JOURNAL OF THE ROYAL SOCIETY INTERFACE

Stepping onto the unknown: reflexes of the foot and ankle while stepping with perturbed perceptions of terrain

Journal:	*Journal of the Royal Society Interface*
Manuscript ID	rsif-2021-0061.R1
Article Type:	Research
Date Submitted by the Author:	11-Feb-2021
Complete List of Authors:	Riddick, Ryan; University of Queensland, School of Human Movement and Nutrition Studies Farris, Dominic; University of Exeter School of Sport and Health Sciences, School of Sport and Health Sciences; University of Queensland Faculty of Health and Behavioural Sciences, School of Human Movement and Nutrition Sciences Cresswell, Andrew; University of Queensland, School of Human Movement and Nutrition Studies Kuo, Arthur; University of Calgary, Faculty of Kinesiology & Biomedical Engineering Program Kelly, Luke; University of Queensland, School of Human Movement and Nutrition Studies
Categories:	Life Sciences - Engineering interface
Subject:	Biomedical engineering < CROSS-DISCIPLINARY SCIENCES, Biomechanics < CROSS-DISCIPLINARY SCIENCES, Systems biology < CROSS-DISCIPLINARY SCIENCES
Keywords:	Intrinsic foot muscles, reflex, short latency response, terrain, perturbation, stepping

Author-supplied statements

Relevant information will appear here if provided.

Ethics

Does your article include research that required ethical approval or permits?:
Yes

Statement (if applicable):
10 participants volunteered for the study with written consent obtained from each prior to the start of the experiment, according to the procedures outlined by the University of Queensland Human Research Ethics Committee.

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
The data from this study and the code to generate the figures and statistics are publically available at 10.6084/m9.figshare.12986223.

Conflict of interest

I/We declare we have no competing interests

Statement (if applicable):
CUST_STATE_CONFLICT :No data available.

Authors' contributions

This paper has multiple authors and our individual contributions were as below

Statement (if applicable):
All authors helped design the experiment. R.R, D.J.F, and L.A.K collected data. R.R. performed data analysis. R.R. and L.A.K. drafted the manuscript. All authors edited and revise the manuscript.

Stepping onto the unknown: reflexes of the foot and ankle while stepping with perturbed perceptions of terrain

Riddick, RC[1], Farris, DJ[2], Cresswell, AG[1], Kuo, AD[3], Kelly, LA[1]

r.riddick@uq.edu.edu
d.farris@exeter.ac.uk
a.cresswell@uq.edu.au
arthur.kuo@ucalgary.ca
l.kelly3@uq.edu.au
[1]School of Human Movement and Nutrition Sciences, University of Queensland, St Lucia, Queensland, Australia
[2]Sport and Health Sciences, College of Life and Environmental Sciences, University of Exeter, Exeter, UK
[3]Faculty of Kinesiology & Biomedical Engineering Program, University of Calgary, Calgary, T2N 1N4 AB CANADA

Abstract

Unanticipated variations in terrain can destabilize the body. The foot is the primary interface with the ground and we know that cutaneous reflexes provide important sensory feedback. However, little is known about the contribution of stretch reflexes from the muscles within the foot to upright stability. We used intramuscular electromyography measurements of the foot muscles flexor digitorum brevis (FDB) and abductor hallucis (AH) to show for the first time how their short latency stretch reflex response (SLR) may play an important role in responding to stepping perturbations. The SLR of FDB and AH was highest for downwards steps and lowest for upwards steps, with the response amplitude for level and compliant steps in between. When the type of terrain was unknown or unexpected to the participant, the SLR of AH and the ankle muscle soleus tended to decrease. We found significant relationships between the contact kinematics and forces of the leg and the SLR, but a person's expectation still had significant effects even after accounting for these relationships. Motor control models of short latency body stabilization should not only include local muscle dynamics, but also predictions of terrain based on higher-level information such as from vision or memory.

Keywords

Intrinsic foot muscles, reflex, short latency response, terrain, perturbation, stepping

Introduction

The foot is the primary interface between the body and the ground. Swinging the foot into an appropriate position ahead of the body is a fundamental and intuitive mechanism for maintaining stability during gait. With the foot pinned to the ground ahead of the main mass of the body, gait can be maintained efficiently by falling like an inverted pendulum (1–4). As the latency of sensing contact increases, the ability to recover from errors and perturbations decreases (5). Part of an effective control strategy would include minimizing the response latency to these types of errors. Reflexes are the primary mechanisms for short latency active compensation in humans, and have been shown in the muscles of the leg to play an important role during tripping (6–8), sudden treadmill accelerations (9–11), and targeted muscle stretching (10,12).

There are fewer data on reflexes in the muscles of the foot, in part due to the difficulty in measuring activity in these muscles via traditional surface electromyography (EMG) techniques. While reflexes of the foot muscle, flexor digitorum brevis, have been recorded during standing with sudden platform rotations (13,14), we have found no data on reflexes in foot muscles during a dynamic task such as stepping, and no measurements of stretch reflexes of other plantar foot muscles in any task. Part of the difficulty in dynamic tasks is that reflexes are known to be influenced by background levels of muscle activity (12). In tasks such as walking, the cyclical patterns of muscle activation may be large enough to obscure reflexes that could be present. In steady-state locomotion on a treadmill, people are presumably accurate enough at predicting where their feet should go and getting them there that there is no obvious indication of reflex contribution in the step-averaged activation of muscles of the foot (15). However, in real world environments where the foot may hit the ground in an unexpected manner, or timing due to an unforeseen variation in the terrain, reflexes may play a larger role.

The behaviour of reflexes in such scenarios may depend on many factors. Mechanoreceptors in the skin of the foot have been shown to contribute to reflexes of short latency (30 ms), medium latency (70 ms), and long latency (>120 ms), in muscles of the ankle while prone (16). At similar time scales, stretch reflexes act via exciting receptors within the muscle spindles that sense stretch or rate of stretch (10). Stimulating the ankle plantar flexors has shown that the size of the H-reflex depends both on the activity (standing, walking, and running) and the phase of gait (17,18). Although the H-reflex methodology bypasses some of the pathways (e.g. gamma motor neurons) within the body that would contribute to naturally evoked stretch reflexes, their results showed that the nervous system is able to tune reflex responses of the lower limb based on task on both the scale of a broad activity, and from second to second as on the scale of a single step or during postural sway (19). A predictive model may play an important role in determining the observed reflex magnitude and could be based on higher level information such as visual feedback or memory of the terrain from previous steps. However, since the instantaneous mechanical state of the body also varies greatly between walking and running, it is difficult to directly attribute the changes in reflex magnitude to the change in output of a predictive model.

We therefore performed an experiment to evaluate whether reflexes can be found in the plantar intrinsic foot muscles, and to what extent reflexes of the foot and ankle are driven by a predictive model of the task. In order to do this, we constructed scenarios in which there could be errors in a participant's predictive model of the terrain during a stepping task. This error was induced by reducing visual feedback while participants stepped onto surfaces of different topologies (level, up, down, and compliant) that were either expected, unknown, or unexpected (Fig. 1A). Firstly, we identify that reflexes are indeed present during stepping in flexor digitorum brevis (FDB), abductor hallucis (AH), and soleus (SOL), and investigate how the magnitude of the reflex depends on the type of terrain. We compare the reflex response of the muscles when the information of the terrain is correct (expected) to the cases in which there is no information given (unknown), and to the case where the information is incorrect (unexpected). We show that this information both together with and separately from mechanics may play a significant role in the reflex response of the foot and ankle during stepping.

Methods

Participants

10 participants volunteered for the study with written consent obtained from each prior to the start of the experiment, according to the procedures outlined by the University of Queensland Human Research Ethics Committee. The participants had a mean +/- sd age of 24.9 ± 5.8 years, height of 179 ± 7.0 cm, and mass of 79.9 ± 13.0 kg. Participants were only included in the study if they had no lower limb injury within the last six months and no known neurological impairments.

Protocol

The experiment was designed to measure the muscle activity and lower-body dynamics of participants as they stepped onto different types of terrains. Participants always started with both feet at rest on a single force plate and could step forward onto either on a level, compliant, upwards, or downwards step, which also had a force plate to measure the force of the step. They were instructed to always first step forward with their right leg, followed by their left, and then to resume standing on the front force plate. Once they completed this step and came to a rest, they were instructed to wait one second and then return to the rear plate to be ready for the next step. For a diagram of the experimental task, see Fig. 1A. The first set of steps consisted of repetitively performing this stepping task onto a level, rigid surface for one minute with full auditory and visual feedback. This set was used as the control condition, since it was most similar to how a normal step would occur in a non-laboratory setting.

Following this set, we added constraints on the participants in order to test the effects of expectation and surprise in regards to the type of step they would encounter. Participants wore partial blinders so they could not see the vertical position or type of surface of the front plate. The blinders prevented participants from seeing the step even if they looked downwards while still allowing vision of the walls and ceiling. As such, participants tended to keep a neutral head posture during the step. They also wore headphones with enough sound insulation to reduce any noise from the experimenters changing the type of step. Because there was a hazard of participants tripping on upwards steps while visual feedback was reduced, a proximity sensor was placed between the two force plates which emitted a piercing beep loud enough to penetrate the headphones if the participant's foot swung low enough to trip on an upwards step. A familiarisation period of at least one minute was performed in which participants acclimated to reduced visual feedback and could reliably avoid triggering the proximity sensor. Following this familiarisation, data were collected of participants performing a one-minute set of stepping onto a level, rigid surface in this manner.

The main body of the experiment consisted of 20 sets of four conditions: steps on to a i) level or ii) compliant surface, iii) where they step up (13 cm) onto the surface, or iv) down (13 cm) onto the surface. The level, up, and down steps were built from wood and fibreboard, whereas the compliant step was a piece of high-density foam. The foam on average compressed 106 mm during a step with a peak force of 717 N, which estimates linear stiffness of the foam at 6.7 N/mm. For the first step of each set/condition, the participant knew only that the step could be any of the four possible types. This step was labelled as the “Unknown” step. The following step was known to be the same as the one they had just encountered and was labelled as the “Expected” step. After repeatedly stepping on the expected terrain, the condition would be suddenly switched after a random number of steps (between 2 and 12), leading to a different step condition than expected. This was labelled as the “Unexpected” step. For the unexpected step, we only paired steps of the opposite type (i.e. rigid vs compliant, and up vs down) although participants were not aware of this paradigm. Additional data of unknown steps were collected in 3 separate sets of 20 steps, in which the terrain was randomly changed in between each step (participants were aware that the surface could change for each step).

Kinetics, Kinematics, & Event Detection

Ground reaction forces were recorded from two force plates (OR 6-7, AMTI, MA, USA) at 4000 Hz. One plate was under the surface where the participant started (rear surface), and one was under the surface they stepped on to (front surface). To identify when contact with the force plate occurred, the vertical force was first smoothed with a second order low-pass Butterworth filter at 30 Hz. This smoothed signal was thresholded at 1% of participant’s body weight to roughly identify when the foot contacted the ground. Because this type of filtering tended to shift rising-edge event detection to an earlier time than appropriate, a second iteration of event identification was used to refine the estimates for each of the events identified by the first iteration. In this second iteration, the raw unfiltered force signal prior to the identified events from the first iteration was used to characterize a normal distribution of the force plate noise. In a 500 ms window centred between the falling edge of the previous step and the rising edge of the identified step, a normal distribution of the force plate noise was estimated using an Ordinary Least Squares estimator. The normal distribution was estimated independently for each step, since both force plate drift and the type of step could influence the parameters of the normal distribution. First contact was then defined as the instant the front plate’s raw force exceeded four standard deviations of the mean noise level of the estimated normal distribution.

Motion capture data were recorded at 200 Hz using a three-dimensional optoelectronic motion capture system (Qualisys, Gothenburg, Sweden). Reflective markers were placed on the pelvis, legs and right foot, with the latter used to construct a 3-segment foot model in a manner described previously (20,21). These data were used to estimate the timing of when the leading right leg departed the rear plate by estimating when the right ankle crossed a level 3 cm above the left ankle. It was used in the same manner to detect when the left leg came into contact with the front force plate. Ankle angle was calculated as the angle between the shank and forefoot segments in the sagittal plane of the shank segment. Contact velocity was defined as the vertical velocity of the forefoot segment’s centre-of-mass at the instant prior to contact with the ground.

During unexpected down steps, contact was delayed since participants were expecting to step up and onto the surface. From the previous steps, we identified the average heights of the three foot segments at first contact with the front plate. During the unexpected down step, we identified when the height of any of the three segments dropped below their corresponding mean contact height and labelled this event as the expected contact (EC). For unexpected up steps, contact occurred earlier than the expected step downwards. For these steps, EC was defined as the mean contact timing of the previous downwards steps of that set.

EMG

We recorded intramuscular electromyography (EMG) from two of the largest plantar intrinsic foot muscles, abductor hallucis (AH) and flexor digitorum brevis (FDB) from the right foot. Bipolar fine-wire electrodes (0.051 mm stainless steel, Teflon coated, Chalgren, USA) with a detection length of 4 mm were inserted under sterile conditions into the muscle bellies of each participant using delivery needles (0.50 mm x 50 mm). The needles were guided into place with the aid of ultrasound imaging (10 MHz linear array, SonixTouch, Ultrasonix, BC, Canada), and the electrodes were situated to have an inter-electrode distance of about 2mm. We also recorded bipolar surface EMG of the ankle plantar flexor, soleus (SOL) using Ag-AgCl electrodes (Tyco Healthcare Group, Neustadt, Germany) with a recording area of 20 mm^2 and a 20 mm inter-electrode distance. All EMG was recorded in the right leg. Signals were amplified by a factor of 350 (MA300, Motion Labs, LA, USA) and recorded at 4000 Hz using a16-bit Power 1401 and Spike2 data collection system (Cambridge Electronics Design).

As movement artefacts often contaminated the intramuscular EMG signals during the first 100 ms of foot contact, a filter was designed and implemented to improve the signal to artefact ratio (Fig. 1B). We manually identified 3 steps from each participant where clear artefact and clear signal could be identified and calculated the average signal level for both. High-pass filters were then applied at frequencies ranging from 1 to 250 Hz, and the frequency which maximized the difference between the two signals was identified. A consistent value to this optimal frequency was not found (ranged between 50 and 200 Hz). A frequency of 150 Hz for the high-pass filter was eventually chosen for all muscles of all participants to err on the side of eliminating the movement artefact at the cost of potentially reducing the valid EMG signal. A root mean square (RMS) signal envelope was then applied to each of the EMG signals using a moving window of 5 ms.

The EMG data are presented at two different scales. The first scale was used to quantify the magnitude of the SLR in relationship to non-reflex based contractions. The maximum value for this scale (a value of 1) was taken as the maximum activation of each muscle for a 26 cm step upwards (averaged across 10 steps). Secondly, in order to gauge how terrain and expectation affected the reflex across participants, we used a second normalization scheme. In this second normalization scheme, instead of representing a maximal level of activation for the muscle in general, a value of 1 represents the average level of activation for the participant during the SLR window across all steps in the experiment. This second scheme was chosen to ensure that the same relative changes in SLR magnitude across conditions for different participants would be identical and not affected by the baseline magnitude of a participant's SLR. For example, a 10 % increase in SLR for two different participants would give the same effect size (0.1) under this normalization scheme, even if the absolute magnitude of the SLR or change in SLR were quite different (as was often the case in the first normalization scheme).

A visual analysis of EMG responses immediately after contact with the front plate was performed (Fig. 1B). Due to background EMG activity, the onset of the SLR window was manually identified for each participant based on the average time-profile of the reflex response across the various conditions, and based on expectation of timing of the reflex from previous studies (13). We observed sporadic evidence of a medium latency response, especially in SOL, but did not attempt to quantify them. Long latency responses were also present but were difficult to differentiate from voluntary activations.

Statistical analysis

To make statistical conclusions, all measures of EMG activation were analysed with linear mixed-effects models. This model was chosen to account for the very unbalanced design (there were many more expected steps than surprise steps, 747 steps vs 195 steps across all participants) and participants having varying levels of average activity for a given muscle. The main variables of interest were Terrain (up, down, level, or compliant), and Expectation (expected, unknown, or unexpected). These two categorical variables were treated as fixed-effects, and the interaction terms between them were included since the type of surprise was coupled to the type of terrain. Unless otherwise reported, quantified values are reported in the format: *estimate ± standard error*, where the estimate and standard error correspond to the corresponding fixed-effect coefficient in the statistical model.

To attribute changes in reflexes purely due to mechanics imposed by the terrain, the vertical contact velocity of the foot, the angle of the ankle at contact, and the mean vertical force during the first 50 ms of contact were included as fixed effects. Interaction terms between the expectation, terrain, and these mechanical measures were also included to account for changes in gain on this mechanical feedback due to differences in planning.

Participants were treated as a random effect such that each participant had their own intercept when fitting the model for each measure. For each of the three muscles, the model in Wilkinson notation can be written as:

$$\text{Activation} \sim \text{Terrain} * (\text{Expectation} + \text{Contact Mechanics}) + \ (1|\text{Participant})$$

A simple effects coding was first used for the coefficients of the model. An ANOVA analysis was used to test whether each fixed and interaction effect was significant, where significance was defined as $p < 0.05$ for the F statistic. To make individual comparisons between two groups, e.g. down expected vs up expected steps, the model was recalculated using dummy variables with reference coding to directly extract significance from the coefficient in the model representing the difference between the reference group and each other group.

Results

Reflex Characterization

For SOL, all 10 participants had consistent SLR activations, whereas for FDB and AH only 6 and 7 participants exhibited consistent activations respectively. The average SLR latencies across participants for FDB, AH, and SOL were 50.06 ± 7.01 ms, 49.49 ± 5.25 ms, and 41.80 ± 6.78 ms respectively. The magnitude of the SLR was small in comparison to the level of activity generally seen throughout a step. For example, the average SLR magnitude of the same three muscles was 8.3 ± 13.3 %, 15.2 ± 12.7 %, and 5.5 ± 6.9 %, respectively, of the maximum activation for a 26 cm step upwards.

Effects of reduced visual feedback

FDB and AH SLR amplitudes were not significantly different ($p = 0.17$, $p = 0.40$) comparing level steps with full and reduced visual feedback (Fig. 2). In contrast, SOL SLR amplitude was greatly increased for steps with reduced visual feedback by 239 ± 1026 % ($p = 0.02$). These comparisons and all further comparisons of reflexes are made using the scaled data based on average per-subject SLR magnitudes and subtracted background levels of activity.

Effects of Terrain

Terrain generally changed the SLR activation patterns of all three muscles (Fig. 3A), with a significant main effect on the SLR magnitudes of FDB, AH, and SOL ($p < 1E-5$ for all).

The SLR magnitudes of the FDB and AH was significantly smaller for upwards steps than downwards steps (Fig. 3B, $p < 0.001$ for both) In contrast, the SLR magnitude for SOL was larger in upwards steps than downwards steps (Table 1, $p < 0.001$). Level steps exhibited SLR magnitudes in between upwards and downwards steps for all 3 muscles (Fig. 3A, 3B).

Effects of Expectation

For AH and SOL SLR, we found that stepping onto unknown or unexpected surfaces generally decreased SLR (Figure 4A). These differences were significant between expected and unexpected steps for both AH and SOL, but between expected and unknown steps this difference was only significant for AH. In contrast, there were no significant main effects of expectation on FDB SLR. When accounting for the interaction of expectation and terrain, there were certain cases in which the effect of expectation was quite different from the main effect. In particular the FDB SLR was significantly increased for unexpected downward steps compared to expected steps (Fig. 4B), whereas there was no significant main effect for the FDB SLR in general. Even when accounting for the effects of both mechanics and terrain, expectation still had significant effects in certain conditions (Fig. 4B).

Contact Dynamics

We found that the contact angle of the ankle was significantly different across terrains and expectations (Fig. 5). The contact angle was more dorsiflexed for expected upwards steps compared to downwards steps. However, when the upwards step was unexpected, this difference was reduced by about half as the foot contacts the unexpected step upwards in a more plantarflexed configuration. This difference was also accompanied by a significant increase in the ground contact force during the first 50 ms of contact (Fig. 5).

We found that contact ankle angle, and contact velocity were weakly related to the SLR of the 3 muscles (Fig. 6). In the statistical model, there were significant interaction effects between these mechanical measures and the SLR of the muscles, especially contact angle and contact velocity. These interactions changed the relationship between SLR and the measure from a negative to a positive relationship in some cases.

Discussion

We found evidence of short latency responses (SLR) present in all three muscles, at ~50 ms for FDB and AH and ~40 ms for SOL. For FDB and AH, the SLR was only consistently measured in 6 and 7 of the participants respectively. For these participants, the SLR was present in most conditions, even in normal stepping without reduced visual feedback (Fig. 1B). This is the first time these reflexes have been measured in the muscles of the foot during stepping. Linear models based on measurements of force and motion of joints and muscles alone may not be sufficient for understanding them. For example, the type of step (level, compliant, up, down) had a significant effect on the SLR for all three muscles. Additionally, we found that as the quality of information about the terrain degraded from expected to unknown to incorrect, that the reflex magnitude of the foot muscles generally decreased. In contrast, reducing visual feedback significantly increased reflex magnitude in SOL. These changes in reflex behaviour do not appear to be controlled entirely by the instantaneous mechanics of the steps as measured by contact forces or landing kinematics. This suggests that measuring reflex behaviour in isolated procedures such as tendon tapping may not be directly transferrable to understanding reflexes in real world tasks.

It is reasonable to hypothesize that reducing sensory information should increase reliance on reflexes in order to compensate. While we found that reducing visual feedback of the environment did increase the magnitude of the SLR of SOL, the same trend did not hold true when the information given to the participant about the type of terrain was absent or incorrect. When there was no prior information about the terrain, or worse yet, that the information of the terrain was biased towards being incorrect, the magnitude of SLR in all muscles decreased. If reflexes are supposed to help stabilize the body in the presence of difficult conditions, why would one of the main potential mechanisms for stabilization have a decrease in magnitude? While the average level of the muscle activity across the entire step increased when stepping onto unknown or unexpected surfaces, it is perhaps counter-intuitive that the short latency reflex response decreased. The observation that the reflex gain decreased in these more difficult scenarios is similar to observations from Rietdyk et al (22). They found that reflex activity of rectus femoris increased when participants were tripped while holding onto handrails for support, compared to trips in which they did not hold the handrails. Since in our experiment we observed increases in reflexes when visual information was removed, and decreases in reflexes when information about expected contact timing was removed or was incorrect, it suggests that the benefit of the SLR depends on the participant accurately estimating when their foot will hit the ground. When a person's predictive model of contact timing is unreliable or incorrect, it appears that the SLR magnitude is reduced and therefore longer-latency contractions must play a larger role in achieving stability for the body.

We observed generally weak relationships between mechanics and the SLR of the three muscles (Fig. 6). Of particular note, the ankle was significantly more plantar flexed for downwards steps than upwards steps (Fig. 5), which could influence reflexes in a nonlinear manner even though the linear model between reflex and contact angle showed only weak relationships. And while the foot and ankle are often thought to work in a very similar fashion, we found that the SLR of the two foot muscles showed opposite trends to SOL when stepping downwards versus upwards (Fig. 3B). This difference could also be in part explained by ankle angle at contact, since the foot experiences a larger load at contact in a more plantar flexed position when stepping downwards. However it could also be explained by other mechanical factors, such as the state of the contralateral limb which has been shown to have an effect on reflex activity (23,24) and in general would be expected to play an important role in stabilizing the body. Nevertheless, even after accounting for the relationship between mechanical measurements and the SLR (Fig. 4B), there still exists significant effects on the reflex related to the participants' expectation. Even though it is possible that these effects of expectation could in principle be explained by dynamics unmeasured in the present study, characterizing these reflexes through the concept of expectation may still be beneficial, since it is generally difficult to measure the mechanical state of muscles directly, particularly for many muscles simultaneously.

The observed latencies of the SLR for the three muscles are in rough accordance with previous literature. For comparison, Schieppati et al. found that the FDB SLR and SOL SLR were between 56 - 61 ms and 44 – 47 ms respectively, depending on the condition. While we measured slightly faster onset latencies (approximately 50 ms and 42 ms for FDB and SOL), the differences could be explained by the fact that the types of perturbations in each experiment are quite different. In their experiment, the start of their platform rotation may be slightly earlier than the physiological detection of the perturbation, which would increase the apparent measured latency of the reflex. Also, as seen in their experiment, the tilt of the platform had a significant effect on latency. Since in the present study the foot often hits the ground at a non-neutral angle, it should then be expected that the latency of the SLR should also have some dependence on how the body is oriented as it hits the ground. Finally, while there are no previous data on the AH SLR, the fact that its latency is similar to the latency of the FDB SLR increases our confidence in the measurement.

While the experimental paradigm of this study allows us to make inferences about reflexes at a higher level, it comes at the cost of working in a less controlled experimental environment. Although the muscle activity during steps on expected terrain shows what appears to be a SLR (Fig. 2), there is no definite way of discounting the effect of planned activations that occur at about the same time. However, in our experiment the actual timing of when the foot would hit the ground was not known to the participant in many conditions, and yet the early bursts of activation remained consistent. This suggests that these bursts of activity must be at least in part be a reflex triggered from contact with the ground. This logic is similar to an experiment in which contact timing was altered with an adjustable platform in hopping which also found that the early burst was dependent on contact timing (25). This is not to say there is no input to this reflex from higher in the nervous system as they also found by inhibiting the motor cortex with a magnetic stimulus it supressed the reflex (25). As noted previously, our results also showed a suppression of the reflex when information about contact timing was less reliable.

Here we discuss the three specific conditions within our experiment that support the idea that the early bursts of EMG activity after contact are reflexes. Firstly, in the unknown stepping conditions, the exact timing of contact with the ground is also unknown to the participant since they could be stepping up or down, yet there are similar activations during the SLR window (Fig 4). Secondly, during the surprise up step, contact occurs much earlier than expected, and therefore activation during the reflex window would have minimal amounts of planned activation. The EMG activity during the first 150 ms after contact can then be mostly understood as reflex, since the minimum voluntary contraction latency after training in SOL is at least 150 ms (26). Since the patterns of activation during these unexpected steps are similar to an expected upwards step, we are confident that the activations during this window of time are generally reflex based. Lastly, during unexpected down steps in which contact with the terrain was delayed, we found minimal amounts of activation of the three muscles during the first 150 ms after expected contact. These observations suggests that the short latency activation patterns observed are dependent on making contact with the ground, and not voluntarily activated via a predictive model of when ground contact will occur.

It must be noted that for 3 and 4 of the participants (for FDB and AH respectively) we could not identify a consistent SLR. One possibility is that some participants simply do not have an SLR in the foot muscles during stepping and that the SLR identified in other participants plays a minor role or even is of a vestigial nature. However, given the consistency of measurement in the SLR of the SOL and the often synchronized nature of the foot and ankle, we believe that the absences of SLR in some of the participants is due to the shortcomings of the intramuscular EMG technique used in the experiment. In comparison to the surface EMG measurement of SOL, the much smaller electrodes and inter-electrode distance used in the intramuscular foot measurements are likely to measure a much more localized region of the muscle (27). As such, since the SLR was quite small in magnitude (< 20 % of the overall activation level), we may have simply situated the electrodes in motor units not involved in the reflex, even though nearby motor units may have exhibited the SLR. Due to the invasive nature of the technique and limited sample size, additional experimentation is required to understand how the SLR is distributed and behaves across a broader population.

The findings of this study have important implications for understanding how the legs are controlled in real world conditions. It shows that it may be important for prostheses and robots to have some level of reflex control to appropriately respond to variations in terrain. The findings of this experiment suggest that the gain on a fast reflex controller should be set based on a high-level model of terrain and errors in this model in addition to mechanical measurements. For example, these results could suggest it is beneficial to turn up the gain on short latency reflexes of the foot when stepping downwards. While direct measurements of muscle length via ultrasound or force via strain gauges may allow better predictions of how the nervous system controls its muscles, the presented methodology allows the study of muscle activation and reflexes from more readily accessible information such as type of terrain and expectation.

References

1. Hof AL. The ‘extrapolated center of mass’ concept suggests a simple control of balance in walking. Hum Mov Sci. 2008 Feb 1;27(1):112–25.

2. Kuo AD, Donelan JM, Ruina A. Energetic consequences of walking like an inverted pendulum: step-to-step transitions. Exerc Sport Sci Rev. 2005 Apr;33(2):88–97.

3. Ramos OE, Hauser K. Generalizations of the capture point to nonlinear center of mass paths and uneven terrain. In: 2015 IEEE-RAS 15th International Conference on Humanoid Robots (Humanoids). 2015. p. 851–8.

4. Vlutters M, van Asseldonk EHF, van der Kooij H. Center of mass velocity-based predictions in balance recovery following pelvis perturbations during human walking. J Exp Biol. 2016 May 15;219(10):1514.

5. Loram ID, Gawthrop PJ, Lakie M. The frequency of human, manual adjustments in balancing an inverted pendulum is constrained by intrinsic physiological factors. J Physiol. 2006 Nov 15;577(1):417–32.

6. Eng JJ, Winter DA, Patla AE. Strategies for recovery from a trip in early and late swing during human walking. Exp Brain Res. 1994 Dec 1;102(2):339–49.

7. Pijnappels M, Bobbert MF, van Dieën JH. Control of support limb muscles in recovery after tripping in young and older subjects. Exp Brain Res. 2005 Jan 1;160(3):326–33.

8. Schillings AM, Van Wezel BMH, Duysens J. Mechanically induced stumbling during human treadmill walking. J Neurosci Methods. 1996 Jul;67(1):11–7.

9. Fouad K, Bastiaanse CM, Dietz V. Reflex adaptations during treadmill walking with increased body load. Exp Brain Res. 2001 Mar 1;137(2):133–40.

10. Grey MJ, Ladouceur M, Andersen JB, Nielsen JB, Sinkjær T. Group II muscle afferents probably contribute to the medium latency soleus stretch reflex during walking in humans. J Physiol. 2001;534(3):925–33.

11. Phanthanourak AL, Cleworth TW, Adkin AL, Carpenter MG, Tokuno CD. The threat of a support surface translation affects anticipatory postural control. Gait Posture. 2016 Oct 1;50:145–50.

12. Toft E, Sinkjær T, Andreassen S. Mechanical and electromyographic responses to stretch of the human anterior tibial muscle at different levels of contraction. Exp Brain Res. 1989 Jan 1;74(1):213–9.

13. Schieppati M, Nardone A, Siliotto R, Grasso M. Early and late stretch responses of human foot muscles induced by perturbation of stance. Exp Brain Res. 1990 Feb 1;105(3):411–22.

14. Schieppati M, Nardone A. Medium-Latency Stretch Reflexes of Foot and Leg Muscles Analysed by Cooling the Lower Limb in Standing Humans. J Physiol. 1997;503(3):691–8.

15. Kelly LA, Lichtwark G, Cresswell AG. Active regulation of longitudinal arch compression and recoil during walking and running. J R Soc Interface. 2015 Jan 6;12(102):20141076.

16. Fallon JB, Bent LR, McNulty PA, Macefield VG. Evidence for Strong Synaptic Coupling Between Single Tactile Afferents From the Sole of the Foot and Motoneurons Supplying Leg Muscles. J Neurophysiol. 2005 Dec 1;94(6):3795–804.

17. Capaday C, Stein RB. Difference in the amplitude of the human soleus H reflex during walking and running. J Physiol. 1987;392(1):513–22.

18. Simonsen EB, Dyhre-Poulsen P. Amplitude of the human soleus H reflex during walking and running. J Physiol. 1999;515(3):929–39.

19. Tokuno CD, Garland SJ, Carpenter MG, Thorstensson A, Cresswell AG. Sway-dependent modulation of the triceps surae H-reflex during standing. J Appl Physiol. 2008 May 1;104(5):1359–65.

20. Leardini A, Benedetti MG, Berti L, Bettinelli D, Nativo R, Giannini S. Rear-foot, mid-foot and fore-foot motion during the stance phase of gait. Gait Posture. 2007 Mar 1;25(3):453–62.

21. Riddick Ryan, Farris Dominic J., Kelly Luke A. The foot is more than a spring: human foot muscles perform work to adapt to the energetic requirements of locomotion. J R Soc Interface. 2019 Jan 31;16(150):20180680.

22. Rietdyk S, Patla AE. Context-dependent reflex control: some insights into the role of balance. Exp Brain Res. 1998 Feb 1;119(2):251–9.

23. Appelberg B, Johansson H, Sojka P. Fusimotor reflexes in triceps surae muscle elicited by stretch of muscles in the contralateral hind limb of the cat. J Physiol. 1986;373(1):419–41.

24. Collins DF, McIlroy WE, Brooke JD. Contralateral inhibition of soleus H reflexes with different velocities of passive movement of the opposite leg. Brain Res. 1993 Feb 12;603(1):96–101.

25. Zuur AT, Lundbye-Jensen J, Leukel C, Taube W, Grey MJ, Gollhofer A, et al. Contribution of afferent feedback and descending drive to human hopping. J Physiol. 2010;588(5):799–807.

26. Andersen JB, Sinkjaer T. The Stretch Reflex and H-Reflex of the Human Suleus Muscle during Walking. Motor Control. 1999 Apr 1;3(2):151–7.

27. Merletti R, Farina D. Analysis of intramuscular electromyogram signals. Philos Trans R Soc Math Phys Eng Sci. 2009 Jan 28;367(1887):357–68.

	FDB SLR	AH SLR	SOL SLR
Rigid	0.39 ± 0.67	0.26 ± 0.69	0.36 ± 1.00
Compliant	0.61 ± 1.00	0.36 ± 0.77	0.40 ± 0.92
Down	0.88 ± 1.36	0.53 ± 1.21	0.29 ± 1.59
Up	0.10 ± 0.82	0.02 ± 0.83	0.67 ± 1.01

Table 1. Magnitudes of FDB, AH, and SOL Short Latency Response (SLR) across various terrain types with reduced audio-visual feedback. Data were normalized per-subject to the average level of response during the SLR window of each muscle. The level of activation prior to this window is subtracted such that a magnitude of zero would represent the presence of no reflex. A magnitude of 1 represents the average level of activation during the window.

	FDB SLR	AH SLR	SOL SLR
Expected	0.58 ± 1.10	0.44 ± 0.94	0.51 ± 1.01
Unknown	0.37 ± 0.91	0.17 ± 0.81	0.39 ± 1.20
Unexpected	0.52 ± 1.02	0.07 ± 0.95	0.26 ± 1.52

Table 2. Magnitudes of FDB, AH, and SOL Short Latency Response (SLR) across various levels of expectation. Data normalization follows same procedure as data for Table 1.

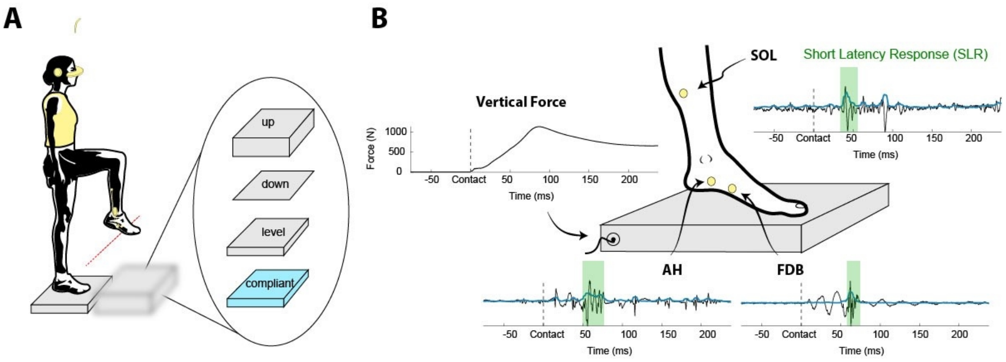

Figure 1. A) Participants wore blinders which blocked vision of the stepping surface while still allowing vision of the walls and ceiling. They stepped onto level, compliant, upwards, and downwards steps. For each step, the type of step was either known and expected, unknown, or unexpected (different than the type of step they expected). B) Intramuscular EMG signals of intrinsic foot muscles flexor digitorum brevis (FDB) and abductor hallucis (AH), as well as surface EMG from the ankle plantar flexor soleus (SOL) as the foot contacts the ground (single step). Dotted vertical line indicates first contact of the foot with the step as detected by in-ground force plate (upper left plot). Raw EMG signal is shown in black (arbitrary units) and the bandpass-filtered, root mean square, signal designed to reduce contact artefact is shown in blue. Reflex responses are observed in all 3 muscles, with the short latency responses highlighted in green.

424x151mm (72 x 72 DPI)

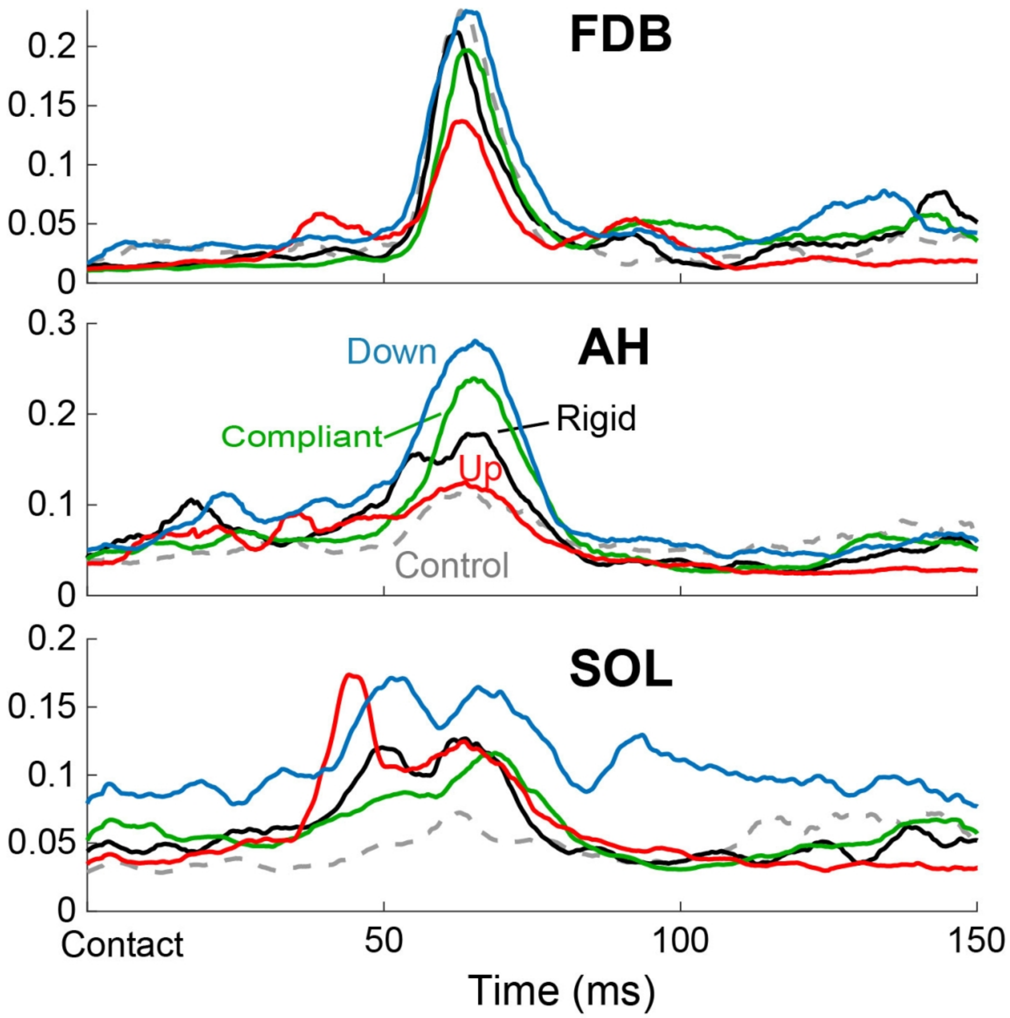

Figure 2. Across-participant average EMG activity (N = 10) of FDB, AH, and SOL during steps with reduced visual feedback for rigid, compliant, down, and up steps (black, green, blue, and red respectively). Average response during normal, level steps with no reduced auditory-visual feedback is shown as the control condition (dashed line). The onset latency of the Short Latency Response (SLR) in FDB and AH is about 50 ms, whereas the onset of the SOL SLR is faster at about 40 ms, with the response dependent on terrain. In comparison to the control, SLR was greatly increased for AH and SOL with reduced audio-visual feedback across most terrains, whereas for FDB it was similar. Signals are scaled to the maximal activation during a 26 cm step upwards.

117x119mm (300 x 300 DPI)

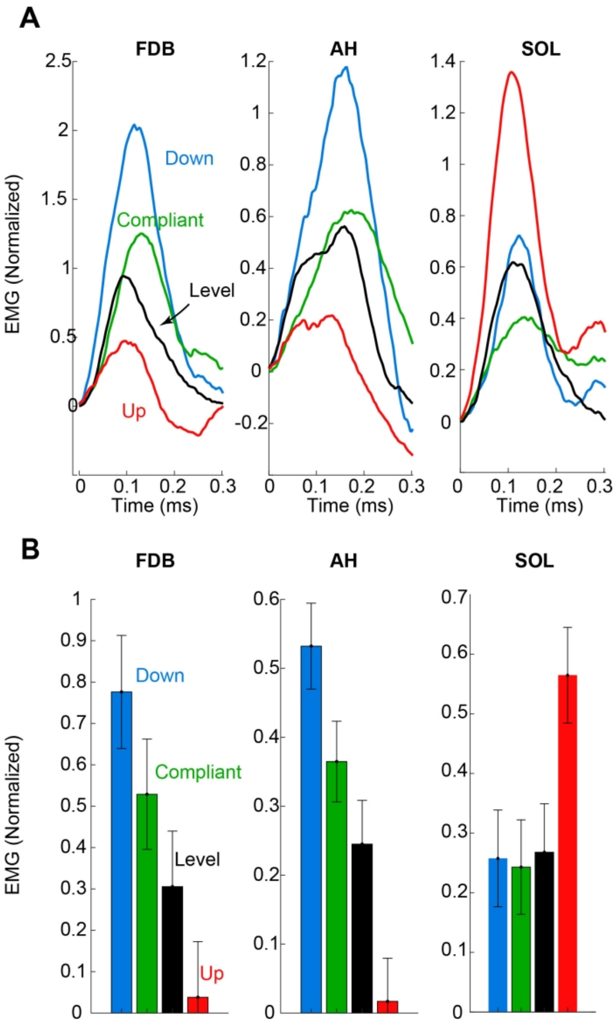

Figure 3. A) A comparison of the normalized short latency responses (SLR) of FDB, AH, and SOL for the three types of rigid terrain (down, level, up) averaged across all participants and levels of expectation. The EMG is scaled to a per-participant average SLR magnitude and the level of background at the start of the reflex is subtracted. Time zero represents the onset of the SLR, which was identified manually for each subject. B) Estimates of the main effect of terrain from the statistical model are shown on normalized SLR magnitude of the same 3 muscles. The results show that the SLR for FDB and AH is larger going from downwards to upwards steps, whereas for SOL this trend is opposite. Error-bars denote the standard error for the corresponding fixed efficient coefficient in the statistical model.

219x224mm (300 x 300 DPI)

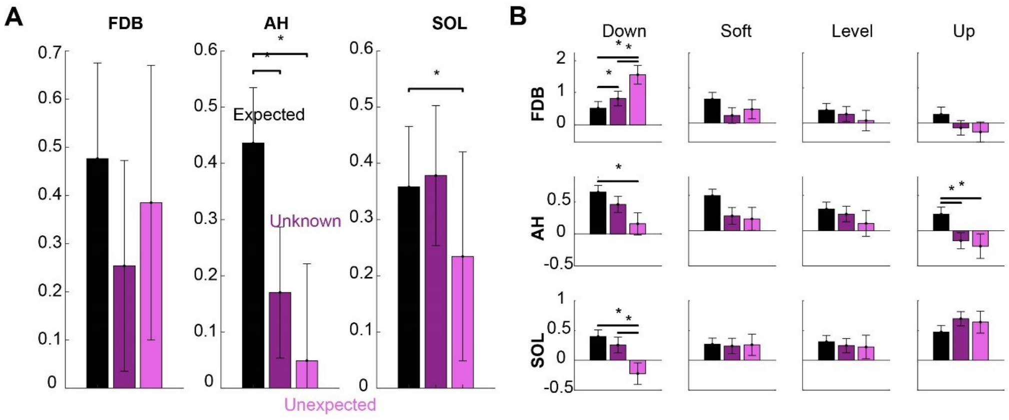

Figure 4. A) Main effects of expectation on the SLR of FDB, AH, and SOL for each terrain using a linear mixed-effects model. Differences between bars within a plot represent differences in the reflex due to the main-effect of expectation across all terrains. The SLR generally decreases when there is no information about the type of terrain (purple) or when the information is incorrect (pink), although for FDB there were no significant differences. Error bars denote the standard error of the model's prediction for these coefficients. Significant differences for all pairwise comparisons between levels of expectation for a given muscle are represented by an asterisk ($p < 0.05$). B) Total effects of expectation (main effect + interaction with terrain) on the SLR of FDB, AH, and SOL for each terrain using a linear mixed-effects model. Holding all mechanical measures constant at their average values, the differences between bars within a plot represent differences in the reflex only due to the type of expectation.

160x66mm (220 x 220 DPI)

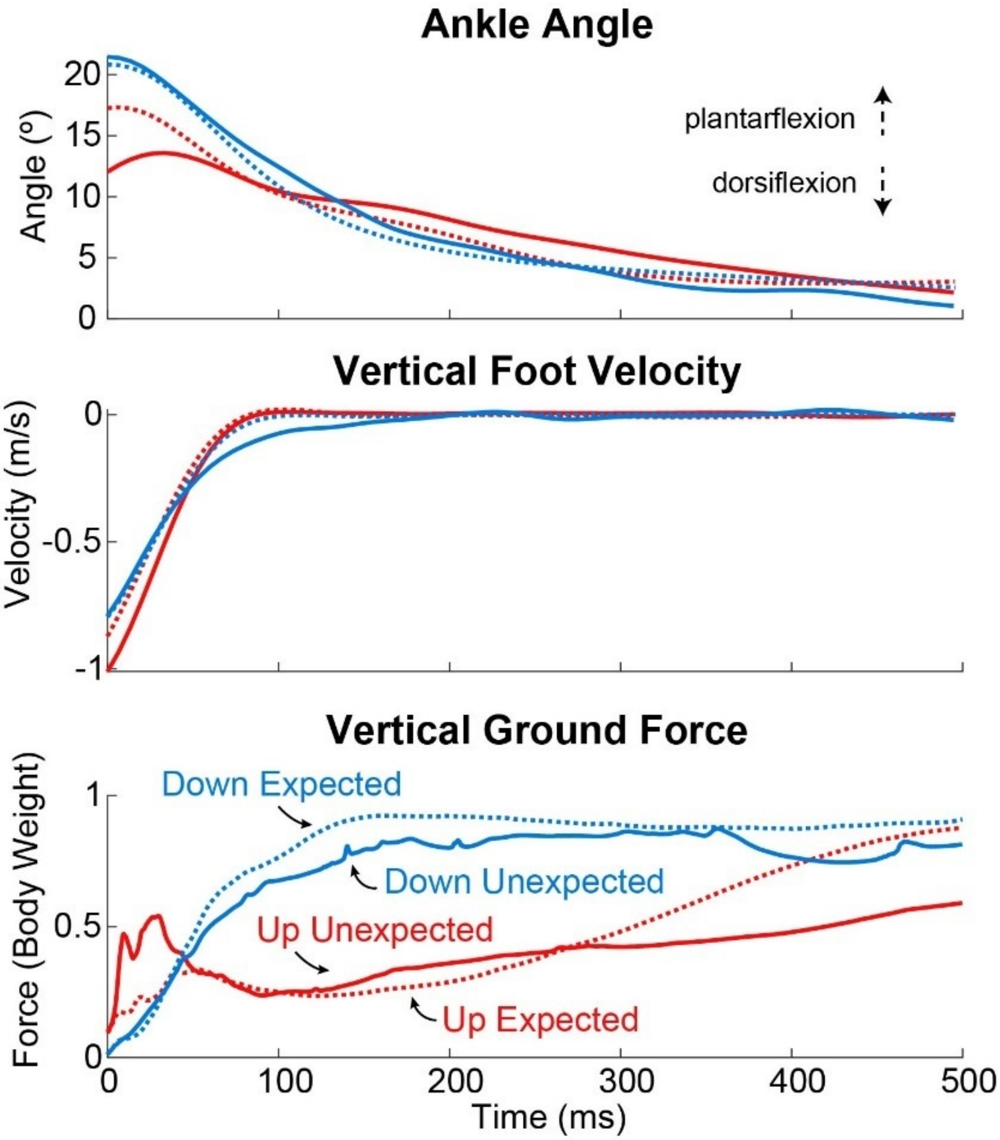

Figure 5. Dynamics of the foot and ankle compared between upwards (red) and downwards (blue) steps, and between expected (solid) and unexpected (dotted) steps. Time zero represents the instant of contact between the foot and the ground. The angle of the ankle at first contact was more dorsiflexed for upwards steps than downwards steps when the terrain was expected (solid red, top plot). However, when the upwards step was unexpected (dotted red), the ankle was significantly more dorsiflexed at first contact, which was accompanied by a large increase in vertical force during the first 50 ms of contact (bottom plot). An unexpected upwards step results in the foot hitting the ground earlier than expected, whereas for an unexpected downward step contact is made later and allows participants to voluntarily compensate sooner relative to contact timing, resulting in smaller differences in dynamics (solid vs dotted blue).

96x109mm (220 x 220 DPI)

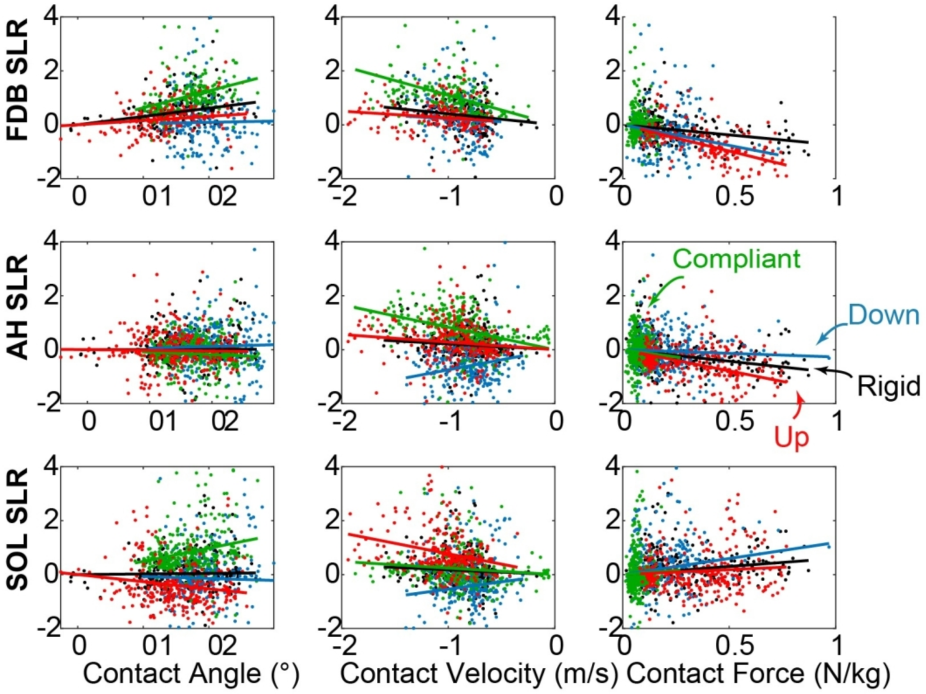

Figure 6. Short Latency Response (SLR) of FDB, AH, and SOL predicted by various mechanical factors for different terrain types within the mixed-effects statistical model. Contact angle is the angle of the ankle at contact (1st column, zero is angle during standing), contact velocity is the vertical velocity of the force at contact (2nd column), and contact force is the peak vertical ground force during the first 50 ms of contact (3rd column). The statistical model showed that these relationships, while often weak or insignificant, depend in some cases on the type of terrain.

148x111mm (300 x 300 DPI)