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RESEARCH ARTICLE

Biomechanics and energetics of running on uneven terrain

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ABSTRACT

In the natural world, legged animals regularly run across uneven terrain with remarkable ease. To gain understanding of how running on uneven terrain affects the biomechanics and energetics of locomotion, we studied human subjects (N=12) running at 2.3 m s^{-1} on an uneven terrain treadmill, with up to a 2.5 cm height variation. We hypothesized that running on uneven terrain would show increased energy expenditure, step parameter variability and leg stiffness compared with running on smooth terrain. Subject energy expenditure increased by 5% (0.68 W kg^{-1}; P<0.05) when running on uneven terrain compared with smooth terrain. Step width and length variability also increased by 27% and 26%, respectively (P<0.05). Positive and negative ankle work decreased on uneven terrain by 22% (0.413 J kg^{-1}) and 18% (0.147 J kg^{-1}), respectively (P=0.0001 and P=0.0008). Mean muscle activity increased on uneven terrain for three muscles in the thigh (P<0.05). Leg stiffness also increased by 20% (P<0.05) during running on uneven terrain compared with smooth terrain. Calculations of gravitational potential energy fluctuations suggest that about half of the energetic increases can be explained by additional positive and negative mechanical work for up and down steps on the uneven surface. This is consistent between walking and running, as the absolute increases in energetic cost for walking and running on uneven terrain were similar: 0.68 and 0.48 W kg^{-1}, respectively. These results provide insight into how surface smoothness can affect locomotion biomechanics and energetics in the real world.

KEY WORDS: Energy expenditure, Joint work, Kinematics, Leg stiffness

INTRODUCTION

Empirical measurements have documented that running on natural surfaces such as sand, grass or irregular trails requires greater metabolic energy expenditure than running on smooth hard surfaces (Jensen et al., 1999; Lejeune et al., 1998; Pinnington and Dawson, 2001; Zamparo et al., 1992). Such natural terrain has many mechanical properties that can influence running biomechanics. For example, humans and animals need to constantly adjust for changes in surface damping, compliance and smoothness during locomotion in the real world. To identify the energetic and biomechanical changes during running caused by increased surface height variability, we studied human running on an uneven surface designed to mimic natural terrain.

Step parameter adjustments are one potential factor that could contribute to increased energy expenditure during running on uneven terrain. In particular, humans adjust step width for maintaining lateral balance during walking (Hak et al., 2012; McAndrew et al., 2010) and could utilize the same strategy to improve running stability as well. A recent study showed that assisting with lateral balance during running resulted in reduced step width variability and energy expenditure in humans (Arellano and Kram, 2012). In contrast, if uneven terrain leads to increased step width variability, it may contribute to increased energetic costs to maintain balance.

Changes in surface height variability are likely to alter muscle activation patterns and mechanical work during running. Running on sand, for example, results in greater muscle activity, greater hip and knee motion, and greater positive mechanical work compared with running on a smooth flat surface (Lejeune et al., 1998; Pinnington et al., 2005). These changes are likely contributors to the increased energy expenditure for running on sand compared with a smooth, hard surface (Pinnington et al., 2005). In addition, we have previously found that human subjects showed greater hip and knee joint flexion motions during swing when walking on uneven terrain compared with even terrain (Voloshina et al., 2013). It is reasonable to expect similar modifications in swing leg dynamics for running on a similar uneven surface. In addition to increased muscle activity, running on the uneven surface may also disrupt patterns of muscle recruitment. Effective energy storage and return during locomotion requires muscle activation to produce a concerted contraction (Hof et al., 1983), or contractions that minimize the change in length of the muscle fiber and maximize tendon and aponeurosis stretch and recoil. Because work produced from elastic energy storage and return contributes to about half of the total mechanical work performed during running (Cavagna et al., 1964), a reduction in elastic work would require increased muscle work and would be more energetically costly. As a result, these factors have the potential to contribute to running energetic costs related to surface smoothness.

Leg stiffness is also likely to change with increased surface height variability. During human reaching in the presence of expected mechanical perturbations (Burdet et al., 2001; Franklin et al., 2007), arm stiffness tends to increase compared with reaching without perturbations. The nervous system may respond to expected lower limb perturbations similarly. In addition, Grimmer et al. have shown that human runners increase leg stiffness in anticipation of a single step-up when running on an uneven track (Grimmer et al., 2008). However, runners then decrease their leg stiffness for the actual step-up, possibly to smooth out the perturbation to the center of mass trajectory. It is likely that runners would also adjust leg stiffness in response to running on uneven terrain.

In this study, we examined the energetic and biomechanical changes during running on uneven terrain when compared with running on smooth terrain. We used an uneven terrain surface that was attached to a standard exercise treadmill (Fig. 1) to collect continuous energetic and kinematic data of human runners. We hypothesized that, on uneven terrain, subjects would show greater energy expenditure and step parameter variability. Based on previous research indicating increased limb stiffness under conditions of anticipated mechanical perturbations, we also

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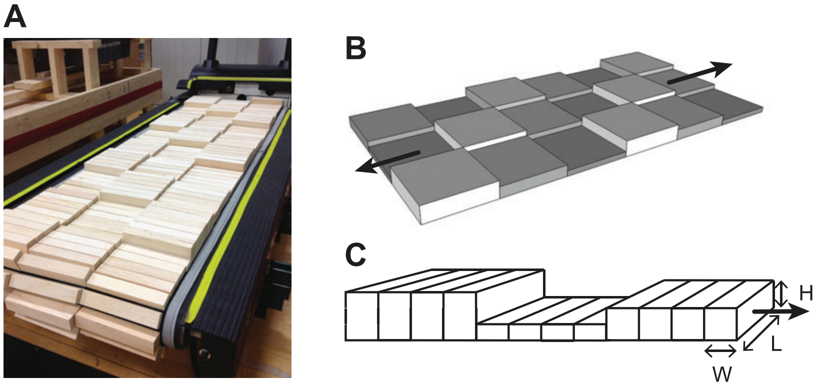

Fig. 1. Study apparatus. (A) Uneven terrain treadmill used for the running studies. (B) Schematic representation of the uneven surface, with stepping areas of three different heights (arrows indicate the treadmill's long axis). (C) Close-up of the blocks comprising the stepping areas. Dimensions: H, 1.27 cm; L, 15.2 cm; W, 2.54 cm.

expected runners to increase leg stiffness on uneven terrain compared with smooth terrain. Our overall objective was to provide insight into how the biomechanical adjustments lead to greater energy expenditure during running on uneven surfaces.

RESULTS

Running on uneven terrain resulted in increased energy expenditure compared with running on smooth terrain. Several biomechanical adjustments contributed to this increase in energetic cost. Subjects did not exhibit changes in mean step parameters between the two conditions, but there were differences in step parameter variability. Joint angle, torque and power were mostly unaffected by the terrain and only the ankle joint showed a significant decrease in joint power. In addition, we observed increased muscle activity in three proximal leg muscles (vastus medialis, rectus femoris and medial hamstring), and increased muscle mutual contraction between the vastus medialis and medial hamstring muscles. Subjects also demonstrated higher leg stiffness when running on uneven terrain compared with smooth terrain.

Metabolic energy expenditure

Running and walking on the uneven terrain resulted in significant increases in energy expenditure when compared with running and walking on the even surface (Fig. 2). During running, energetic cost increased from 9.72±0.65 to 10.2±0.94 W kg^{-1} (mean±s.d., *P*=0.008), or about 5% from even to uneven terrain. This percentage increase in running energy expenditure was much lower than the percentage increase found during walking on uneven terrain. In contrast to running, metabolic energy expenditure during walking on uneven terrain increased from 2.51±0.24 to 3.19± 0.14 W kg^{-1} (*P*=0.0004), or by ~27%. This increase in metabolic cost was consistent with the 28% energy increase found in our previous study on walking on uneven terrain (Voloshina et al., 2013). This suggests that the biomechanical adaptations during walking in this study are likely the same as we have previously described, even though walking surfaces and subject footwear differed between the two studies. Although the percentage increases in energy expenditure were different between walking and running, the absolute increases in energetic cost were similar: 0.68 and 0.48 W kg^{-1} for walking and running, respectively. The mean standing metabolic rate was 1.46±0.17 W kg^{-1}.

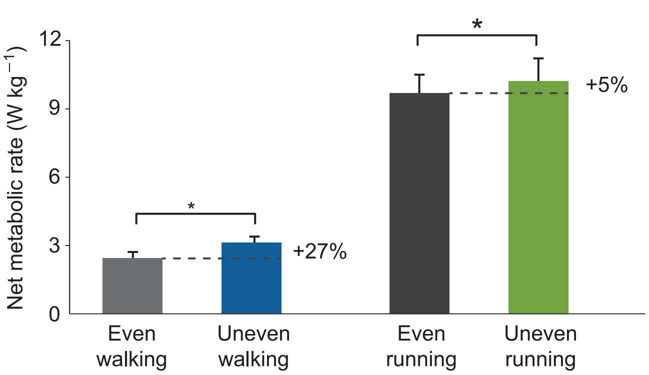

Fig. 2. Net metabolic rate for walking and running on the even and uneven surfaces. All net metabolic rates are normalized to subject mass and show the absolute changes in energetics when walking and running on uneven terrain compared with smooth terrain. Percentages indicate the increases in energetic cost caused by uneven terrain when compared with even walking or running. Asterisks signify a statistically significant difference between the even and uneven walking and running conditions (*post hoc* pair-wise comparisons, α=0.05).

Kinetics and kinematics

We saw no changes in mean step parameters (width, length, height and period), although step variability increased for all parameters during running on uneven terrain compared with even terrain (Table 1). In particular, step width, length and height variability all increased significantly by approximately 27%, 26% and 125%, respectively (*P*<0.05) on uneven terrain. In addition, step period variability on uneven terrain increased significantly by 30% (*P*<0.05).

Subjects showed few changes in joint kinematics and kinetics during running on uneven terrain compared with even terrain, with most notable changes occurring at the ankle joint. During running on uneven terrain, joint angles in the sagittal plane showed slightly higher peak flexion angles in the knee and hip during mid-stance, possibly to allow for greater leg clearance (Fig. 3). Qualitative examination of the ankle angle showed a slightly decreased range of motion on uneven terrain compared with even terrain, although subjects appeared to maintain a similar heel-strike footfall pattern on the two surfaces. This reduced range of ankle motion suggests that subjects ran with slightly flatter feet when on uneven ground. The ankle joint also showed an approximately 14% decrease in peak joint moment, around mid-stance. In contrast, the knee and hip joints showed little change. Changes in joint power were only seen around the ankle and knee, with the two joints showing decreases in power around mid-stance (by 29% and 23%, respectively), when running on uneven terrain. Ankle power also decreased by 25% prior to push-off and at ~40% of stride time. The timing of toe-off with respect to stride timing did not differ between the two running conditions.

Joint motion variability was also greater on uneven terrain compared with even terrain (Fig. 3). Surface unevenness increased ankle and knee angle variability by approximately 25%, and hip angle variability by 35% when compared with even terrain (all

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Table 1. Step parameters for running on the even and uneven surfaces

	Even		Uneven		*P*-value	
	Mean±s.d.	Variability (mean±s.d.)	Mean±s.d.	Variability (mean±s.d.)	Mean	Step variability
Step width	0.055±0.029	0.022±0.004	0.059±0.033	0.028±0.006*	0.353	<0.0001
Step length	0.881±0.051	0.035±0.009	0.884±0.044	0.044±0.011*	0.385	0.0002
Step height	–	0.004±0.001	–	0.009±0.002*	–	<0.0001
Step period (s)	0.729±0.041	0.010±0.003	0.731±0.033	0.013±0.003*	0.427	0.0014

Parameters include step period and the mean step width, length and height and their respective variabilities (all normalized to subject leg length, mean 0.944 m). Step variability is defined as the s.d. of step distances over a trial, reported as the mean (±s.d.) across subjects.
Asterisks signify a statistically significant difference between the even and uneven running conditions (*post hoc* pair-wise comparisons, α=0.05).

P<0.05). Ankle moment variability also increased by about 60%, while knee and hip moment variability more than doubled on uneven terrain (all *P*<0.05). Joint power variability increased by 50% for the ankle and ~70% for the knee and hip (all *P*<0.05).

Running on the uneven surface also affected the amount of positive and negative joint work done at the ankle (Fig. 4). Positive ankle work decreased by 0.413 J kg^{-1} (22%) while negative ankle work decreased by 0.147 J kg^{-1} (18%; *P*=0.0001 and *P*=0.0008, respectively). Positive and negative joint work for the knee and hip were not statistically different between the two running conditions.

Muscle activation

Subjects showed increases in muscle activity variability, mean muscle activity and muscle co-activation in the thigh muscles when running on uneven terrain compared with running on even ground (Fig. 5). Significant increases in mean muscle activity were only noted in three of the thigh muscles; vastus medialis (VM), rectus femoris (RF) and medial hamstring (MH) activity increased by 7%, 20% and 19%, respectively (*P*<0.05). However, the vastus lateralis (VL) and all muscles in the lower leg showed no significant differences in mean muscle activity between conditions (Fig. 6).

All but three muscles showed a significant increase in electromyographic (EMG) variability when running on the uneven terrain (Fig. 5). Only two muscles in the lower leg and three muscles in the thigh showed increases in variability (s.d. of muscle activity), with the mean increase in variability being slightly higher in the thigh muscles (mean increase of 14% and 25% in the lower leg and thigh muscles, respectively). In the lower leg, both the soleus (SO) and lateral gastrocnemius (LG) showed 14% increases in s.d. (*P*<0.05), while the tibialis anterior (TA) and medial gastrocnemius (MG) showed no significant changes. For the thigh muscles, VM, RF and MH showed 15%, 35% and 26% increases in muscle variability, respectively (*P*<0.05).

Out of the three pairs of antagonistic muscles, we observed increased muscle co-activation over the entire stride only in the MH/VM muscle pair (Table 2). However, when we broke down the stride into 1% increments, we noticed significant increases in muscle co-activation in the first 5% of the stride in the MH/VL muscle pair as well. Similarly, the MH/VM pair showed increased muscle co-activation during the first 5% of the stride but also slightly before and during toe-off. The muscle pair also demonstrated increased muscle co-activation during swing, although, because of minimal muscle activity of the two muscles during this time, these increases are likely

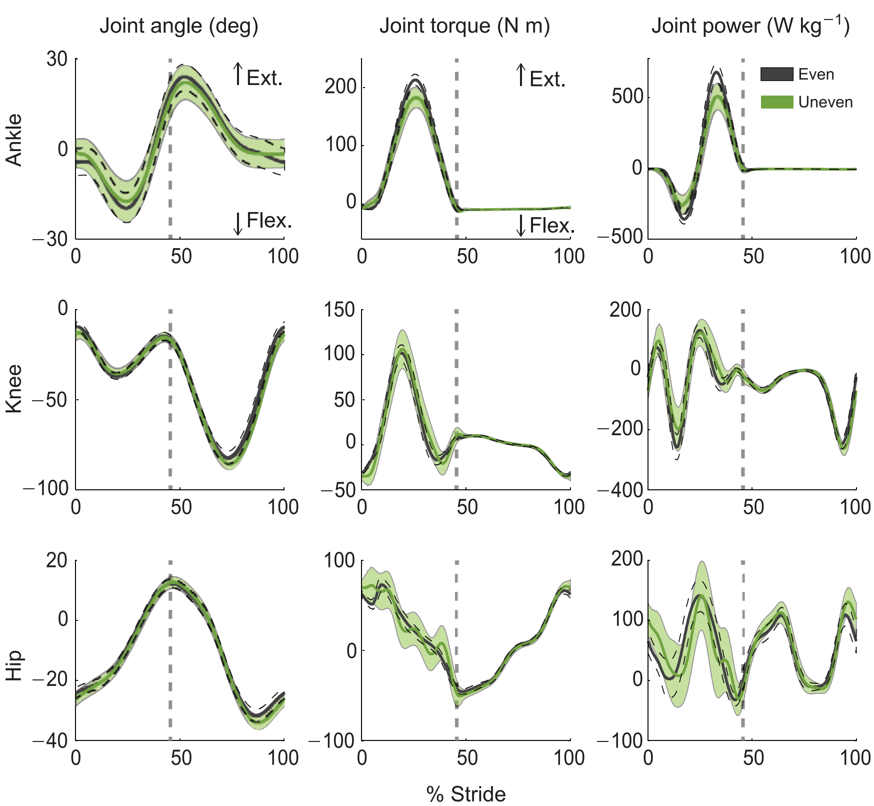

Fig. 3. Joint angle, torque and power versus stride time for running on even and uneven terrain. Plotted in solid lines are the mean trajectories for the ankle, knee and hip against percentage stride time for running during uneven and even terrain conditions. Shaded areas denote the mean s.d. envelopes across subjects for the uneven condition, dashed lines for the even condition. Strides start and end at same-side heel-strike. Dashed vertical gray line indicates toe-off. Ext., extension; Flex., flexion.

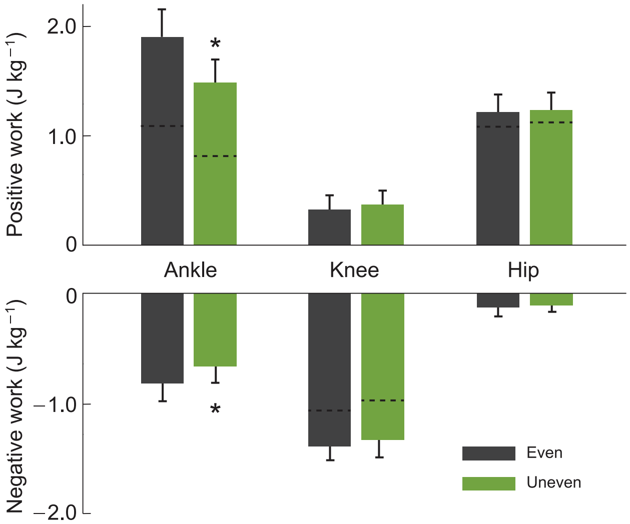

Fig. 4. Ankle, knee and hip work per stride for the two running conditions. Values are shown for positive and negative work for the three joints, with error bars denoting s.d. Dashed lines indicate net work for the specific joint and condition, and asterisks signify a statistically significant difference between the even and uneven running conditions (*post hoc* pair-wise comparisons, α=0.05).

inconsequential. The TA/SO muscle pair showed no significant increases in muscle co-activation at any point in the stride (Fig. 5).

Vertical ground reaction forces and leg stiffness

Vertical ground reaction forces, normalized to subject weight, remained largely unchanged for running on uneven terrain compared with even terrain (Fig. 7A). The maximum force, f_{max}, occurred around 40% of stance and had a peak at 2.19±0.11 (dimensionless; *P*=0.753). The peak maximum force was not statistically different for the two running conditions. However, the impact peak increased by approximately 17% (from 1.34±0.19 to 1.57±0.25, dimensionless) when running on uneven terrain compared with even terrain (*P*=0.0002). In addition, vertical ground reaction force variability more than tripled when running on uneven terrain (*P*<0.05).

Subjects ran in a slightly more crouched posture when on uneven terrain compared with running on the even surface (Fig. 7A). Subjects contacted the ground at heel-strike with a more bent leg, and hence a shorter leg length (0.992±0.022 and 0.984±0.022, dimensionless, for even and uneven terrains, respectively; *P*=0.0018), defined as the straight-line distance from the greater trochanter marker to the fifth metatarsal marker of the stance foot and normalized to mean subject leg length. Similarly, leg length before toe-off decreased significantly from 1.02±0.011 to 1.01±0.015 (dimensionless; *P*<0.0001). In addition, the minimum leg length during mid-stance was longer on uneven terrain (0.907±0.014 and 0.912±0.015, dimensionless, for even and uneven terrains, respectively; *P*=0.0041). This resulted in a 15% decrease in the maximum change in leg length, from 0.085±0.023 on even ground to 0.072±0.019 on uneven terrain (dimensionless; *P*<0.0001).

Primarily due to different leg length dynamics, subjects ran on stiffer legs when running on uneven terrain compared with running on even ground (Fig. 7B). Using the more traditional leg stiffness calculation (defined as the ratio between the maximum vertical ground reaction force and the maximum leg length displacement), we found a 20% difference in leg stiffness between the two surfaces (from 27.9±6.40 on even terrain to 33.4±7.54 on uneven terrain, dimensionless; *P*<0.0001). Similarly, the second leg stiffness calculation (defined as the linear fit to the vertical ground reaction force versus leg displacement) showed a 10% increase in leg stiffness (from 19.7±2.10 on even terrain to 21.8±2.74 on uneven terrain, dimensionless; *P*<0.0001).

DISCUSSION

In this study we quantified the changes in energetics and biomechanics between running on uneven terrain and on flat, smooth terrain. Our findings supported our hypotheses, primarily

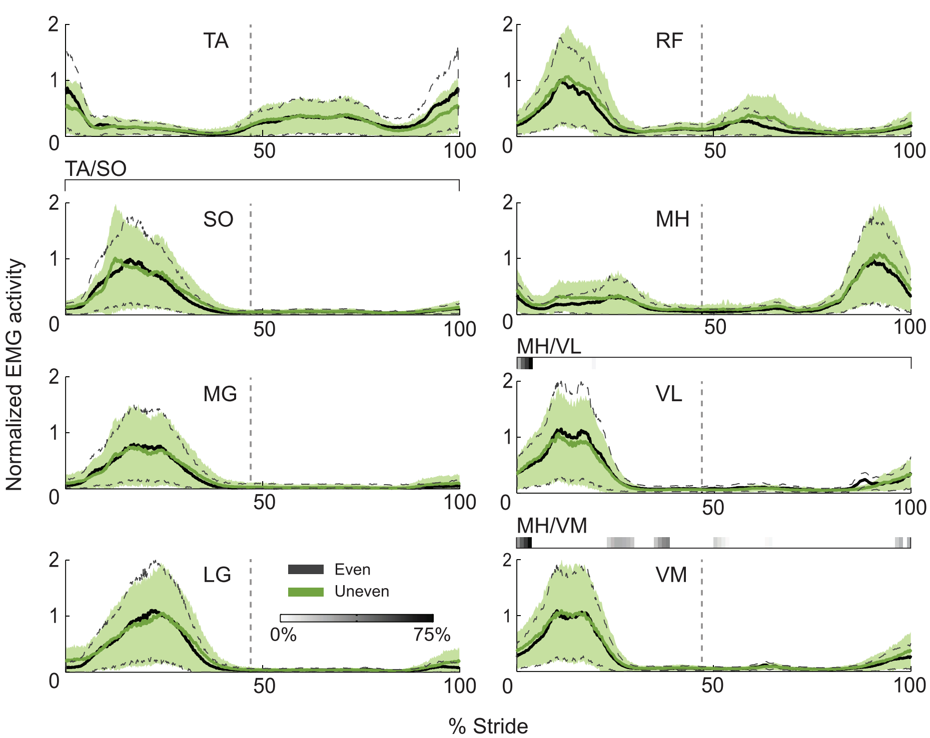

Fig. 5. Averaged electromyographic (EMG) activity versus stride time for running on even and uneven terrain. All EMG profiles were normalized to the maximum mean muscle activity over the two running conditions, for each muscle and subject. Strides start and end at same-side heel-strikes. Dashed vertical gray line indicates toe-off. Shaded areas denote the mean s.d. envelopes across subjects for the uneven condition, dashed lines for the even condition. Gray bars indicate statistically significant increases in mutual muscle contraction, with darker colors indicating larger percentage increases from the even to the uneven running condition. TA, tibialis anterior; SO, soleus; MG, medial gastrocnemius; LG, lateral gastrocnemius; RF, rectus femoris; MH, medial hamstring; VL, vastus lateralis; VM, vastus medialis.

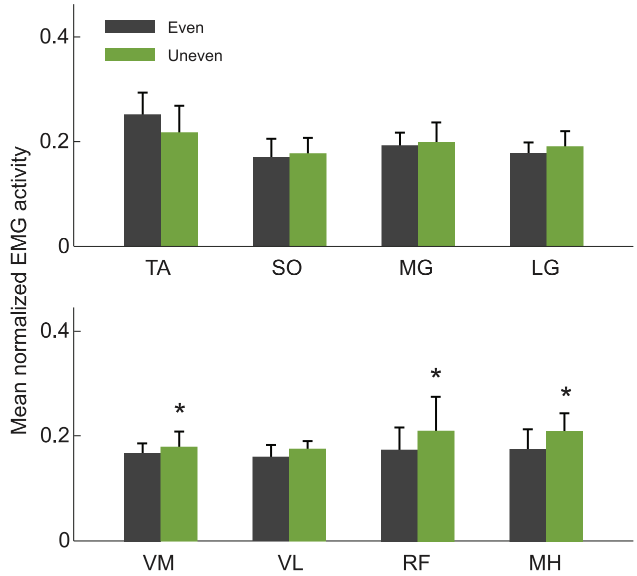

Fig. 6. Mean rectified EMG activity values. Mean subject EMG profiles were first normalized to maximum mean muscle activity over the two running conditions, for each muscle and subject, and then averaged over stride time to produce subject average EMG activity values. Subject average EMG activity was then averaged over subjects to produce mean EMG activity values. Bars indicate s.d. across subjects. Asterisks signify a statistically significant difference between the even and uneven running conditions (*post hoc* pair-wise comparisons, α=0.05).

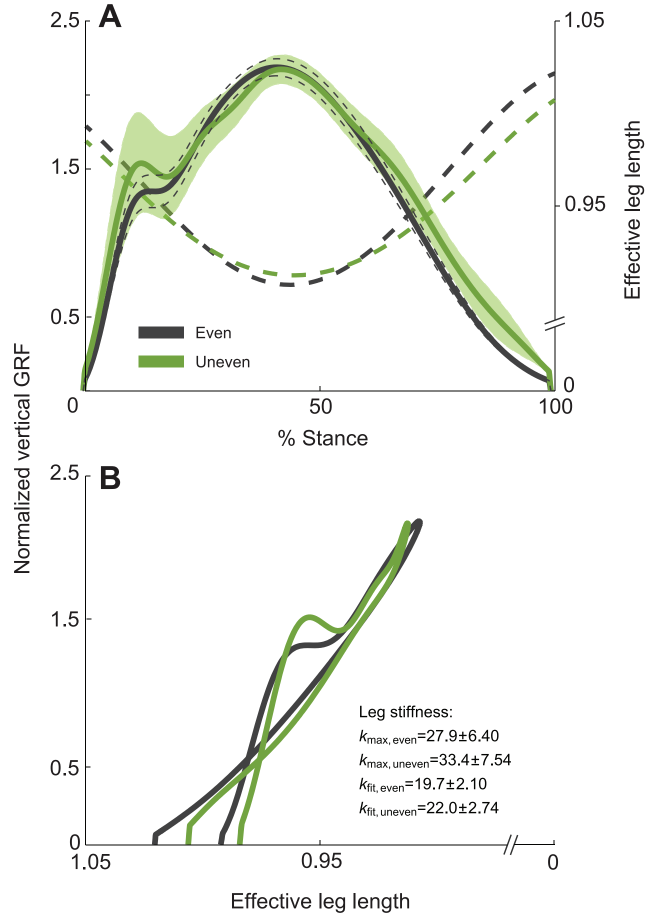

Fig. 7. Vertical ground reaction forces, effective leg length and leg stiffness calculations for the two running conditions. (A) Mean vertical ground reaction forces normalized to subject weight (solid lines), and effective leg lengths normalized to mean subject leg length (thick dashed lines), versus stance duration for running on even and uneven terrain. Shaded area denotes the mean s.d. envelope across subjects for the vertical ground reaction force on the uneven condition, thin dashed lines indicate the envelope for the even condition. (B) Normalized vertical ground reaction force plotted against the normalized effective leg length for the two running conditions. Mean leg stiffness values are presented for two leg stiffness calculation methods: k_{max} equals the maximum force divided by the maximum leg length displacement and k_{fit} is the slope of the linear fit to the leg stiffness curve. s.d. values are across subjects.

that running is more energetically costly on uneven terrain compared with even terrain. However, this increase was much smaller than the increase caused by the same surface during walking. More specifically, we found a 0.68 W kg^{-1} (27%) increase in metabolic cost during walking and a 0.48 W kg^{-1} (5%) increase during running. Although the percentage changes were quite different between the two locomotion types, it is important to note that the absolute increases were very similar. These absolute energetic increases could be related to the total mechanical energy fluctuations caused by the uneven surface. For example, running uphill and downhill for an equal distance would result in greater energy expenditure than running on level ground for the same total distance (Margaria, 1968). If we equate the uneven surface to a series of steps up and down an incline, it would be reasonable to expect an increase in energy expenditure as well. If we consider the mean step length of our runners (0.884 m) and the maximum step height change of the uneven terrain (0.025 m), our uneven terrain surface would be roughly equivalent to running up and down a 1.6% incline. In addition, we could expect this incline to result in an energy increase of ~0.35 W kg^{-1} (Margaria et al., 1963). However, the true energetic increase due to incline variations is likely much smaller. This suggests that factors other than changes in mechanical work contribute to energy expenditure on uneven terrain during running.

Table 2. Muscle mutual contraction over the entire stride

	Even (mean±s.d.)	Uneven (mean±s.d.)	*P*-value
TA/SO	105.7±36.34	109.5±32.83	0.6527
MH/VM	106.4±28.05	134.7±34.31*	0.0168
MH/VL	123.3±66.60	125.5±28.02	0.9244

Values signify the dimensionless area under the minimum of the normalized EMG curves for the two muscles of interest. Three muscle antagonist pairs are compared: tibialis anterior/soleus (TA/SO), medial hamstring/vastus medialis (MH/VM) and medial hamstring/vastus lateralis (MH/VL). s.d. are calculated across subjects. Asterisks signify a statistically significant difference between the even and uneven running conditions (*post hoc* pair-wise comparisons, α=0.05).

As expected, we saw changes in step length and width variabilities across the two surfaces. On uneven terrain, runners showed 33% and 26% increases in step width and length variability, respectively (P<0.05). This is consistent with past research, which has shown that challenges to locomotor stability tend to produce more step variability during walking (Thies et al., 2005; Voloshina et al., 2013). Greater step variability during walking also seems related to active stabilizing adjustments for maintaining lateral balance (Bauby and Kuo, 2000; Donelan et al., 2001). In contrast, during running, humans tend to prefer narrow step widths close to the midline of the body (Cavanagh, 1987). This is because narrow step widths result in reduced lateral moments about the center of mass and tend to reduce energetic cost compared with larger step widths. Based on previous research (Arellano and Kram, 2011), reducing step width and step width variability during running leads

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to a reduction in energy expenditure. However, our subjects only showed a 27% increase in step width variability and no change in the mean step width. These changes are relatively small and nowhere near the magnitude necessary to produce a 5% increase in energy expenditure (Arellano and Kram, 2011). This suggests that the energetic increase caused by changes in step parameters was negligible.

A significant finding of our study is that the absolute changes in energetic cost are independent of locomotor gait. Although percentage increases in energetic cost were significantly different (27% and 5% for walking and running, respectively) the absolute changes were relatively close (0.68 and 0.48 W kg^{-1} for walking and running, respectively). The similar absolute changes for walking and running suggest that the dominant factor responsible for increases in metabolic cost during locomotion on uneven surfaces may be related to surface height variability and the corresponding vertical motion of the center of mass. It would be interesting to examine a range of surface height variabilities and their effects on walking and running energetics. This could provide insight into whether walking and running have similar biomechanical mechanisms responsible for energetic cost differences.

Another important finding of this study is that the lower limb joints that compensate for locomotion on uneven terrain are very different between walking and running. During walking, ankle joint dynamics remain invariable while the knee and hip joints compensate with greater positive work production (Voloshina et al., 2013). In contrast, running on uneven terrain only significantly affects work done at the ankle joint. The most likely explanation for this contrast in joint kinetic adaptations is the reliance on different biomechanical mechanisms for the two gaits. Running can be compared to a spring-mass system, with the lower limb functioning as if it were a single compression spring (Farley and Ferris, 1998; McMahon and Cheng, 1990). In contrast, walking has inverted pendulum dynamics with differentiation by joint that is unlike running (Alexander, 1992; Farley and Ferris, 1998; Kuo, 2001; McGeer, 1990). These differences in fundamental dynamics suggest that each gait has different benefits and drawbacks to joint-specific adaptations on uneven terrain.

The decrease in ankle work seen during running on uneven terrain compared with even ground is likely due to the high load sensitivity of the ankle joint. Muscles at the distal joints rely on high-gain proprioceptive feedback and are often the first to encounter perturbations due to uneven terrain (Daley and Biewener, 2006). In contrast, the more proximal knee and hip joints are largely feed-forward controlled. This control strategy improves running stability by maintaining consistent limb cycling but has a more pronounced effect on the distal joints (Daley et al., 2007). In addition, we saw a small reduction in the ankle range of motion, which could have also led to a reduction in joint work. This reduction in ankle motion likely stabilized the joint in response to the unpredictable running surface. However, it could also have led to a reduction in energy storage and return in the Achilles tendon, leading to reduced work at the ankle joint. Recently, a number of research groups have demonstrated that ultrasound imaging can track both muscle fiber and tendon displacements during human running. Future experiments using ultrasound imagining could provide greater insight into the muscle–tendon mechanics on uneven terrain.

In conjunction with our hypotheses, subjects exhibited greater leg stiffness when running on uneven terrain compared with even terrain. There were changes in muscle co-activation but they were small in magnitude and were likely not the major drivers of leg stiffness adjustments across the surfaces. Vertical ground reaction force profiles were also largely unchanged, with only the impact peak magnitude increasing by 17%. This increase suggests that subjects landed with a higher contact force, likely due to flatter feet at ground contact. However, the main cause of increased leg stiffness is the change in lower limb posture. When running on uneven terrain, subjects contacted the ground at heel-strike with a shorter leg length, and had a longer leg length during mid-stance and a shorter leg length at toe-off. This change in posture, and in turn in leg stiffness, can be the result of several factors. Previous research on upper limb movements has shown that humans tend to stiffen their joints when presented with unfamiliar tasks, likely in anticipation of potential perturbations. Similarly, Blum and colleagues (Blum et al., 2011) have shown that a more crouched leg posture during avian running may be an adaptation mechanism, as it allows for lengthening and shortening of the limb. As a result, the more crouched running posture and overall larger leg stiffness on uneven terrain is likely an adaptation response to an unfamiliar environment. In future studies, it may be interesting to look into the changes in leg stiffness throughout training periods, where subjects are allowed to become familiar with the surface over longer periods of time.

This study had several limitations related to kinetic measurements. The accuracy of the force measurements during uneven terrain running was one such limitation. As described previously, the uneven terrain treadmill was placed atop two supports, each of which was placed on top of a force platform. The forces recorded from each platform were then added together to obtain the total ground reaction forces. The treadmill was not rigidly attached to the supports and there was some slack in the belt to which the uneven surface was attached. As a result, the force data were noisier than data collected with our in-ground, instrumented treadmill. To account for the additional noise, we low-pass filtered the ground reaction force data using a cut-off frequency of 6 Hz, rather than a more traditional cut-off frequency of 25 Hz. We used the same filtering techniques for both surface conditions. To test the validity of comparing running for these different experimental setups, we compared a representative subject running on the in-ground instrumented treadmill with the same subject running on the regular treadmill on supports with a bare belt. Average peak vertical and anterior–posterior ground reaction forces, as well as average peak ankle moments, were within 4% of each other and highly correlated (i.e. R>0.997). Mean center of pressure trajectories on the regular treadmill were also within 6% of mean center of pressure trajectories recorded on the instrumented treadmill. For the uneven surface, the terrain attached to the supported treadmill likely introduced additional variability to calculations of the center of pressure, because foot orientation during ground contact is highly variable on uneven terrain. However, this error would have been multidirectional and likely did not affect the mean results of the inverse dynamics calculations. Instead, the main effect on the inverse dynamics calculations would have been increased variability in parameters throughout the stance phase. Examination of s.d. in the ankle profiles in Fig. 3 shows slightly greater variability in the ankle moment calculations but increased variability is also present in the ankle angle data. The ankle angle data are independent of center of pressure calculations, so similar changes in variability seen in other parameters suggest that the effect of the center of pressure variability from the uneven terrain surface was not large.

Another limitation of the study was that subjects ran at only one prescribed speed. They could not negotiate the terrain by altering their speed as is possible when running on natural surfaces. We chose a slow running speed to maximize our subjects' comfort level and did not test a range of speeds. Running at faster speeds could have resulted in more pronounced biomechanical differences. We also tested only one pattern of stepping areas and one range of surface heights for the uneven terrain surface. However, as subjects did not appear to get accustomed to the surface, we do not believe the inherent pattern of the uneven terrain affected gait dynamics. Larger surface height variability would have likely caused amplified biomechanical and energetic effects.

Additional limitations relate to subject training and the inherent difference between treadmill and overground running. For one, subjects were also not allowed multiple days to train and adjust to the terrain. It may be helpful in future studies to determine whether there are long-term adaptation effects. In addition, subjects ran with a limited visibility of the terrain because of the length of the treadmill. All subjects were comfortable running on the treadmill and did not appear to be affected by limited visibility. However, it is possible that subjects may negotiate the terrain differently if more visibility were allowed. For overground locomotion, runners typically have extended visual feedback on the terrain and may choose different paths and foot placements in response to terrain properties.

In summary, we found that changes in mechanical work can explain approximately half of the energetic cost increase when running on uneven terrain surfaces compared with flat, smooth surfaces. The other half of the energetic cost increase may be related to less efficient energy storage and return in elastic tendons and ligaments. Future studies using ultrasound imaging could provide greater insight into muscle fiber and tendon dynamics on various terrains. We did find that human runners did not vary mechanical work done at their knee and hip joints when running on uneven terrain compared with smooth terrain. Instead, subjects reduced limb mechanical work done at the ankle joint when running on the uneven surface. Using a similar control approach for legged robots with biomimetic limb architectures might have benefits in increasing the relative stability of running as it alters the limb biomechanics closest to the foot–ground interface (Daley et al., 2007).

MATERIALS AND METHODS

We modified a regular exercise treadmill by attaching an additional belt with wooden blocks of varying heights to the original treadmill surface. The blocks simulated an uneven surface on which subjects could run continuously while we collected biomechanical and metabolic data. Subjects also ran on a separate, smooth treadmill surface, resulting in two testing conditions termed ‘uneven’ and ‘even’. For both surfaces, the running speed was maintained at 2.3 m s^{-1}, while we collected kinematic, kinetic, metabolic and EMG data.

Subjects

Twelve young, healthy subjects participated in the study (seven males, five females; mean±s.d.: age 24.3±4.0 years, mass 68.6±7.1 kg and height 175.5± 7.1 cm). Subjects ran on the even and uneven surfaces during the same data collection. For running on both surfaces, we collected oxygen consumption (N=11), step parameter (N=12), EMG (N=10) and joint kinematics and kinetics data (N=11). Because of technical issues, some data were not collected for particular subjects, resulting in a value of N less than 12 in some data subsets.

Prior to the experiment, all subjects provided written informed consent. Experimental procedures were approved by the University of Michigan Health Sciences Institutional Review Board.

Running surfaces and trial procedures

We created an uneven surface treadmill belt (Fig. 1) that we attached to the regular treadmill belt of a modified exercise treadmill (JAS Fitness Systems, Trackmaster TMX22, Dallas, TX, USA). To create the uneven surface belt, we sewed one side of the hook-and-loop fabric on to thick, non-stretch fabric. The other side of the hook-and-loop fabric was glued on to wooden blocks with a width of 2.55 cm and length of 15.2 cm, and of three varying heights (1.27, 2.54 and 3.81 cm). Then, we attached the blocks to the belt, oriented lengthwise across the belt. As a result, the blocks could curve around the treadmill rollers, because of their relatively short width. The blocks comprised 15.2×15.2 cm stepping areas (after Voloshina et al., 2013), in a pattern that was difficult for subjects to adopt. We then placed the uneven surface belt on top of the regular treadmill belt and connected the ends of the second belt using zip-ties to form one continuous surface. Subjects also ran on a separate, custom-built in-ground instrumented treadmill (Collins et al., 2009). The even surface served as the control condition and allowed us to determine the biomechanical effects of the uneven surface on gait biomechanics and energetics.

For both surfaces, subjects ran at a speed of 2.3 m s^{-1} and with the trial order randomized for every participant. Subjects participated in just one trial for each condition, with each trial lasting 10 min and with a minimum of 5 min rest allowed between trials. On both surfaces, subjects were instructed to run normally and not look down at their feet unless they felt it was necessary. Generally, subjects chose not to look at their feet during running. After the running trials were completed, subjects walked at 1.0 m s^{-1} for an additional 10 min on each surface, while we collected metabolic data to use as a comparison with our previous study on walking on uneven terrain (Voloshina et al., 2013). Subjects wore running shoes of their choice for the experiments.

Metabolic rate

We measured the rate of oxygen consumption ($\dot{V}_{O_2}$) for all running trials using an open-circuit respirometry system (CareFusion Oxycon Mobile, Hoechberg, Germany). We recorded respirometry data for all 10 min of the running and walking trials and also for 7 min during quiet standing prior to each data collection. We allowed subjects the first 7.5 min of the trial to reach steady-state energy expenditure and only used the last 2.5 min of data to calculate the metabolic energy expenditure rate of each subject. To find the metabolic rate, $\dot{E}_{met}$ (W), we used standard empirical equations as described elsewhere (Brockway, 1987; Weir, 1949). The net metabolic rate was found by subtracting the standing metabolic power from the metabolic power of all running conditions. All net metabolic power data were normalized by subject body mass (kg).

Kinetics and kinematics

For both even and uneven conditions, we recorded the positions of 31 reflective markers using a 10-camera motion capture system (frame rate: 100 Hz; Vicon, Oxford, UK). We placed markers on the pelvis and lower limbs as described previously (Voloshina et al., 2013) and taped them on to the skin or spandex shorts worn by the subjects. Although trials lasted for 10 min, the first 7.5 min allowed subjects to reach steady-state dynamics and we only used the last 2.5 min of data to calculate step parameters such as step width, length and height. For each subject and trial, the 2.5 min of data analyzed consisted of a minimum of 250 steps and up to 400 steps. To reduce motion artifact, we low-pass filtered all marker data at 6 Hz (fourth-order Butterworth filter, zero-lag). We defined step width, length and height as the distance between the lateral, fore–aft and vertical distances between the calcaneous markers on the two feet at their respective heel-strike instances. Step height measurements were used only to determine changes in step height variability caused by the uneven surface. We calculated the effective leg angle as the angle relative to horizontal made by the straight-line distance from the greater trochanter marker to the calcaneous marker of the stance foot. The effective leg angle and the position of the calcaneous markers acted as a means to determine the time of heel-strike. This method of determining heel contact agreed well with the onset of the vertical ground reaction force. In addition, we normalized all measurements to subject leg length measured prior to each data collection and defined as the mean distance between the greater trochanter and calcaneous markers of both legs.

We recorded ground reaction forces using a custom-built in-ground instrumented treadmill (Collins et al., 2009) for the even condition and two in-ground force platforms for the uneven condition. For the uneven condition, we placed the treadmill on top of two supports, each of which rested solely on an in-ground force platform (sample rate: 1000 Hz; AMTI, Watertown, MA, USA). To obtain total ground reaction forces, we added the recorded forces from each of the force plates. For the even condition, subjects ran on one belt of the split-belt instrumented treadmill and we recorded only one set of forces (sample rate: 1000 Hz). Force platforms were re-zeroed prior to each trial. Force data used to determine the time of heel contact and to calculate the average vertical ground reaction forces for each subject were low-pass filtered at 25 Hz (fourth-order Butterworth filter, zero lag). However, forces synced to kinematic data and used for inverse dynamics analysis were low-pass filtered at 6 Hz (fourth-order Butterworth filter, zero lag) because of the high noise sensitivity of the inverse dynamics calculations. We used Visual-3D (C-Motion, Germantown, MD, USA) to conduct inverse dynamics analysis and to determine joint angles, moments and powers in the sagittal plane for the stance limb. For both running conditions, we determined any position offset of the force vector relative to the running surface and corrected for its location in Visual-3D. For the even condition, this correction was minimal. However, for the uneven condition, the ground reaction force was measured across two force plates located substantially below the surface of the treadmill. To compensate for this, we transformed the measured forces and torques at the force platforms into a common reference frame with an origin at the height of the treadmill surface, and added them together. This introduced a small error into the inverse dynamics calculations, as the actual ground reaction force was applied on the terrain, which was up to 2.54 cm higher than the surface of the treadmill. We estimate the center of pressure error introduced by this simplification to be less than 1.5 cm based on projecting a force from the highest point on the terrain to the surface of the treadmill. Mean subject forces were normalized to subject weight and then averaged over subjects.

Electromyography

For all trials, we recorded and processed EMG signals as previously described (Voloshina et al., 2013). Bipolar surface electrodes (sample rate: 1000 Hz; Biometrics, Ladysmith, VA, USA) were placed over the belly of four lower leg and four thigh muscles. In particular, we recorded EMG data from the tibialis anterior (TA), soleus (SO), medial gastrocnemius (MG), lateral gastrocnemius (LG), rectus femoris (RF), vastus medialis (VM), vastus lateralis (VL) and the semitendinosus of the medial hamstring (MH) muscles of the right leg only. The surface electrodes had a diameter of 1.0 cm, an inter-electrode distance of 2.0 cm, and an EMG amplifier bandwidth of 20–460 Hz. Only the last 2.5 min of data were used for analysis. EMG data were first high-pass filtered at 20 Hz (fourth-order Butterworth filter, zero lag) and then full-wave rectified. For each subject, we then averaged the data over steps to create EMG means for each muscle and normalized these means to the maximum mean value for the two running conditions to minimize inter-subject variability (Yang and Winter, 1984). These signals were then averaged over subjects to create representative EMG profiles. We also found the s.d. of the EMG signal at each time point, for each subject. These s.d. were also averaged over subjects, to create mean s.d. envelopes for each running condition. Although variability in muscle activity cannot directly be related to changes in energy expenditure, it can demonstrate the amount of perturbation experienced due to uneven terrain. In addition, we quantified changes in muscle activation by averaging, over the stride time, the normalized subject EMG profiles for each subject and condition. These subject average values were then averaged over subjects to produce one mean value, for each muscle and condition, indicative of muscle activity. We also used the mean subject EMG profiles to calculate muscle mutual contraction (MC), or 'wasted' contraction as defined by Thoroughman and Shadmehr (1999), for three pairs of antagonistic muscles (SO/TA, MH/VM and MH/VL):

$$\mathrm{MC} = \int \min(f_1, f_2)\ \mathrm{d}t, \tag{1}$$

such that f_1 and f_2 are the mean EMG profiles of the two antagonistic muscles and $\min(f_1, f_2)$ is the minimum of the two profiles at each time point (Voloshina et al., 2013). In other words, when mean EMG profiles from two muscles do not overlap, we can expect zero mutual contraction, whereas any overlap would produce a non-zero, shared activity level. We computed the integrals over the entire stride and in 1% increments, to determine where in the stride cycle mutual contraction occurred. The purpose of calculating mutual contraction was not to determine the amount of co-activation relative to what each muscle pair could have done during running, but to test for differences in co-activation strategies between the two surfaces.

Leg stiffness

In order to compare the sensitivity of our results, we calculated leg stiffness values using two methods. First, we reduced subject dynamics to that of a spring-mass model (McMahon and Cheng, 1990) and defined leg stiffness to be the ratio between the vertical ground reaction force and the change in effective leg length:

$$k_{\max} = \frac{F_{\max}}{\Delta L_{\max}}, \tag{2}$$

where the effective leg length was the straight-line distance from the greater trochanter marker to the fifth metatarsal marker of the stance foot, normalized to subject leg length. We defined ΔL as the difference in leg length at heel-strike and any other point during stance, such that maximum leg length deflection, $\Delta L_{\max}$, occurred near mid-stance when leg length was shortest. In addition, we defined $F_{\max}$ as the maximum vertical ground reaction force after the impact force. We then calculated leg stiffness, $k_{\max}$, for each stride as the ratio between the peak vertical ground reaction force and the maximum leg length deflection (Günther and Blickhan, 2002).

We used an alternative method for calculating leg stiffness as a means to ensure that methodology did not alter the conclusions of the study. We computed the second leg stiffness, k_{fit}, by finding a linear fit to the curve produced by plotting effective leg length against the vertical ground reaction force over a stride. The slope of this linear fit defined the approximate leg stiffness (Günther and Blickhan, 2002). For both calculations, we found leg stiffness at each step for every subject and then averaged the strides to find subject means for both running conditions. The mean inter-subject leg stiffness for each running surface was the average leg stiffness across subjects.

Data and statistical analyses

We defined variability for step parameters, joint parameters (consisting of joint angles, torques and powers) and EMG data as the average s.d. of each parameter across subjects, per running trial. For example, for step parameter data, variability was calculated by averaging the s.d. of consecutive step distances or periods over time for each subject, across subjects. Similarly, joint parameter and EMG variability were found by averaging the s.d. of the parameter at each time point, per condition, across subjects. We then reported the mean variability (and the s.d. of the variability over subjects) for each condition. We used repeated-measures ANOVA to assess differences between conditions. The significance level, α, was set at 0.05, and *post hoc* Holm–Sidak multiple comparison tests were conducted where appropriate.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
A.S.V. and D.P.F. developed the concepts and design of the experiments, interpreted the results and prepared and revised the article. A.S.V. executed the experiments and performed data analysis.

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