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RESEARCH ARTICLE

# Lower limb biomechanical analysis during an unanticipated step on a bump reveals specific adaptations of walking on uneven terrains

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## ABSTRACT

Although it is clear that walking over different irregular terrain is associated with altered biomechanics, there is little understanding of how we quickly adapt to unexpected variations in terrain. This study aims to investigate which adaptive strategies humans adopt when performing an unanticipated step on an irregular surface, specifically a small bump. Nine healthy male participants walked at their preferred walking speed along a straight walkway during five conditions: four involving unanticipated bumps of two different heights, and one level walking condition. Muscle activation of eight lower limb muscles and three-dimensional gait analysis were evaluated during these testing conditions. Two distinct adaptive strategies were found, which involved no significant change in total lower limb mechanical work or walking speed. An ankle-based strategy was adopted when stepping on a bump with the forefoot, whereas a hip-based strategy was preferred when stepping with the rearfoot. These strategies were driven by a higher activation of the plantarflexor muscles (6–51%), which generated a higher ankle joint moment during the forefoot conditions and by a higher activation of the quadriceps muscles (36–93%), which produced a higher knee joint moment and hip joint power during the rearfoot conditions. These findings provide insights into how humans quickly react to unexpected events and could be used to inform the design of adaptive controllers for wearable robots intended for use in unstructured environments that can provide optimal assistance to the different lower limb joints.

**KEY WORDS: Electromyography, Preferred walking speed, Unanticipated bump, Irregular surface**

## INTRODUCTION

Humans walk over different types of terrains on a daily basis. These might consist of composite surfaces such as grass, sand, ballast or asphalt, but can also include irregularities such as potholes, bumps or cracks. While it is clear that walking on uneven surfaces alters the biomechanics of walking, there is relatively little understanding of how humans adapt to isolated irregularities in walking surface. Previous studies investigating uneven terrains by means of continuous walking analysis reported slower walking speeds (Voloshina et al., 2013; Wade et al., 2010; Gates et al., 2012; Menant et al., 2009) and an associated average decrease in step or stride length (Voloshina et al., 2013; Wade et al., 2010; Menant et al., 2009), compared with walking on a flat surface.

To gain insight into how humans may adapt their gait when walking on uneven terrain, these select studies have investigated changes in kinematics, kinetics, muscle activity and energy cost. Typically, researchers have simulated an uneven surface in a biomechanics laboratory on a modified overground walkway (Gates et al., 2012; Wade et al., 2010; Marigold and Patla, 2008; Grimmer et al., 2008; Thies et al., 2005) or on a treadmill with attached wooden blocks and foam (Voloshina et al., 2013), and collected measurements over a number of consecutive strides. For both the overground and treadmill studies, foot-falls varied on a step-by-step basis due to the random nature of the surface variations. Findings from these studies indicated that, on average, humans exhibit increased knee and hip flexion during swing, perhaps linked with greater toe clearance requirements (Voloshina et al., 2013; Gates et al., 2012). These kinematic changes were also associated with a 28% and 62% increase in positive knee and hip work, respectively, and a 26% increase in negative knee work (Voloshina et al., 2013). A similar increase in muscle activation for both the thigh and the calf muscles, together with higher co-contraction to stabilize the joints, along with differing changes in joint moments at the knee and hip, was also reported (Voloshina et al., 2013). Most likely, these alterations of the lower limb function also impact the energetics of locomotion, because walking on different uneven terrains increases the metabolic cost of locomotion (Pandolf et al., 1976; Lejeune et al., 1998; Davies and McKinnon, 2006; Voloshina et al., 2013; Soule and Goldman, 1972; Strydom et al., 1966).

While these prior studies highlighted differences between walking on flat and uneven terrain, a consistent finding was the larger variability displayed by the joints and muscles across the parameters investigated (Voloshina et al., 2013; Gates et al., 2012; Thies et al., 2005). This suggests that, on a step-by-step basis, different lower limb mechanical changes take place depending on the specific irregularities of the walking surfaces, thus penalizing consistency in joint moment and power traces. For example, if landing on an irregular surface with different parts of the foot elicits distinct negotiation strategies, in turn, it leads to an increased variability that has been reported by previous studies, when taking the average over multiple steps. However, to the best of our knowledge, only one study to date has quantified adaptations that take place at each joint and at different muscles in response to a well-defined irregularity, specifically when transitioning from a flat surface to an elevated surface by stepping on a wedge (Earhart and Bastian, 2000). In that study, the authors reported non-linear changes in timing of peak joint angles and muscle activity,

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suggesting that humans use two different strategies to traverse the wedges due to the different biomechanical constraints imposed by each wedge angle. Specifically, when traversing a 10 deg wedge, the peak hip flexion was reached at mid-swing and the peak ankle dorsiflexion was reached during late stance, whereas traversing a 20 deg (or 30 deg) wedge led to peak hip flexion being delayed by 12% of the gait cycle and peak ankle dorsiflexion 12% earlier. A similar behavior was reported also in the onset of rectus femoris, gluteus maximus and vastus lateralis, with an earlier activation when traversing a 10 deg wedge and a later activation when traversing a 20 deg wedge (or steeper). Similar to that study, we were interested in investigating if a specific lower limb strategy was adopted by the control system as a consequence of the biomechanical constraints imposed by a different type of uneven surface.

Investigating these mechanisms could be helpful not only for increasing the understanding of specific uneven terrain negotiation strategies of the musculoskeletal system, but also to guide the design and control of lower limb wearable robotic devices that can effectively mimic or assist human walking over variable terrain. Recently developed assistive devices have shown the importance to implement adaptive control systems that assist different lower limb joints with specific timings and magnitude (Ding et al., 2016; Lee et al., 2016; Zhang et al., 2016). Although representing a remarkable advancement in the field, these investigations have been mainly conducted in a laboratory-based environment on flat surfaces.

Therefore, the aim of the present study was to investigate how the control system regulates specific kinematic and kinetic parameters in response to biomechanical constraints imposed by an irregular surface, specifically a small bump. We specifically tested the hypothesis that the ankle push-off work would be higher in forefoot conditions and lower in rearfoot conditions. We focused our analysis on the investigation of two different classes of foot contact with the bump (forefoot and rearfoot) in combination with bumps of two different heights, and we compared them with level walking. To minimize the potential for participants to develop anticipatory motor control strategies when approaching the irregularities, as observed by Menz et al. (2003), we decided to obstruct participants' view of the exact bump location before stepping on it. This choice was taken because vision has been reported to play an important role in regulating negotiation strategies (Patla, 1997) and because it reproduced more accurately the conditions of an unanticipated step on an irregular surface, a frequent event in everyday walking.

We specifically hypothesized that the biomechanical constraint would impose an increased dorsiflexion angle in the forefoot landing with respect to the rearfoot landing, thus necessitating more positive work production at the ankle during push-off. Conversely, we hypothesized that when stepping on a bump with the rearfoot, the different biomechanical constraint imposed by an already plantarflexed ankle before push-off would reduce the amount of mechanical work produced at the ankle in favor of other joints.

## MATERIALS AND METHODS

### Participants

Nine healthy male participants (age 29.1±4.8 years; mass 76.8±10.2 kg; height 176.3±4.7 cm; mean±s.d.) were recruited for this study. All participants were free from musculoskeletal injury and other musculoskeletal diseases and provided written informed consent prior to participating in the study. The participants whose images appear in this manuscript have provided written consent for the publication of their images according to the policies of Journal of Experimental Biology. The study was approved by the Harvard Medical School Committee on Human Studies (MA, USA).

### Testing protocol

Participants walked at their preferred walking speed along a straight walkway (~10 m) covered with rubber mats (Ultimate RB, McMinnville, OR, USA) during five randomized conditions: four involving unanticipated bumps of two different heights (High 4.76 cm and Low 3.18 cm, Medium Rubber Ducts, Cable Organizer, Ft Lauderdale, FL, USA), and one level walking condition used as a baseline comparison (FLAT). The static friction coefficient between the rubber mat and the boot outsole was $\mu_s$~1.2, and the compressive Young's modulus of the bumps was 20.1 MPa. The high friction coefficient and elastic modulus ensured that there were no slip and no deformation on the bump itself when stepping on it.

In the four conditions with bumps, participants stepped on small and large bumps with their right forefoot (High-FF and Low-FF) or with their right rearfoot (High-RF and Low-RF). The bumps were placed on a force platform (OR-6, AMTI, Watertown, MA, USA; 1000 Hz) embedded into the ground to measure ground reaction forces and calculate inverse dynamics. An investigator positioned near the bump judged if the participant stepped on the bump with the desired part of the foot. If the participant missed the bump, the trial was discarded and the participant's starting position was moved accordingly for the next trial. Participants were instructed to look straight ahead. They also wore a pair of specialized glasses similar to those used in Rhea and Rietdyk (2011) to obstruct their view of the full walkway and prevent them from anticipating the exact bump location (Fig. 1).

### Joint kinematics and kinetics

Three-dimensional (3D) gait analysis was performed during the testing protocol. The marker set used for 3D motion capture (VICON, Oxford Metrics, Yarnton, UK; 120 Hz) was composed of 41 markers placed on selected anatomical bony landmarks. Single markers were placed on both legs on calcanei, toes, heads of the first and fifth metatarsals, medial and lateral malleoli, medial and lateral epicondyles of the femurs, greater trochanters, posterior superior iliac spines, anterior superior iliac spines, iliac crests, and on the sternum. Clusters of four markers were attached to the thighs and shanks of both legs.

All markers and force trajectories were filtered using a zero-lag fourth-order low-pass Butterworth filter with a 6 Hz optimal cut-off frequency. Joint angles, net joint moments and powers were calculated in the sagittal plane using filtered markers and forces by a kinematic and inverse dynamic approach (Visual 3D, C-Motion, Germantown, MD, USA). Net joint moments and powers were normalized by each participant's body mass. Onset timing of plantarflexion moments was defined as the percentage of the gait cycle when the moment traces crossed zero. Positive and negative joint work was calculated by integrating over time the positive and negative intervals of hip, knee and ankle power curves within each gait cycle. Total positive and negative joint work was calculated by summing ankle, knee and hip joint work. For the four conditions with bumps, which were in random order, the stride of interest was defined as the initial contact of the right foot on the bump to the following right heel strike. Heel strike and toe-off events were defined using a kinematic-based automatic gait detection algorithm (Stanhope et al., 1990) implemented in Visual 3D (C-Motion), followed by visual inspection. These events were used to calculate duty factor, defined as stance-phase duration divided by the stride time. Walking speed was calculated by dividing the horizontal displacement of the sternum marker by the stride time. Twelve strides per condition were used for generating mean kinematic and kinetic data for each individual participant, which were combined to calculate condition mean data.



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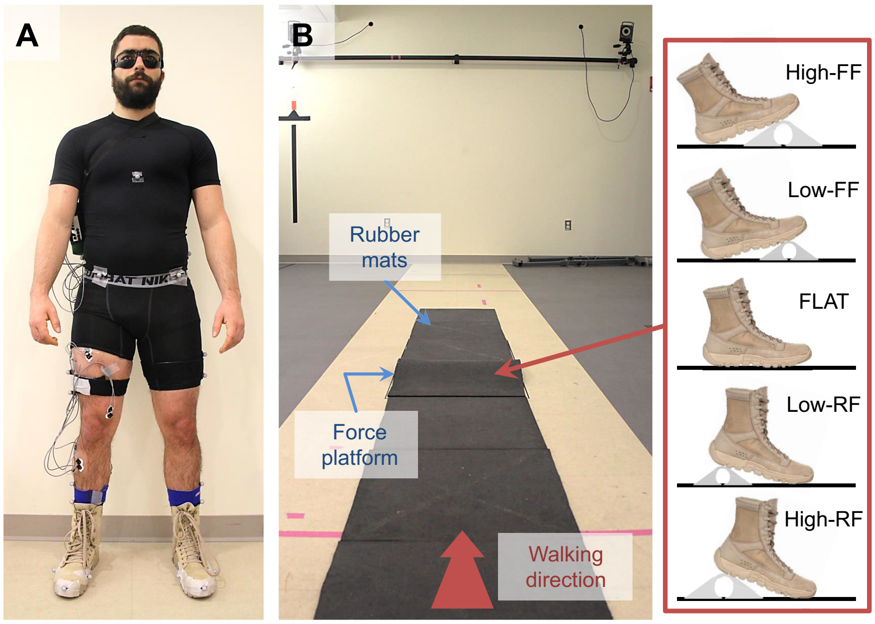


**Fig. 1. Images showing an instrumented participant, the experimental set-up and the different classes of foot contact.** (A) Instrumented participant. (B) Experimental setup. Straight walkway, highlighting the bump placement and its different sizes. The panel on the right shows the contact of the foot with the bump in the five different walking conditions (High-RF, Low-RF, FLAT, Low-FF and High-FF), highlighting the different classes of foot contact. RF, rearfoot; FF, forefoot.

During the data processing, some trials were found to be corrupted or incomplete. They were excluded from the analysis, resulting in 10.6±1.6 (mean±s.d.) strides investigated per condition for every participant.

### Muscle activity

During the walking trials, surface electromyography (EMG) from eight lower limb muscles was measured using a wireless system (TELEmyo 2400 G2, Noraxon, Scottsdale, AZ, USA; 1500 Hz) and synchronized with the motion data from the VICON system. Muscles investigated were: biceps femoris (BF), rectus femoris (RF), vastus medialis (VM), vastus lateralis (VL), soleus (SOL), medial gastrocnemius (MG), lateral gastrocnemius (LG), and tibialis anterior (TA). EMG signals were band-pass filtered (fourth-order Butterworth, cut-off 20–450 Hz), rectified, then low-pass filtered (fourth-order Butterworth, cut-off 6 Hz) to obtain an EMG linear envelope. For each participant and muscle, the EMG linear envelope was normalized to the peak value averaged across the strides collected during FLAT. The same strides used for kinematics and kinetics were used for generating average of muscle activation across each condition of testing, which we refer to as mean EMG (from the entire gait cycle). Muscle co-contraction index (CCI) was calculated for each pair of antagonist muscles (BF–RF, BF–VM, BF–VL, TA–SOL, TA–MG and TA–LG) using the methods described in Chambers and Cham (2007).

### Statistical analysis

Statistical analysis was performed using MATLAB (The MathWorks Inc., Natick, MA, USA). A two-tailed Student's paired *t*-test was performed to assess the differences between High-RF, Low-RF, Low-FF and High-FF condition and FLAT. Variables analyzed were chosen to compare the present study with the one conducted by Voloshina et al. (2013). We chose to examine peak power rather than average power because peak power is commonly used to describe the behavior of joint power (Pires et al., 2014; Franz and Kram, 2014). The statistical analysis included the following variables: spatio-temporal parameters (walking speed, duty factor, stride length), hip, knee and ankle joint kinematics (minimum, maximum and total range of motion), kinetics (average moments, onset plantarflexion moment, peak powers, positive and negative joint work) and muscle activity (mean EMG activation and CCI). The significance level was set at $P<0.05$ for all analyses. Where significance was detected, Bonferroni *post hoc* tests were performed to identify differences between conditions.

## RESULTS

### Spatio-temporal parameters

No differences were found in walking speed between FLAT and High-RF, Low-RF, Low-FF and High-FF, nor were any differences found in stride length between FLAT and the other four conditions. Significantly higher duty factor was found in both rearfoot conditions (High-RF and Low-RF) compared with FLAT. A complete overview of the spatio-temporal parameters, including means and s.d. values, is presented in Table 1.

### Joint kinematics and kinetics

Differences in joint kinematics with respect to FLAT were reported in all four conditions with bumps. As expected, a significantly higher peak ankle dorsiflexion angle was found in the forefoot conditions and a significantly lower peak ankle dorsiflexion angle was found in the rearfoot conditions. A different result was found for the peak ankle plantarflexion angle, with significantly higher values in the rearfoot conditions and significantly lower values in

**Table 1. Spatio-temporal parameters across the five different conditions of testing**

| | | FLAT | High-RF | Low-RF | Low-FF | High-FF |
|---|---|---|---|---|---|---|
| Spatio-temporal parameters | Walking speed (m s$^{-1}$) | 1.22±0.15 | 1.22±0.13 | 1.18±0.17 | 1.19±0.14 | 1.20±0.13 |
| | Stride length (m) | 1.42±0.11 | 1.41±0.10 | 1.38±0.12 | 1.41±0.11 | 1.43±0.11 |
| | Duty factor | 0.66±0.01 | 0.68±0.01* | 0.68±0.01* | 0.65±0.01 | 0.65±0.01 |

Values are means±s.d. across participants. *Significantly different from FLAT ($P<0.05$). RF, rearfoot; FF, forefoot.

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**Table 2. Joint kinetics and kinematics across the five different conditions of testing**

| | FLAT | High-RF | Low-RF | Low-FF | High-FF |
|---|---|---|---|---|---|
| Joint angle (deg) | | | | | |
| Ankle dorsiflexion (peak) | 13.86±4.78 | 6.29±5.63* | 7.39±7.43* | 19.77±3.96* | 21.25±4.76* |
| Ankle plantarflexion (peak) | −10.78±4.59 | −17.74±7.82* | −16.76±7.49* | −4.16±4.15* | 0.39±5.16* |
| Knee flexion (peak) | 17.56±8.95 | 22.79±9.81* | 21.18±9.40 | 17.53±9.78 | 16.89±10.75 |
| Hip flexion (peak) | 27.97±8.06 | 34.24±7.74* | 31.88±7.93* | 28.77±8.39 | 28.22±9.36 |
| Joint moment (N m kg$^{-1}$) | | | | | |
| Ankle plantarflexion (peak) | 0.31±0.04 | 0.21±0.02* | 0.26±0.04* | 0.40±0.05* | 0.42±0.07* |
| Knee flexion (average) | 0.16±0.08 | 0.23±0.11* | 0.20±0.09* | 0.12±0.07* | 0.11±0.07* |
| Hip extension (average) | 0.36±0.10 | 0.40±0.12 | 0.35±0.12 | 0.29±0.07* | 0.28±0.09* |
| Joint power (W kg$^{-1}$) | | | | | |
| Ankle plantarflexion (peak) | 2.67±0.39 | 2.06±0.35* | 2.29±0.48* | 2.47±0.40* | 2.35±0.48 |
| Knee flexion (peak) | −2.09±0.75 | −2.47±0.90* | −2.28±0.86 | −2.11±0.68 | −2.22±0.62 |
| Hip flexion (peak) | 0.79±0.30 | 1.19±0.50* | 1.01±0.37 | 0.79±0.35 | 0.87±0.40 |
| Onset moment (% GC) | | | | | |
| Ankle plantarflexion | 19.82±2.34 | 29.99±7.23* | 26.61±4.19* | 13.27±2.14* | 9.08±2.88* |

Values are means±s.d. across participants. *Significantly different from FLAT ($P$<0.05). RF, rearfoot; FF, forefoot.

the forefoot conditions with respect to FLAT (Table 2). Peak knee flexion angle was significantly higher in High-RF compared with FLAT. Peak hip flexion angle and range of motion were significantly higher in High-RF and Low-RF compared with FLAT.

The average ankle moment significantly decreased in both rearfoot conditions and increased in both forefoot conditions relative to FLAT. Conversely, the knee showed a significantly higher average moment in the rearfoot conditions and a smaller value in the forefoot conditions compared with FLAT. Significantly lower average moment at the hip was found in the forefoot conditions with respect to FLAT (Table 2). Significantly earlier onset of plantarflexion moment was reported in High-FF and Low-FF and significantly later onset of plantarflexion moment was reported in High-RF and Low-RF relative to FLAT (Table 2).

Peak ankle positive power was significantly reduced in three of the four conditions with bumps (High-RF, Low-RF and Low-FF) as compared with FLAT. Peak knee negative power and peak hip positive power were significantly increased in High-RF condition with respect to FLAT. Joint kinematics, kinetics and power traces for the five conditions of testing are presented in Fig. 2.

Alterations in joint work were reported when stepping on the bump; negative lower limb total joint work was found to be higher in the rearfoot conditions and lower in the forefoot conditions than in FLAT. Analyses at the single-joint level revealed significantly less positive ankle joint work in the rearfoot conditions and significantly more negative ankle work in Low-RF with respect to FLAT. Significantly higher positive hip work was found in High-RF and significantly smaller negative hip work was found in Low-FF relative to FLAT. No differences were found in positive and negative knee work in the bump conditions with respect to FLAT. Positive and negative joint work for the five conditions of testing is presented in Fig. 3.

### Muscle activity

Higher muscle activations were reported in the bump conditions relative to FLAT, with differences in muscle activation depending on the class of foot contact. Significantly higher average muscle activation was reported in the thigh muscles during rearfoot conditions with respect to FLAT. Specifically, higher muscle activation was reported in the BF, RF, VM and VL during the

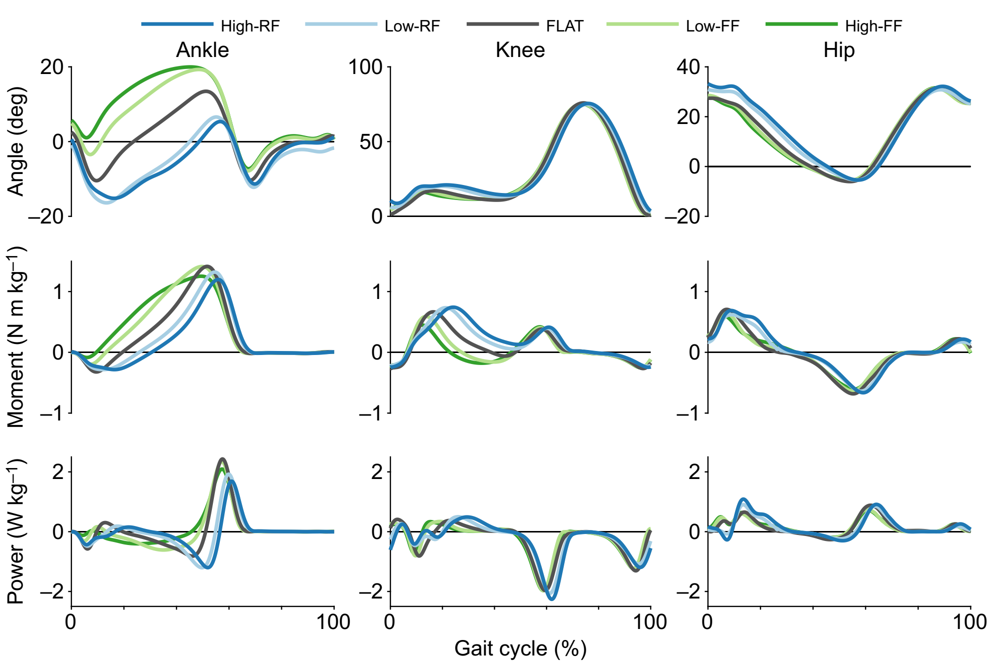


**Fig. 2. Joint kinematics and kinetics.** Comparison of joint angles, moments and powers (from top to bottom) for the five conditions of testing across the gait cycle. The curves represent the five different conditions: High-RF, Low-RF, FLAT, Low-FF, and High-FF. Ankle, knee and hip joints are displayed from left to right. Data are group means. Positive joint angles represent flexion (dorsiflexion at the ankle) and negative angles represent extension (plantarflexion at the ankle). Positive moments represent net extension joint moments (plantarflexion at ankle) and negative moments represent net flexion joint moments (dorsiflexion at ankle). Positive powers represent instantaneous joint power generation and negative powers represent instantaneous joint power absorption.



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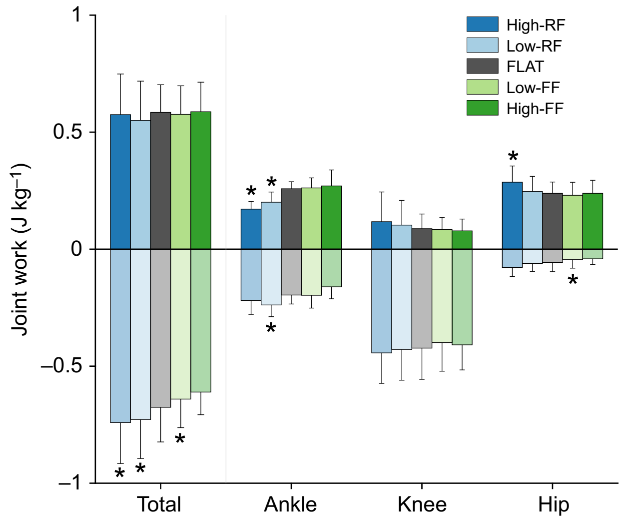


**Fig. 3. Negative and positive work across the lower limb joints and for each single joint.** The bars represent the five different conditions: High-RF, Low-RF, FLAT, Low-FF, and High-FF. Data are means±s.d. across participants. *Significant difference ($P$<0.05) with respect to FLAT. RF, rearfoot; FF, forefoot.

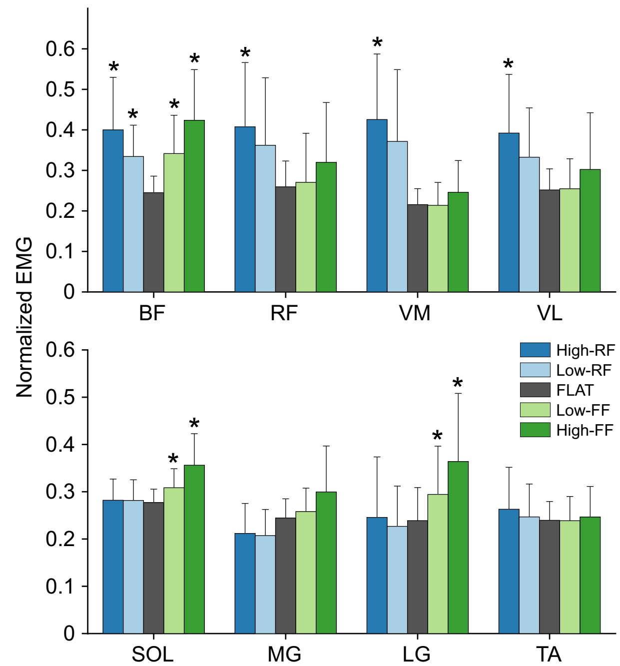


**Fig. 4. Average muscle activations.** Results are normalized to the peak value averaged across the strides collected during FLAT: biceps femoris (BF), rectus femoris (RF), vastus medialis (VM), vastus lateralis (VL), soleus (SOL), medial gastrocnemius (MG), lateral gastrocnemius (LG), and tibialis anterior (TA). The bars represent the five different conditions: High-RF, Low-RF, FLAT, Low-FF, and High-FF. Data are means±s.d. across participants. *Significant difference ($P$<0.05) with respect to FLAT. EMG, electromyography; RF, rearfoot; FF, forefoot.

High-RF with respect to FLAT and in the BF in Low-RF with respect to FLAT (Table 3, Figs 4, 5). Only BF showed significantly higher activation during the two forefoot conditions than in FLAT. Instead, significantly higher average muscle activation was reported in the shank muscles in the forefoot conditions; SOL and LG were significantly higher during Low-FF and High-FF with respect to FLAT (Table 3, Figs 4, 5). No differences in muscle activation were reported in the MG and in the TA during the bump conditions with respect to FLAT. An overview of average muscle activations for the eight muscles investigated is presented in Table 3 and Figs 4 and 5.

A significantly higher (in the range of 23–134%) CCI with respect to FLAT was found in the thigh muscles during the conditions with bumps. Specifically, a significantly higher CCI was found during High-RF (BF–RF, BF–VM, BF–VL), Low-RF (BF–RF, BF–VM, BF–VL), Low-FF (BF–VL) and High-FF (BF–RF, BF–VM) with respect to FLAT. A significantly higher CCI relative to the shank muscles was found only during High-RF (TA–SOL) compared with FLAT (Table 4).

## DISCUSSION

The aim of the present study was to investigate how the control system regulates specific kinematic and kinetic parameters in response to biomechanical constraints imposed by a small bump, specifically testing the hypothesis that the ankle push-off work would be higher in forefoot conditions and lower in rearfoot conditions. Moreover, by investigating discrete steps and different classes of foot landing, this work builds on previous studies that have focused on quantifying changes across consecutive strides on different types of uneven terrains (Voloshina et al., 2013; Wade et al., 2010; Thies et al., 2005).

Although similar walking speeds were maintained between conditions (Table 1), differences were reported at each joint depending on the class of foot contact, indicating that two different strategies were adopted in response to the specific nature of the constraints. In the forefoot conditions, our results confirmed the hypothesis that a larger amount of joint work was produced at the ankle relative to the rearfoot conditions, which was probably a mechanically necessitated choice in response to the biomechanical constraint imposed by the forefoot landing on the bump. This result can be attributed to different ankle moment patterns associated with foot contact classes (Fig. 2). Specifically, onset timings of plantarflexion moments were earlier in the forefoot conditions as compared with the rearfoot conditions, resulting in higher average plantarflexion moments during the forefoot conditions.

At the same time, the increased dorsiflexion during the stance phase reported in the forefoot conditions may be associated with an increased stretch reflex because the muscle–tendon complex is lengthening. Previous work has shown that the presence of a short-latency stretch reflex can contribute to force enhancement during gait (Ishikawa and Komi, 2007), and it has an important role in stiffness regulation of muscle fibers (Toft et al., 1991). To this extent, previous studies have shown that humans adjust ankle joint stiffness mainly as a response to the presence of perturbations or

**Table 3. Muscle activation percentage change with respect to FLAT condition**

| | High-RF (%) | Low-RF (%) | Low-FF (%) | High-FF (%) |
|---|---|---|---|---|
| BF | +64.34±55.34* | +36.29±22.78* | +37.88±18.37* | +72.77±47.30* |
| RF | +55.47±37.92* | +36.87±47.27 | +5.76±47.40 | +25.03±60.90 |
| VM | +92.64±43.28* | +68.91±66.46 | −1.37±16.31 | +12.98±22.51 |
| VL | +60.35±38.79* | +36.10±30.45 | +0.77±17.78 | +15.90±33.20 |
| SOL | +2.13±15.32 | +1.70±12.97 | +11.36±10.40* | +28.47±19.37* |
| MG | −14.48±14.19 | −14.41±19.75 | +6.39±17.33 | +20.73±25.44 |
| LG | −1.50±28.33 | −6.45±19.90 | +22.51±14.77* | +51.12±29.49* |
| TA | + 8.10±25.11 | +2.32±18.67 | −0.20±12.67 | +2.26±15.28 |

Values are means±s.d. across participants. *Significantly different from FLAT ($P$<0.05). RF, rearfoot; FF, forefoot; BF, biceps femoris; RF, rectus femoris; VM, vastus medialis; VL, vastus lateralis; SOL, soleus; MG, medial gastrocnemius; LG, lateral gastrocnemius; TA, tibialis anterior.

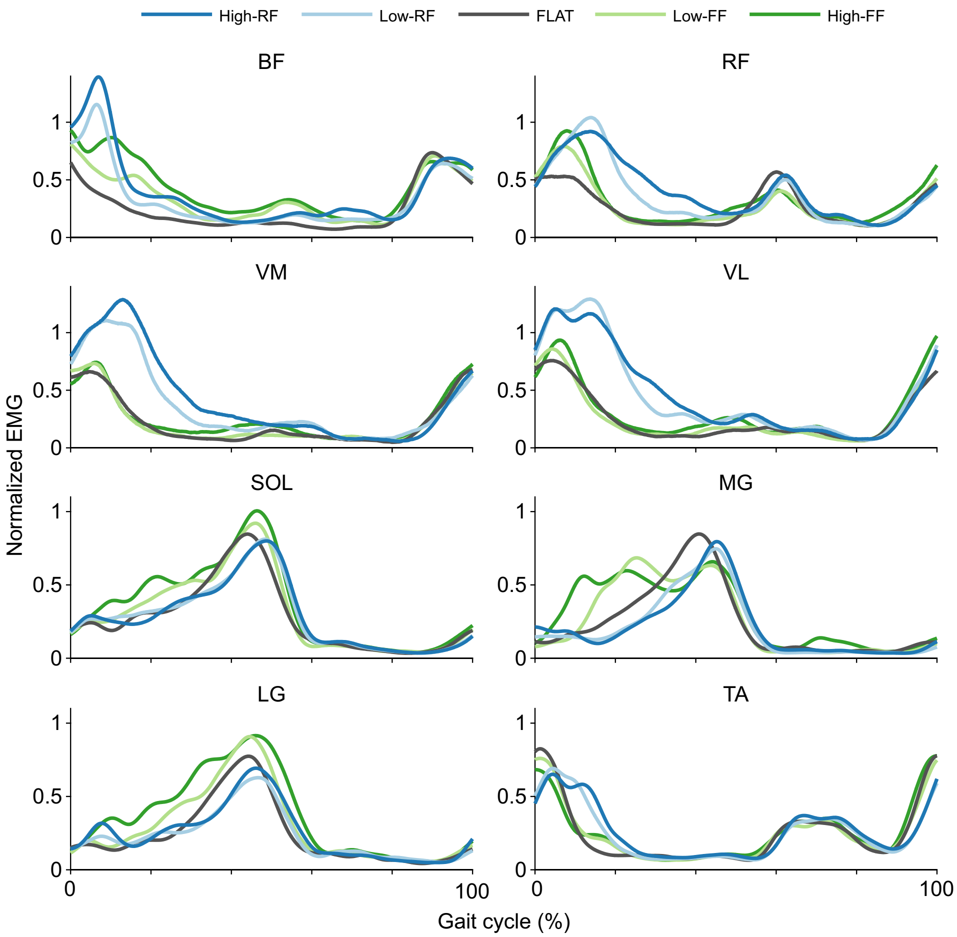


**Fig. 5. Muscle activation patterns.** Results are normalized to the peak value averaged across the strides collected during FLAT: biceps femoris (BF), rectus femoris (RF), vastus medialis (VM), vastus lateralis (VL), soleus (SOL), medial gastrocnemius (MG), lateral gastrocnemius (LG), and tibialis anterior (TA). The curves represent the five different conditions: High-RF, Low-RF, FLAT, Low-FF, and High-FF. EMG, electromyography; RF, rearfoot; FF, forefoot.

biomechanical constraints during walking and running (Müller et al., 2010). These are in line with our results indicating that the majority of the adaptations took place at the ankle in the forefoot conditions, and higher muscle activation in the plantarflexor muscles (SOL and LG) seems to support this mechanism because it is associated with the generation of the stretch reflex (Kao et al., 2010; Sloot et al., 2015).

It is interesting that, whereas individual joint behavior differed, the total mechanical work produced by the lower limbs was the same in all foot-landing conditions. This may suggest that the total mechanical work could be an optimized parameter when reacting to an unexpected perturbation on a single-step basis, such that the control system regulates only the work distribution over different joints in reaction to different classes of foot contact. This is probably because the forward momentum produced by the entire lower limb should be maintained, given that the perturbation was applied unexpectedly to a single step, while the walking speed was maintained. This is in line with the previous study that local control of individual joints is combined to generate appropriate patterns for the whole limb, as well as for inter-limb coordination (Ivanenko et al., 2002).

During rearfoot landing, however, the knee and the hip had a larger role while several adaptations occurred at these joints in both foot contact classes; in contrast to the ankle moment and power, knee moment and hip power increased in the rearfoot conditions relative to FLAT. Possibly, this increase compensated for lower moments at the ankle during rearfoot conditions; a compensation that was unnecessary in the forefoot conditions, which were marked by increased ankle moments. This may be because the kinematic constraint in the rearfoot conditions was applied directly to the heel rather than to the toe, so the kinematic compensation that could be provided by the ankle joint was limited. As a consequence of this, it is reasonable to hypothesize that a more proximal joint (hip) was responsible in maintaining the forward momentum needed to propel the body forward.

**Table 4. Muscle co-contraction index (CCI) for each pair of antagonist muscles in the thigh and shank**

| | FLAT | High-RF | Low-RF | Low-FF | High-FF |
|---|---|---|---|---|---|
| BF–RF | 15.01±7.48 | 28.04±13.29* | 24.74±11.98* | 19.35±10.78 | 22.19±11.60* |
| BF–VM | 12.67±4.46 | 29.56±11.93* | 24.21±7.66* | 15.62±5.79 | 19.54±8.91* |
| BF–VL | 14.24±6.60 | 30.52±11.61 | 26.14±10.68 | 19.21±9.93 | 24.02±13.46 |
| TA–SOL | 9.12±2.98 | 11.70±3.32* | 10.64±2.26 | 9.93±3.32 | 10.06±4.08 |
| TA–MG | 7.41±5.08 | 7.65±2.99 | 6.79±2.36 | 7.53±2.00 | 9.11±4.52 |
| TA–LG | 8.61±5.20 | 10.08±4.96 | 9.38±4.43 | 8.79±3.99 | 9.88±5.87 |

Values are means±s.d. across participants. *Significantly different from FLAT (*P*<0.05). RF, rearfoot; FF, forefoot; BF, biceps femoris; RF, rectus femoris; VM, vastus medialis; VL, vastus lateralis; SOL, soleus; MG, medial gastrocnemius; LG, lateral gastrocnemius; TA, tibialis anterior.

Additionally, this increase in hip power generation during rearfoot landing could be adopted by the control system to increase stability, which may also be associated with where the kinematic constraint was applied. Increased power at proximal joints may increase the joint stiffness and, in turn, the overall stability and resistance to external perturbation while walking, which has also been reported in other studies on uneven terrain walking (Marigold and Patla, 2002; Ochi et al., 2014). The high duty factor may have a similar effect on stability because a relatively prolonged double-support phase may contribute to improving static stability of locomotion (Gordon et al., 2017). This increased emphasis on stability may be because the kinematic constraint directly applied to the heel alters not only the ankle joint angle during stance but also the position (height) of the ankle joint center relative to the ground, where the kinematic linkage of the rest of the body starts from. Therefore, a rearfoot contact may affect the overall postural stability to a greater extent compared with a forefoot contact, and thus increase the importance of stability-related strategies.

We are aware of only one study investigating walking over uneven surfaces (Voloshina et al., 2013) that reported both ankle angles and moments, in which the authors did not report differences between the average ankle moment in walking on uneven terrain and the same moment in normal walking. However, the authors did report an approximately 50% increase in variability when walking over uneven terrain. This divergence from previous research may stem from the combination of foot contact classes contributing to the results from Voloshina et al. (2013); indeed, if we compare rearfoot and forefoot conditions from our study together, ankle moments could be similar to flat walking. In addition, we found no change in walking speed – a result that would likely change if the subject encounters multiple consecutive bumps.

Two of the most relevant literature reported seemingly contrasting findings on these adaptations at the knee and hip on uneven terrains. Voloshina et al. (2013) observed increased knee flexion and hip extension moments at mid-stance and a reversed pattern during push-off with greater knee extension and hip flexion moments, whereas Wade et al. (2010) reported lower hip and knee joint moments compared with walking on a flat surface. This discrepancy could be due to the different aims and methodological procedures, and in turn to the different types of irregular surfaces investigated. Voloshina et al. (2013) used a treadmill with wooden blocks and foam to relate the biomechanics of walking on uneven terrain to an increased metabolic rate, whereas Wade et al. (2010) analyzed the impact of ballast size on gait with a specific focus on occupational biomechanics. With these different aims, neither Wade et al. (2010) nor Voloshina et al. (2013) separated foot contacts into distinct classes, instead investigating interactions happening during continuous walking on an uneven surface. However, the present study aimed to isolate different foot contact classes, providing complementary information with respect to the previous studies. Moreover, it is also relevant to mention the different aims of the previous studies, which could have driven the methodological procedures of these studies and consequently could have affected the results. Voloshina et al. (2013) investigated how the changes in the biomechanics of walking on uneven terrain relate to an increased metabolic cost, whereas Wade et al. (2010) analyzed the impact of ballast size on gait, with a specific focus on occupational biomechanics.

From a muscle perspective, the previous study (Voloshina et al., 2013) showed higher muscle activation in six of the eight muscles investigated, with the thigh muscles presenting a higher increase in muscle activation than the plantarflexors. Although we also generally reported higher activation of the thigh muscles with respect to the calf muscles, our results revealed specific muscle-group activations as a response to the two classes of foot contact, providing further insights on the two distinct negotiation strategies at muscle level (Fig. 5). Also, this finding, in agreement with the kinematics and kinetics data, suggests a higher reliance on the plantarflexor muscles for the forefoot conditions and on the thigh muscles for the rearfoot condition. Last, higher co-contraction of the thigh muscles (BF–RF, BF–VM, BF–VL) was reported in the present study (Table 4). Higher co-contraction in walking has been reported as a strategy to stiffen the lower limb joints to enhance stability when individuals perceive a high risk of falling (Marigold and Patla, 2002; Ochi et al., 2014). This phenomenon has also been previously reported when walking on irregular surfaces, specifically on different lower limb muscles (Wade et al., 2010; Voloshina et al., 2013).

It is worth mentioning some of the present study's limitations. First, the investigations were limited to forefoot and rearfoot classes of foot contact, and did not include other possible stepping conditions. As more terrain irregularities are introduced, it is likely that additional negotiation strategies would take place. In this study, we strove to limit the number of irregularities to best highlight the specific information available through this new methodological approach. Second, the analysis was limited to the leg stepping on the bump, although some adaptations might have happened to the contralateral limb. This choice was imposed by the setup of our testing facility, which included only one force platform and limited motion capture volume. To avoid any anticipatory adaptation in the lower limb mechanics (i.e. participants remembering the exact location of the bump), we restricted the participants' field of view and changed the starting position for each trial. Despite this, we cannot rule out the possibility that some of the findings reported in the present study are due to anticipatory changes. Perhaps, an analysis of the steps prior to bump contact or a survey given to participants after the experiments would have provided further insights on this aspect.

In conclusion, these findings provide insights to how humans quickly react to unexpected events and explore the specific effects of different perturbations. Although further validation studies are required, the neuromotor system seems to control the amount of mechanical work needed at each lower limb joint to perform a step on a bump, with no significant change in total mechanical work and a constant walking speed. This finding highlights the conservation of a biomechanical parameter (total mechanical work) by the control system. Because of the different biomechanical constraints imposed by the two different classes of foot landing, we reported two different strategies involving a redistribution of joint work across lower limb joints. An ankle-based strategy was adopted when stepping on a bump with the forefoot, which generated a higher ankle joint moment driven by a higher activation of the plantarflexor muscles. However, a hip-based strategy was preferred when stepping on a bump with the rearfoot, which was driven by a higher activation of the quadriceps muscles, producing a higher knee moment and hip power and, in turn, a higher generation of mechanical work by these two joints; this might be adopted by the control system to increase stability.

Moreover, these results may be helpful to develop controllers for assistive devices (Mooney et al., 2014; Asbeck et al., 2015; Panizzolo et al., 2016) that can adapt to different terrains, extending the applicability of such systems to environments with complex terrain. Previous studies proposed to control lower limb exoskeletons by applying external assistance that mimics the biological joint moment (Collins et al., 2015; Panizzolo et al., 2016; Quinlivan et al., 2017), power (Lee et al., 2016) or muscle activity patterns (Ferris et al., 2006) while walking on flat surfaces. The findings from the present study on how specific biological parameters, e.g. the onset timing of biological joint moment (Table 2), change due to uneven surfaces could be of practical applicability to researchers in this field by providing insights on how assistive devices should react to certain changes in walking terrain.

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**Competing interests**

The authors declare no competing or financial interests.

**Author contributions**

Conceptualization: F.A.P., S.L., T.M., D.M.R., C.S., I.G., C.J.W.; Methodology: F.A.P., S.L., T.M., D.M.R., C.S., I.G., C.J.W.; Software: S.L., T.M., D.M.R., C.S.; Formal analysis: F.A.P., S.L., T.M., D.M.R., C.S., J.S.; Investigation: F.A.P., S.L., T.M., D.M.R.; Resources: C.J.W.; Writing - original draft: F.A.P., S.L., T.M., D.M.R., C.S., C.J.W.; Writing - review & editing: F.A.P., S.L., T.M., D.M.R., C.S., J.S., I.G., C.J.W.; Visualization: T.M., D.M.R., C.S.; Supervision: F.A.P., C.J.W.; Project administration: F.A.P., C.J.W.; Funding acquisition: C.J.W.

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