878±23	794±20*	794±17*	808±22*

Values are means ± SE for all 8 subjects. The time of peak moment after minimum angle gives the time lag between when the joint reaches minimum angle and when the joint moment is greatest for the ankle, knee, and hip. *Significant difference from the elastic surface, $P < 0.05$.

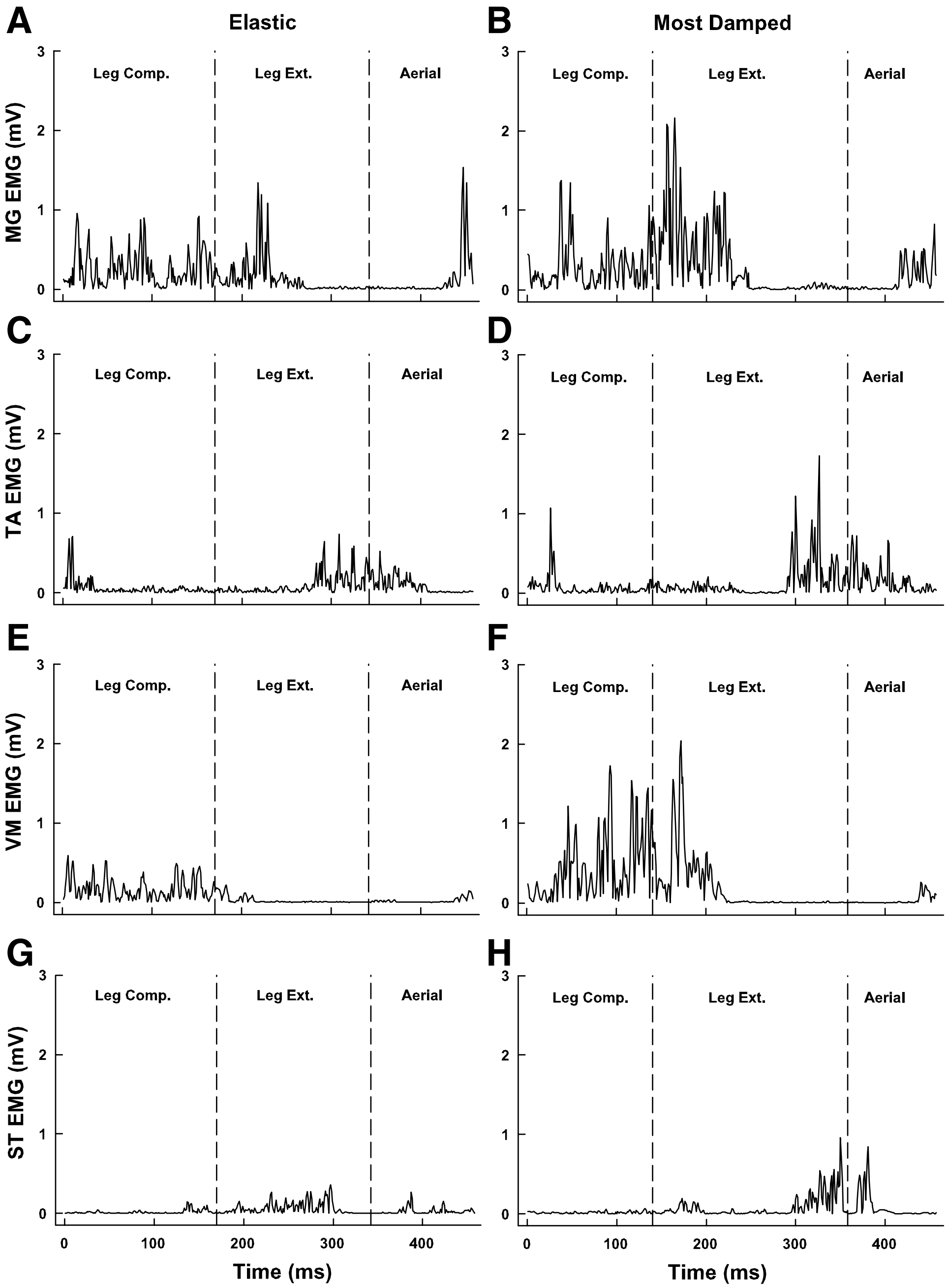


Fig. 6. Rectified electromyographic signals (EMG) vs. time for example hops on elastic surface (*A*, *C*, *E*, and *G*) and most damped surface (*B*, *D*, *F*, and *H*). Muscles shown are medial gastrocnemius (MG; *A* and *B*), tibialis anterior (TA; *C* and *D*), vastus medialis (VM; *E* and *F*), and semitendinosus (ST; *G* and *H*). Traces begin at touchdown, and dashed vertical lines indicate the times of maximum leg compression and takeoff. EMG increased markedly on the most damped surface compared with on the elastic surface.

With greater surface damping, mean EMG of the knee extensor muscles increased more in the stance phase (262–441%) than in the aerial phase (113–138%; Figs. 6 and 7). In contrast, semitendinosus EMG increased more in the aerial phase (211%) than in the stance phase (81%, Figs. 6 and 7).

DISCUSSION

Humans modulate the mechanics of all three leg joints during hopping as the leg transitions from springlike mechanics on elastic surfaces to actuator-like mechanics on damped surfaces. On damped surfaces, our finding that over one-half of the leg mechanical work appears at the ankle supports our hypothesis that the ankle replaces most of the energy lost to damped surfaces. Thus the ankle dominates both leg stiffness adjustment (10, 11) and leg work output during hopping in place. This finding that the greatest fraction of mechanical leg work appears at the ankle, however, seems to be counter to the previous hypothesis that long-fibered proximal muscles are best suited for power output (2).

Hopping on a damped surface requires that hoppers perform net positive work on the environment at a similar rate as when running up a hill (19, 24), into a headwind (6), or across sand (21). When hopping on our most damped surface, hoppers replace the energy dissipated by the surface at an average rate of 140 W (i.e., net positive work rate). This power output exceeds the net positive power required to run on sand (77–92 W; Ref. 19) and the power required to run into a strong headwind (64 W; Ref. 6). Moreover, it is similar to the power

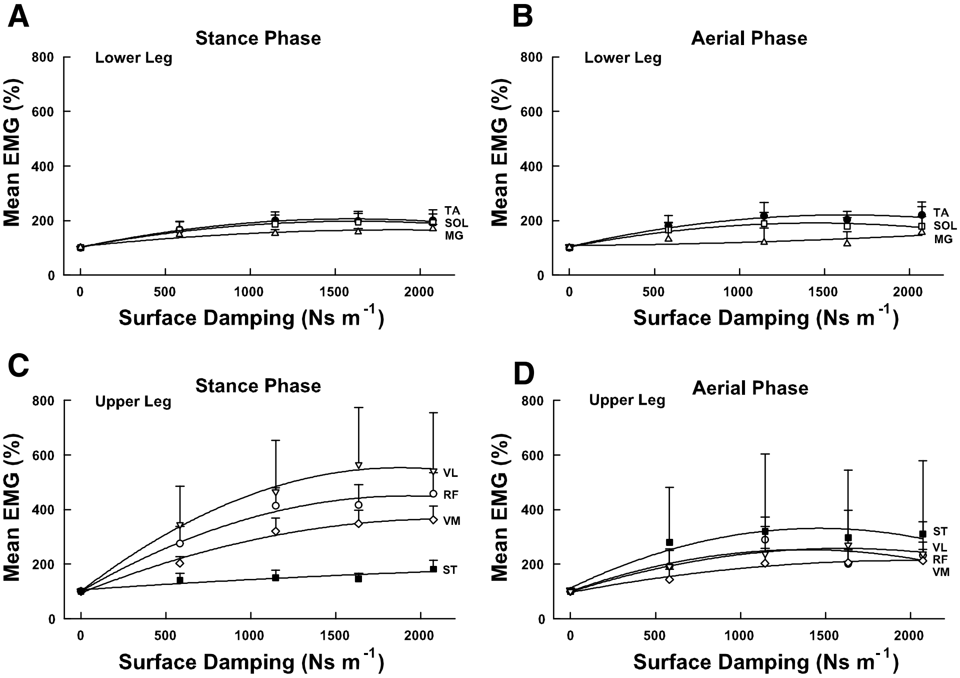


Fig. 7. Mean EMG vs. surface damping (means + SE). Stance phase (*A* and *C*) is from touchdown to takeoff, whereas aerial phase (*B* and *D*) is from takeoff to touchdown. *A* and *B*: lower leg. *C* and *D*: upper leg. Values are shown for the TA, soleus (Sol), MG, VM, vastus lateralis (VL), rectus femoris (RF), and ST. EMG values are expressed as a percentage of mean EMG of that muscle during the respective phase of the hop cycle (i.e., stance or aerial phase) on the elastic surface. All lines are least squares regressions, and only positive error bars are shown for clarity. EMG of ankle muscles increased by up to 92% with damping during both the stance and aerial phase ($P < 0.05$ for all). In contrast, EMG of knee extensors increased much more during the stance phase ($P < 0.05$ for all) than during the aerial phase ($P < 0.05$ for all). Finally, ST increased twice as much in the aerial phase ($P < 0.05$) as in the stance phase with increased damping.

required for humans to run at a moderate speed up a 4.4° incline (151 W; Ref. 19). Even when humans run aerobically up extremely steep inclines (e.g., 24°), net positive power output (218 W; Ref. 24) is not dramatically higher than when hopping on a heavily damped surface.

Little is known about individual joint mechanical work when humans must perform net positive work in situations like running across sand, into a headwind, or up a hill. Therefore, we must compare our findings to data from maximum height vertical jumping, another activity requiring net positive work output (18, 29). When hopping on the most damped surface in the present study, the ankle contributes about twice as much mechanical work as the knee or hip. In contrast, in two-legged maximum height squat jumps and countermovement jumps, the ankle contributes less than either the knee or hip alone to net leg work (18, 29). Thus, unlike our findings for hopping, these findings for maximal vertical jumping support the hypothesis that long-fibered proximal muscles are best suited for power output (2).

A potential explanation for the difference in joint mechanical work contributions between hopping and jumping is that hopping on a damped surface is not a maximal power-output activity, whereas jumping is maximal. When hopping on the most damped surface, the average positive power of all three joints combined is 512 W, about one-fourth of the power output for countermovement jumping (29). Thus it may not be possible to produce sufficient power for a maximal vertical jump while relying primarily on power appearing at the ankle. An alternative explanation is that the ankle can produce positive power more economically than other joints. The ankle, unlike the knee and hip, operates in a sufficiently flexed posture during hopping on elastic surfaces that it has the capacity to produce net joint extension, and also net power output, on damped surfaces without dramatically decreasing its touchdown angle or increasing its peak moment (Fig. 4*A*; Table 2). In contrast, to achieve net joint extension and net positive power output at the knee and hip, hoppers touch down with these joints more flexed on more heavily damped surfaces. This strategy likely incurs a substantial metabolic cost because it leads to longer moment arms of the ground reaction force about the knee and hip (Fig. 5*B*), as well as greater net muscle moments (Table 2). A final potential explanation is that much of the power appearing at the ankle in hopping is actually produced by proximal muscles (32).

Hoppers on a damped surface increase joint mechanical work output by extending the joints further during takeoff than they flex during landing and by changing the timing of peak muscle moments. Net joint extension results in longer legs at takeoff than at landing on the damped surfaces. Similarly, when humans run up an incline, they perform positive mechanical work against gravity by extending the stance leg during takeoff more than it compresses during landing (19). Net muscle fascicle shortening during stance, indicative of net joint extension, is also observed when turkeys (28) and rats (16) run up an incline and in simulations of animal accelerations (27). An alternative strategy for increasing net joint work would be to increase net muscle moments during extension. Although the ankle and hip moments do not change, hoppers do increase the average knee moment during extension by 3.5-fold between our elastic surface and most damped surface. Moreover, hoppers reach peak joint flexion earlier in the stance phase on more heavily damped surfaces. In addition to allowing more time for extension, this timing shift causes the peak muscle moment to occur during extension. Consequently, it increases the average moment during knee extension, decreases the average moment during flexion (Table 2), and thus increases net work.

Aside from performing mechanical work, there are two other potential reasons for the dramatically greater extensor and flexor muscle EMG with increased surface damping. First, greater extensor muscle EMG likely helps cause the 2.5- to 4.5-fold increase in extensor angular acceleration of the joints during the leg compression phase that leads to the earlier start of the extension phase on more heavily damped surfaces (Table 1; Fig. 5*A*). Leg extensor EMG is 69–441% greater during hopping on the most damped surface than on the elastic surface (Figs. 6 and 7) and likely causes the nearly significant 2.4-fold increase in knee net muscle moment during flexion ($P = 0.07$; see Table 2). The increase in net muscle moment at the knee may also accelerate the ankle and hip into extension through linked segment dynamics (32). In addition, the mean ground reaction force during leg compression is 18% lower on the most damped surface than on the elastic surface (Table 2). Because the ground reaction force is aligned so that it tends to accelerate all three leg joints into flexion, this reduction assists the joints in beginning to extend earlier on more heavily damped surfaces. Therefore, the combination of the greater net muscle moments and the lower ground reaction force leads to the substantially greater angular acceleration of all three joints into extension on more heavily damped surfaces (Table 1).

The second reason for increasing EMG with surface damping is that flexor muscles are active before takeoff and during the early part of the aerial phase on the damped surfaces. These flexor muscles likely act to shorten the legs while the hopper is in the air. During the aerial phase on the most damped surface, hoppers retract their legs by ~4 cm between takeoff and landing to allow net leg extension during the subsequent stance phase (see Fig. 4*D*). Two flexor muscles that may be responsible for leg retraction, the tibialis anterior and semitendinosus, have 120–210% greater EMG activity levels in the aerial phase on the most damped surface than on the elastic surface.

Despite the smaller mechanical work contribution at the knee than at the ankle, hoppers increased knee extensor muscle EMG proportionally more than ankle extensor EMG as surface damping increased. One reason for the high knee extensor EMG on the most damped surface is that the knees are 21° more flexed and the moment arm of the ground reaction force is fourfold longer at midstance than on the elastic surface. This posture facilitates net knee extension but has a trade-off of higher muscle forces and EMG for a given ground reaction force. A second explanation for the relatively large percent increase in knee extensor EMG is that it is very low during hopping on the elastic surface, and thus percent increases are magnified.

Another possible reason for the relatively large increase in knee extensor EMG on the most damped surface is that the knee extends 140% faster than on the elastic surface while ankle extension velocity changes much less. The knee extensor muscles probably shorten faster to extend the knee more rapidly and, therefore, likely generate less muscle force for a given level of EMG (17). Of course, tendon strain complicates estimates of muscle shortening velocity from joint kinematics. Positive work due to elastic energy release, however, cannot exceed negative work. In this case, positive work at the knee is threefold greater than negative work, and thus the knee extensor muscles must shorten to yield net mechanical work. A final possible explanation for the relatively large increase in knee extensor EMG is that mechanical work performed by knee extensor muscles may be transferred via the biarticular gastrocnemius muscles and appear at the ankle. Forward dynamic simulations of squat jumps reveal that 22% of ankle mechanical work is transferred by the biarticular gastrocnemius muscles from the upper leg muscles (30). This strategy would allow hoppers to rely on more proximal leg extensor muscles for power, and those muscles are thought to be better suited to produce power due to their long fibers (2).

In summary, humans modulate the mechanics of all three leg joints during hopping as the leg transitions from springlike mechanics on elastic surfaces to actuator-like mechanics on damped surfaces. During the stance phase of hopping on damped surfaces, all three leg joints extend more than they flex to contribute net mechanical work output. Net leg extension, net joint extension, and net muscle shortening are closely linked strategies used for increasing mechanical work output during hopping, incline running, and running accelerations (19, 27, 28). The ankle produces most of the work needed to replace the energy lost by the damped surfaces. Taken together with previous findings that the ankle dominates adjustments to leg stiffness, our findings show that adjusting ankle mechanics is an important neuromuscular strategy of humans for hopping on a variety of surfaces. Furthermore, the findings that the joints produce mechanical work through both net joint extension and a shift in the timing of peak flexion have implications for the design and control of artificial limbs for prostheses and robots that can adapt to the variety of terrain in the natural world.

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