Title:

The influence of sagittal trunk leans on uneven running mechanics

Running title:

Uneven running with altered trunk postures

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Summary statement:

Modulations in running mechanics induced by changes in trunk sagittal posture are less relevant for accommodating expected substrate height changes. However, the observation of posture- and step-specific adjustments in global and local mechanics appear to be influenced by an anticipation of changes to running pattern, likely reflecting the utilisation of task-dependent strategies during perturbed running.

List of symbols and abbreviations

ATL	anterior trunk lean
BW	body weight
CoM_{TD}, CoM_{TO}	normalised centre of mass at touchdown and at toe-off
F_{z}	peak normalised vertical ground reaction force
GRF	ground reaction force
k_{ankle}	normalised ankle stiffness
k_{knee}	normalised knee stiffness
k_{leg}	dimensionless leg stiffness
l_{TD}, l_{TO}	normalised leg length at touchdown and at toe-off
M_{ankle}	peak normalised ankle extension moment
M_{knee}	peak normalised knee extension moment
PTL	posterior trunk lean
STL	self-selected trunk lean
$\overline{step}$	control step
$\overrightarrow{step}$	approach step
$step\downarrow$	stepdown
t	time
ΔL_{max}	dimensionless amount of maximum leg compression
$\theta_{leg(TD)}$, $\theta_{\mathrm{leg(TO)}}$	leg orientation at touchdown and at toe-off

Abstract

The role of trunk orientation during uneven running is not well understood. This study compares the running mechanics during the approach step to and the stepdown of a 10-cm expected drop, positioned halfway through a 15-m runway, with that of the level step in twelve participants at a speed of 3.5 m/s while maintaining self-selected (17.7±4.2°; mean±S.D.), posterior (1.8±7.4°) and anterior (26.6±5.6°) trunk leans from the vertical. Our findings reveal that the global (i.e., the spring-mass model dynamics and centre-of-mass height) and local (i.e., knee and ankle kinematics and kinetics) biomechanical adjustments during uneven running are specific to the step nature and trunk posture. Unlike the anterior-leaning posture, running with a posterior trunk lean is characterized with increases in leg angle, leg compression, knee flexion angle and moment, resulting in a stiffer knee and a more compliant spring-leg compared with self-selected condition. In the approach versus level step, reductions in the leg length and stiffness through the ankle stiffness yield lower leg force and centre-of-mass position. Contrariwise, significant increases in the leg length, angle and force, and the ankle moment, reflect in a higher centre-of-mass position during the stepdown. Plus, the ankle stiffness significantly decreases, owing to a substantially increased leg compression. Overall, the stepdown appears to be dominated by centre-of-mass height changes, regardless of having a trunk lean. Observed adjustments during uneven running can be attributed to anticipation of changes to running posture and height. These findings highlight the role of trunk posture in human perturbed locomotion relevant for design and development of exoskeleton or humanoid bipedal robots.

Introduction

Running is a low cost and easy accessibility form of physical activity that enhances health and increases longevity (Lee et al., 2017). The popularity of running continues to grow worldwide. In 2019 alone, for instance, millions of recreational participants around the world covered 1.3 billion total miles with an average distance of 4.1 miles per run (Strava, 2019). Running outdoor in a natural environment often entails a frequent negotiation of the terrain irregularities such as variations in ground compliance, slipperiness, or substrate height. In running over changing surfaces, human runners appear to use spring-mass dynamics to help passively stabilise their locomotion (Blickhan, 1989; McMahon and Cheng, 1990). The spring-mass model (Blickhan, 1989) is comprised of a mass-less spring and the body (represented by a point mass), and is simply described by: the leg stiffness (k_{leg}), leg orientation (θ_{TD}) and leg length (l_{TD}) at touchdown (TD) (Blickhan, 1989; McMahon and Cheng, 1990). Albeit the model does not account for the trunk movements, this is a simplistic approach to describe the basic mechanics of human locomotion.

The mechanics of the body's interaction with the ground is influenced by k_{leg}, which is indicative of the average stiffness of the overall musculoskeletal system during the ground contact phase. For running on uneven ground, the θ_{TD} and the k_{leg} appear to be adjusted relative to the nature of changes in the substrate height. This involves a flatter θ_{TD} and a more compliant leg when stepping up, whilst a steeper θ_{TD} and a stiffer leg when stepping down. For the latter situation, runners reduce the k_{leg} in the preceding step, possibly to lower the centre of mass (CoM) in preparation for the safe negotiation of expected changes in substrate height, e.g. a drop (Ernst et al., 2014). As for traversing an obstacle, the k_{leg} decreases in the penultimate step and increases in the final step prior to the barrier in order to accelerate the CoM upward and take-off velocity (Mauroy et al., 2014). Therefore, the fine adjustments of the leg properties not only in the perturbed contact, but also in the preceding contacts (Mauroy et al., 2014; Müller and Blickhan, 2010; Müller et al., 2012a; Müller et al., 2010) potentially enhance the stability in response to ground perturbations.

The global k_{leg} is determined by the combination of the local stiffness of the joints and the leg geometry at touchdown (Farley et al., 1998; Farley and Morgenroth, 1999; Günther and Blickhan, 2002). Adjustments in both joint stiffness and k_{leg} during the stance phase seem to be governed by initial conditions like the l_{TD}, θ_{TD} and landing velocity (Blickhan et al., 2007; Farley et al., 1998; Farley and Morgenroth, 1999; Grimmer et al., 2008; Mauroy et al., 2014), which are previously geared by a swing-leg retraction throughout the second half of the swing phase prior to landing (Seyfarth et al., 2003). Therefore, the muscle pre-activation plays a major role in adjusting the leg posture in preparation for traversing, e.g., an obstacle. While adjustments in the leg mechanics have been widely proven key towards the accommodation of uneven ground, in such context, little is known about the role of trunk posture during uneven running. Given the ~50% contribution of the trunk segment to the total body mass (De Leva, 1996), mechanical demands of the lower limb can be potentially influenced by even slight alterations in the trunk kinematics. On the other hand, the analysis of how the deviations from the cyclic motion (i.e., mechanical adaptations against an expected change in substrate height) are controlled can help further understanding of human locomotion.

There are a limited number of studies that have addressed the influence of an anterior trunk lean on the knee joint energetics (Arendse et al., 2004; Teng and Powers, 2015), knee muscles activity (Teng and Powers, 2016), patellofemoral joint stress (dos Santos et al., 2019; Teng and Powers, 2014), and impact loading (Huang et al., 2019) during running over uniform ground surfaces. As for running along an uneven terrain, one study showed that runners adopt a more crouched posture and larger k_{leg} (Voloshina and Ferris, 2015), possibly to facilitate adaptations to an unfamiliar environment. As recently shown by a study (Shih et al., 2019) on recreational runners, the modifications in the trunk orientation can be achievable with simple postural instructions following one-month training. However, it is unknown how the modification of sagittal plane trunk posture can potentially impact the lower limb operation during uneven running. In walking with increasing trunk flexion angles against changes in substrate height, we previously demonstrated that trunk plays a functional role through extending its angle during stepping down, necessary to control the angular momentum of the whole body (AminiAghdam and Blickhan, 2018; Aminiaghdam et al., 2017a). This contributed to an observed elevated CoM trajectory during the stepdown, presumably to ease the drop negotiation.

An overall objective of our study is providing insight into the contribution of sagittal plane trunk lean to the running mechanics against an expected change in substrate height. Anticipation of changes to running pattern can facilitate the stability and manoeuvrability (Dhawale et al., 2019; Müller et al., 2015; Qiao and Jindrich, 2012). Runners are expected to exhibit step-to-step modulations in local and global running mechanics to account for expected change in the substrate height. We hypothesize that runners would exhibit strategies in the global and local running mechanics that are task-specific, owing to anticipatory nature of the changes to posture and substrate height. Especially, running with a posterior versus anterior trunk lean is expected to be associated with greater compensatory kinematic adjustments, due to a further shift of the GRF's line of action from the knee joint axis of rotation, resulting in augmented changes in the magnitude of lower limb local and global kinetic parameters.

Materials and methods

Participants

A convenience sample of twelve (six females, six males) volunteer recreational runners (mean±standard deviation (S.D.); age = 28.5±5.7 years, body mass = 65.5±8.6 kg, body height = 168.9±6.4 cm) gave written, informed consent and participated in the study. The experimental protocol was approved by the local Ethics Committee of Friedrich-Schiller-University Jena and conducted according to the Declaration of Helsinki.

Experimental design and protocol

Data were collected on a 15-m long instrumented track halfway embedded with two consecutive force plates (1000Hz; 9281B, 9287BA, Kistler, Switzerland) and twelve infrared system cameras (250 Hz; MCU1000, Qualisys, Sweden). Force plates were set at a distance of one step from each other, allowing step lengths ranging from 1.40 to 2.30 m. Kinematics and ground reaction forces (GRF) data were synchronized by using the Kistler's external trigger and BioWare data acquisition software (Kistler Instrument AG, Switzerland). A twelve-body segment model was defined using nineteen reflective markers. The International Society of Biomechanics joint coordinate standards (Wu et al., 2002; Wu et al., 2005) were applied. Trunk angle was defined by the angle sustained by the line connecting the midpoint between the L5–S1 junction (L5) and the seventh cervical spinous process (C7) with respect to the vertical. Following running with self-selected (STL) trunk lean (17.7±4.2°; mean±S.D.), participants were instructed to run with anterior (ATL; 26.6±5.6°) and posterior (PTL; 1.8±7.4°) trunk leans within a range in which they felt comfortable when running across (un)even runways (Fig. 1). Mean trunk flexion angle was calculated as the average sagittal plane trunk posture during the stance phase of running over the level step across all trials and all participants. The order of the ATL and PTL conditions was randomized for each participant. After running on the even, uniform runway, the variable-height force plate at the site of the second contact was visibly lowered by 10-cm and participants ran along the uneven runway (Fig. 1). Practice trials were permitted to allow participants to become familiar with the running velocity and with the desired trunk postures. The participants accomplished ten valid trials per condition in which each force plate was fully struck with a single foot, whilst the first force plate was set to be hit by the left foot.

Parameters of interest

The ensemble average of the following parameters in the sagittal plane during the stance phase across the level, unperturbed step ($\overline{step}$), approach step ($\overrightarrow{step}$) and stepdown ($step\downarrow$) were determined: 1) vertical position of the CoM relative to the ground determined by the body segmental analysis method relative to the laboratory coordinate system (De Leva, 1996; Gard et al., 2004); 2) leg length, defined as the length between the hip and the ball of the foot marker (Fig. 1); 3) leg angle, the angle between the leg and the ground (Fig. 1) calculated with respect to the negative x-axis; 4) knee and ankle joint angles; 5) peak vertical GRF (F_z); 6) maximum leg compression (Dl_{max}) by subtracting the minimum leg length between TD and toe-off (TO) from l_{TD}; 7) leg stiffness (k_{leg}) as the ratio between the F_z and Dl_{max}; 8) net knee and ankle joint moments calculated using a rigid linked segment model, anthropomorphic data, and an inverse dynamics analysis (Zatsiorsky, 1983); 9) knee (k_{knee}) and ankle (k_{ankle}) joint stiffness calculated from the ratio of the change in net muscle moment to joint angular displacement between TD and the instant when the joints reached maximal flexion. A vertical GRF threshold of 0.03 body weight was used to determine the instants of TD and TO at each contact

(Aminiaghdam et al., 2017b). The leg length, Dl_{max} and CoM were normalised to the distance between the greater trochanter marker and the lateral malleoli marker at the instant of TD (l_0). The F_z was normalised to the participant's body weight (N/BW). Each joint moment (Nm/kg) and joint stiffness (Nm/deg/kg) were normalised to the subject's body mass, respectively.

Data processing

For data analysis, we chose all those trials that were distributed in a narrow range of each participant's running steady-state velocity (3.5 m/s). From the calculated mean horizontal velocity of the L5 marker for each of two force plates, we discarded the trials which contained two values differed by more than 5%. Kinetic and kinematic data of all successful trials were analysed using custom written Matlab (Mathworks Inc., MA, USA) code. The raw coordinate data were filtered using a fourth-order low-pass, zero-lag Butterworth filter with 12 Hz cutoff frequency (Aminiaghdam et al., 2017b). Following confirming that the data were normally distributed, a two-way repeated measurements ANOVA was used to examine interactions between *Posture* (STL, ATL and PTL) and *Step* ($\overline{step}$, $\overrightarrow{step}$ and *step*↓) on the parameters of interest (outlined earlier) in SPSS (ver 21.0, IBM® Co., USA). In case of a significant interaction, simple main effects were used to compare between-postures changes across each step as well as between-steps changes for each individual posture using one-way ANOVA and *post-hoc* comparisons with Bonferroni adjustments for multiple comparisons. In case of a non-significant interaction, the main effects of the *Posture* and *Step* were evaluated on each dependent variable of interest. Where Mauchly's test indicated a violation of sphericity, *p*-values and degrees of freedom were corrected using the Greenhouse-Geisser correction factor. Results were expressed as mean±S.D. over all participants and parameters. The statistical significance level of all tests was set to p=0.05.

Results

The data analyzed includes 720 trials with a total of 2160 step cycles. Participants were successful in maintaining their stability (no falls) on every trial while running across the level and uneven track. Table 1 summarizes the kinematic and kinetics parameters (mean±S.D.) of uneven running with altered sagittal plane trunk orientations along with the the main effects of *Step* and *Posture* and their interaction effects. Fig. 2 illustrates ensemble-averaged global and local sagittal plane kinematic waveforms, and Fig. 3 illustrates ensemble-averaged joint moment and vertical GRF waveform of running with three various trunk orientations across $\overline{step}$, $\overrightarrow{step}$ and *step*↓.

Two-way repeated measures ANOVAs indicated *Step*-specific effects of *Posture* on $\theta_{\mathrm{ankle(TD)}}$, ΔL_{max}, $\theta_{ankle\mathrm{(TO)}}$, $\theta_{\mathrm{leg(TO)}}$ and t_{contact} (Table 1). *Post-hoc* comparisons (simple main effects) revealed significant changes in a few of kinematic parameters during the stepdown (*step*↓) as compared to those during the level step ($\overline{step}$) and the approach step ($\overrightarrow{step}$) with no between-posture changes across each step (Table 1). In the *step*↓, the ankle angle demonstrated substantial increases in plantarflexion at TD for all running conditions. Likewise, the maximum leg compression in the *step*↓ significantly increased by ~35%, ~70% and 75% during ATL, STL and PTL postures, respectively compared with those of $\overline{step}$ and $\overrightarrow{step}$ (Table 1). The ankle angle at TO of the *step*↓ increased by ~45% and ~60% during STL and ATL conditions, respectively, compared with that of $\overrightarrow{step}$ (Table 1). Furthermore, the leg became more vertical across all running conditions by demonstrating significant decreases in leg angle (~4.5° during the STL and ATL conditions, and ~7° during the PTL condition), presumably in preparation to accelerate the body CoM for surmounting the drop. The contact time significantly decreased in the *step*↓ compared with the $\overrightarrow{step}$, irrespective to the trunk orientation (Table 1).

Analyses considering the main effect of *Posture* revealed significant alterations in running mechanics due to changes in the sagittal trunk lean angle. Looking at the global leg parameters, the k_{leg} significantly reduced during the PTL condition by 15% compared with the STL condition, and by ~12% compared with the ATL condition (Fig. 4A), whilst F_z remained unchanged. However, the k_{leg} did not significantly differ during the ATL running compared with the STL condition (Fig. 4A). In addition, the PTL running was characterized with a slightly more vertical leg at TD as compared to the ATL condition (Fig. 4D). As for the local leg parameters, the knee flexion angle at TD was slightly higher in both PTL and ATL conditions when compared to the STL condition (Fig. 4E). The peak knee extension moment (M_{knee}) was significantly lower by ~7% during the ATL condition, and was significantly higher by ~15% during the PTL condition when compared to the STL condition (Fig. 4C). As compared to the STL condition, the knee stiffness (k_{knee}) were significantly higher by ~13% during the PTL condition, whereas it remained unchanged during the ATL condition (Fig. 4B). At TO, the knee flexion angle was greater by ~11% during the PTL condition when compared to the STL condition (Fig. 4F).

Furthermore, analyses considering the main effect of *Step* revealed significant changes in kinetic and kinematic parameters of running during the $\overrightarrow{step}$ and *step*↓ when compared with the $\overline{step}$. In the $\overrightarrow{step}$, runners reduced their k_{leg} by ~24% (Fig. 5G), resulting in a ~13% decrease in the magnitude of F_z (Fig. 5H). At the ankle level, k_{ankle} (Fig. 5I) and M_{ankle} (Fig. 5J) were reduced by ~24% and 12%, respectively. At the end of the $\overrightarrow{step}$, runners lowered their CoM by ~6% (Fig. 5B) using an increased knee flexion (Fig. 5F). This was associated with a ~2% significant decrease in the leg length (Fig. 5D). At TD of the *step*↓, landing involved an increased leg length (Fig. 5C) and a more extended knee joint angle (Fig. 5E), leading to a ~5% higher vertical position of the CoM (Fig. 5A). As compared to the $\overline{step}$, the M_{ankle} increased by ~40% (Fig. 5J), while the k_{ankle} demonstrated a ~36% decrease (Fig. 5I). The k_{leg} reduced (Fig. 5G), despite of ~27% increase in F_z (Fig. 5H). However, the difference did not reach significance. This was mainly due to a much greater increase in the ΔL_{max} (Table 1) across all running conditions. At the end of the stance, the vertical position of the CoM was enhanced by ~4% (Fig. 5B), possibly in preparation to surmount the drop.

Table 1. Kinematics and kinetics of uneven running with altered sagittal plane trunk orientations (mean±S.D).

	Reference mean – trunk lean mean	p-value/F-value

							ES	
Variable	Reference mean	Step	Self-selected	Anterior	Posterior	Step	Posture	Interaction
CoM_{TD} (l_0)	0.99±0.04	$\overline{step}$		0.02±0.04	0.02±0.06	0.001/7.42	0.26/1.41	0.21/1.53
		$\overrightarrow{step}$	0.05±0.09	0.05±0.07	0.03±0.08	0.41	0.11	0.12
		$step\downarrow$	-0.04±0.04	-0.03±0.03	-0.02±0.05			
CoM_{TO} (l_0)	1.01±0.04	$\overline{step}$		0.02±0.04	0.02±0.06	0.001/9.61	0.18/1.83	0.32/1.21
		$\overrightarrow{step}$	0.08±0.09	0.09±0.07	0.06±0.07	0.46	0.14	0.09
		$step\downarrow$	-0.04±0.05	-0.02±0.03	-0.02±0.05			
l_{TD} (l_0)	0.93±0.02	$\overline{step}$		0.01±0.02	0.01±0.02	0.001/25.7	0.65/0.22	0.27/1.36
		$\overrightarrow{step}$	0.01±0.01	0.01±0.02	0.01±0.05	0.71	0.02	0.11
		$step\downarrow$	-0.06±0.03	-0.05±0.03	-0.06±0.06			
l_{TO} (l_0)	1.01±0.02	$\overline{step}$		0.01±0.02	-0.01±0.01	0.001/6.68	0.53/0.43	0.39/0.88
		$\overrightarrow{step}$	0.01±0.01	0.02±0.02	0.03±0.05	0.37	0.03	0.07
		$step\downarrow$	-0.01±0.01	-0.01±0.02	0.01±0.05			
$\theta_{leg(TD)}$ (°)	65.9±2.45	$\overline{step}$		0.37±3.43	-0.97±3.51	0.001/8.74	0.001/9.22	0.35/1.13
		$\overrightarrow{step}$	0.05±2.94	0.88±3.95	-1.71±3.61	0.44	0.45	0.09
		$step\downarrow$	-2.65±1.47	-2.13±1.83	-3.85±1.66			
$\theta_{leg(TO)}$ (°)	115±2.99	$\overline{step}$		-1.11±2.91	-2.51±2.96	0.001/97.7	0.001/8.06	0.001/12.3
		$\overrightarrow{step}$	-3.51±2.53	-3.97±2.61	-5.11±2.66	0.89	0.42	0.52
		$step\downarrow$	4.56±2.61^{a,b}	3.31±2.46^{a,b}	4.51±2.24^{a,b}			
$\theta_{knee(TD)}$ (°)	24.1±4.88	$\overline{step}$		-2.03±3.74	-4.81±5.21	0.001/15.5	0.001/34.1	0.06/3.11
		$\overrightarrow{step}$	-1.41±4.62	-2.27±4.83	-5.69±6.06	0.58	0.75	0.22
		$step\downarrow$	3.91±3.97	1.83±5.11	2.63±4.21			
$\theta_{knee(TO)}$ (°)	17.9±5.32	$\overline{step}$		0.26±5.98	-1.22±5.08	0.001/62.7	0.001/5.85	0.14/1.81
		$\overrightarrow{step}$	-7.75±4.01	-9.16±5.61	-10.5±4.03	0.85	0.34	0.14
		$step\downarrow$	2.11±4.66	0.88±5.69	-0.64±4.84			
$\theta_{ankle(TD)}$ (°)	4.71±7.42	$\overline{step}$		0.11±7.12	1.56±7.21	0.001/84.5	0.03/4.05	0.001/7.72
		$\overrightarrow{step}$	1.65±5.41	0.87±6.54	1.21±7.56	0.88	0.26	0.41
		$step\downarrow$	-24.9±9.1^{a,b}	-23.5±11.7^{a,b}	-31.9±5.7^{a,b}			
$\theta_{ankle\ (TO)}$ (°)	30.7±6.19	$\overline{step}$		0.74±6.51	-2.18±7.39	0.001/21.1	0.002/12.1	0.001/4.62
		$\overrightarrow{step}$	7.07±4.26	9.06±4.92	3.24±7.02	0.65	0.52	0.29
		$step\downarrow$	-3.77±6.37^{b}	-3.71±6.54^{b}	-5.07±6.91			
F_z (BW)	2.61±0.22	$\overline{step}$		0.06±0.29	0.08±0.31	0.001/266	0.18/1.85	0.32/1.21
		$\overrightarrow{step}$	0.35±0.21	0.39±0.21	0.39±0.26	0.96	0.14	0.09
		$step\downarrow$	-0.68±0.29	-0.62±0.29	-0.64±0.32			
k_{leg} (BW/l_0)	36.9±10.8	$\overline{step}$		2.07±11.8	5.34±11.1	0.04/4.74	0.001/17.6	0.15/1.77
		$\overrightarrow{step}$	9.06±9.03	10.9±7.47	12.3±9.44	0.31	0.61	0.13
		$step\downarrow$	8.62±9.68	8.19±9.42	14.1±4.41			
ΔL_{max} (l_0)	0.07±0.01	$\overline{step}$		-0.01±0.01	-0.01±0.01	0.001/22.4	0.001/28.6	0.01/4.01
		$\overrightarrow{step}$	-0.01±0.02	-0.01±0.02	-0.02±0.02	0.67	0.72	0.26
		$step\downarrow$	-0.05±0.02^{a,b}	-0.04±0.02^{a,b}	-0.07±0.02^{a,b}			
M_{knee} (Nm/kg)	2.18±0.52	$\overline{step}$		0.16±0.51	-0.31±0.49	0.07/2.97	0.001/35.3	0.71/0.38
		$\overrightarrow{step}$	0.13±0.44	0.22±0.48	-0.23±0.41	0.21	0.76	0.03
		$step\downarrow$	-0.12±0.33	0.03±0.41	-0.42±0.44			
k_{knee} (Nm/deg/kg)	0.11±0.02	$\overline{step}$		-0.01±0.03	-0.01±0.03	0.12/2.25	0.001/6.51	0.07/2.29
		$\overrightarrow{step}$	0.01±0.02	0.01±0.03	-0.01±0.02	0.17	0.37	0.17
		$step\downarrow$	-0.01±0.02	-0.01±0.02	-0.01±0.02			
M_{ankle} (Nm/kg)	3.26±0.52	$\overline{step}$		0.05±0.57	-0.01±0.58	0.001/73.1	0.09/2.63	0.46/0.79
		$\overrightarrow{step}$	0.41±0.42	0.46±0.43	0.33±0.45	0.86	0.19	0.06
		$step\downarrow$	-1.33±0.85	-1.32±0.86	-1.34±0.89			
k_{ankle} (Nm/deg/kg)	0.22±0.11	$\overline{step}$		0.01±0.11	0.01±0.11	0.04/4.56	0.04/3.73	0.16/1.95
						0.29	0.25	0.15
		$\overrightarrow{step}$	0.05±0.05	0.06±0.05	0.05±0.07			
		$step\downarrow$	0.07±0.11	0.07±0.08	0.11±0.04			
$t_{contact}$ (s)	0.23±0.01	$\overline{step}$		0.01±0.01	-0.02±0.02	0.001/51.6	0.001/9.33	0.01/5.11
		$\overrightarrow{step}$	-0.01±0.02	-0.01±0.02	-0.03±0.02	0.82	0.45	0.31
		$step\downarrow$	0.02±0.01^{b}	0.02±0.01^{b}	0.01±0.02^{a,b}			

The last three columns outline the p-values, F-value, and effect size (ES, partial eta-squared) pertaining to the main effects of *Step* and *Posture* as well as *Step*×*Posture* interaction, respectively. In case of an interaction effect, significant differences (simple main effect) from $\overline{step}$ and $step\downarrow$ across each running posture are indicated by 'a' and 'b', respectively ($p<0.05$). The leg length (l), maximal leg compression (Dl_{max}) and centre of mass *(CoM)* were normalised to the distance between the greater trochanter marker and the lateral malleoli marker at the instant of TD (l_0). $\overline{step}$, control step; $\overrightarrow{step}$, approach step; $step\downarrow$, stepdown; *k*, stiffness; θ, angle*; M*, peak net joint moment; F_z; peak vertical ground reaction force; *t*, time; TD, touchdown; TO, toe-off.

Discussion

An overall objective of our study was providing insight into how changing the sagittal plane trunk orientation influences the running mechanics against an expected substrate change. It was postulated that runners would exhibit strategies in the global and local running mechanics that are task-specific, facilitated by anticipatory nature of changes to posture and substrate height. This was confirmed by the findings of the present study, as running with a posterior versus anterior trunk lean was associated with greater compensatory kinematic adjustments resulting in augmented changes in the magnitude of lower limb local and global kinetic parameters. On the other hand, runners exhibited step-to-step modulations in local and global running mechanics to account for expected change in the substrate height. Interestingly, the control of body motion for the accommodation of expected substrate height changes appears not to be affected by trunk orientation in running humans.

Posture-related adjustments in running mechanics

When considering the main effect of *Posture* (averaging across the steps), we observe the posture-specific adjustments in locomotor behaviour. These results are consistent with those of our previous studies analyzing trunk-flexed walking (with the same experimental setup), which revealed that leaning trunk forward up to 30° does not lead to between-steps changes in the kinematic (Aminiaghdam et al., 2017a) and the kinetics of the braking phase of the stance (Aminiaghdam, 2017) in able-bodied gait. Running with ATL is characterized with a slightly more crouched configuration than that of the STL condition, induced possibly by a forward shift of the CoM. Further, along with an increased knee flexion at TD (Fig. 4E), the knee moment reduced significantly by ~7% (Fig. 4C), when compared with the STL condition. This finding is in agreement with a previous study by Teng and Powers (2014) showing a ~7% decrease in the knee extensor moment at the time of peak patellofemoral joint stress during level running when increasing sagittal trunk lean by ~7° from a self-selected trunk posture (Teng and Powers, 2014). By contrast, the study by (dos Santos et al., 2019) revealed no significant decrease in the peak knee extensor moment (1.55±0.32 versus 1.62±0.36 Nm/kg) when runners increase the trunk inclination angle (by ~9°) from their self-selected trunk posture. Moreover, an anterior lean of the trunk does not induce significant changes in the joint stiffness across the knee and ankle joints and thus the leg stiffness tends to remain virtually the same as for the STL running (Fig. 4A, Table 1). Likewise, the ankle moment appears not to be influenced by an alteration in the trunk orientation. These results match those observed in an earlier study (Teng and Powers, 2014) that an increase of the sagittal plane trunk inclination redistributes the energetics across the hip and knee without imposing the biomechanical demands on the ankle plantar-flexor muscles during level running.

On the other hand, a posterior lean of the trunk yields increases in the knee flexion at TD (3.4°) and TO (2.2°) as well as in the knee moment (~15%) when compared with STL running (Fig. 4). An increased extension moment implies a higher muscle activation of the knee extensors, leading to a higher k_{knee} (Fig. 4B). Teng and Powers (2014) reported a ~5% increase in the peak knee extensor moment when running with a more extended sagittal trunk lean (Teng and Powers, 2014). A lower extent of the decrease in the extension moment compared with that of our study can be explained by the fact that the degree of a posterior lean in our study was profoundly greater. This, in turn, induces more compensatory kinematic adaptations in the leg posture. In another similar study, Teng and Powers (2016) demonstrated that weak hip-extensor muscles prompt adopting a more upright trunk posture during running (Teng and Powers, 2016). Such postural adaptation appears to reduce the demand on the hip extensors; however, at the cost of imposing higher demands on the knee extensors. Moving trunk backward shifts the line of action of GRF away from the axis of rotation at the knee joint, and therefore the larger moment arms result in greater net external moments. This, in turn, increases the angular displacement at the knee joint, and subsequently the compression of the spring-leg. Runners demonstrate adaptations in the local stiffness by decreasing k_{ankle} by ~10% and increasing k_{knee} by ~13% (Fig. 4B). The local regulation of the joint stiffness coupled with the combination of an increased leg compression and a decreased F_z yields a reduction in the k_{leg} for the PTL condition (Fig. 4B). Consequently, the sagittal plane trunk posture has an influence on biomechanical demands (global and local) of the lower limb during running; however, independent of changes in the substrate height.

Step-related adjustments in running mechanics

It appears that the anticipation of substrate height change governs the control scheme of running. Runners exhibit substantial adjustments in body mechanics, namely feed-forward strategies to accommodate substrate height changes while adopting various trunk orientations. This includes changes in the spring-mass properties (i.e., l_{TD}, $\theta_{\mathrm{leg(TD)}}$ and k_{leg}) and local mechanics across knee and ankle joints. The properties of the spring-mass model are modulated with an attenuation bias in the preceding contact when coping with drops and downward steps, and with an augmentation bias in the lowered level (Müller et al., 2012a). These adjustments are utilized to smooth the CoM kinematics (Blickhan et al., 2007). In our study, the analysis of the main effect of *Step* reveals the global and local adjustments in the locomotor behaviour specific to the step nature during uneven running. In the approach step, runners demonstrate a ~24% reduction in the leg stiffness in preparation to step down when compared with the control step (Fig. 5G). Likewise, the ankle stiffness reduces by ~24% (Fig. 5I). As a result, the global leg stiffness appears to be mainly adjusted locally at the level of the ankle joint. These modulations in local and global stiffness yield changes in the magnitude of the leg force, which decreased by ~13% (Fig. 5H). Given the joint stiffness also depends on the activation level of the muscles acting on the joint (Müller et al., 2010; Müller et al., 2012b), an attenuation of the global leg stiffness may be due to a decreased muscle activation, and a more flexed leg configuration. Here, runners demonstrate a 12% reduction in the ankle moment (Fig. 5J). On the other hand, as they approach the end of the stance, the knee flexion (Figs 2K and 5F) increases so that the leg length (Figs 2H and 5D) decreases by ~2% and subsequently the CoM is lowered by ~6% at TO (Figs 2E and 5B). As for an obstacle negotiation, the k_{leg} decreases in the penultimate step and then increase in the final step prior to a 0.65 m-high barrier in an attempt to enhance the movement of the CoM while leaping the obstacle (Mauroy et al., 2013). It seems that the runners take resort to the spring-leg stiffness attenuation on the obstacle or upward step, but also in the preparatory step(s) prior to a drop or downward step (Müller et al., 2012a). The findings observed in our study mirror those of the previous studies that have reported decreases in the stiffness of the ankle joint proportional with the elevation of the next step during running (Grimmer et al., 2008; Mauroy et al., 2013; Mauroy et al., 2014; Müller et al., 2012a; Müller et al., 2010). The authors of these studies (Müller et al., 2012a; Müller et al., 2010) suggested that the modulation of the leg stiffness appears to be actively achieved.

In the stepdown (drop), the perturbed leg lands in a more vertical orientation with more extended knee and ankle joint positions, resulting in an elongated leg (Figs 2I and 5C). Similarly, (Müller et al., 2012a) demonstrated increases in the leg angle and the leg length when accommodating (un)expected drops and expected steps during running. However, they noted that the negotiation of the unexpected versus expected perturbations is associated with greater leg adjustments at TD, due possibly to the lack of feed-forward control of motion prior to the perturbation. It seems that the modulation of the TD leg angle plays a crucial role in dynamics of stance following the perturbation. Such mechanical behavior appears to be also exploited by small birds as (Daley and Biewener, 2006) noted that the extended limb posture at TD of an unexpected drop accounts for 80% of their stance limb loading. Furthermore, given a relatively straight architecture of the human leg, the longer leg at TD is achieved greatly by the ankle plantar flexion (Müller and Blickhan, 2010; Müller et al., 2012a) and slightly by the knee extension. The coupling of these adjustments in the perturbed leg with a posterior motion of the trunk across all running conditions (Fig. 2C) slightly enhances the vertical position of the CoM at TD (Fig. 2F). (Seethapathi and Srinivasan, 2019) showed that runners adjust the leg force over the whole stance and foot placement in a manner to recover CoM trajectory back to steady state as they run. They further demonstrated the application of these control strategies for locomotion in simulation, showing the robustness of a simple biped against larger discrete perturbations or constant noise-like perturbations. Here, the peak leg force increased by 27% in the perturbed step whilst decreased by 13% in the preparatory step when compared with the level step. In agreement with (Seethapathi and Srinivasan, 2019), running human exhibit adjustments in the leg loading and the CoM motion in the approach step and the stepdown (Figs 2D-F and 5A-B) to facilitate the traverse of expected substrate height changes.

In locomotion, the foot segment enables a forward propulsion by serving as the link between the ground and the kinetic chain of the lower limb and trunk. Compared with other lower limb moments and forces, the primary contributor to the vertical GRF is the ankle moment (Chen, 2006). The ankle extensor moment exhibits a ~40% increase (Figs 3F and 5J), due potentially to a higher activation of the plantar-flexor muscles, which stems particularly from an increased pre-activation of the M. gastrocnemius medialis (Müller et al., 2015). Our findings accord with those of previous studies in terms of modulation of the leg stiffness (Müller and Blickhan, 2010; Müller et al., 2012a) that have shown stepping down off an elevation (e.g., single drop of different elevations) is not associated with changes in the leg stiffness. This can be due to a great extent of the leg compression displayed across all running conditions. On the other hand, the duration of the ground contact during the lowered (perturbed) step is significantly shorter than during the level steps, irrespective to the running postures (Table 1). As approaching to the end of the drop, the CoM raises (by ~4%) through a greater plantar-flexion and a more vertical leg orientation (regardless of trunk posture), possibly in preparation to surmount the drop

(Figs 2F and 5B). The stepdown therefore appears to be dominated by CoM height changes, regardless of having a trunk lean.

When interpreting the findings of this study, several limitations need to be acknowledged. First, the runway utilized in the present may not fully resemble running outdoors, which represents a wide range of (un)expected and/or varied magnitudes of surface perturbations, and thus possibly elicit different locomotor outputs. Secondly, the sample size of the study might be relatively small to reach a convincing conclusion. Thirdly, our results also do not exclude the possibility of being influenced by using an overly conservative Bonferroni correction for multiple comparisons which preserves type I error of the global null hypothesis. In overall, the step-to-step adjustments in various running mechanical parameters exhibit no dependency on the sagittal trunk orientation. It is most likely that the observed adjustments to be influenced by feed-forward control as both postural and environmental changes were imposed experimentally in an anticipatory fashion. The reliance of stability of running's sagittal-plane dynamics on anticipatory strategies on rough terrains (i.e., slope and height variations) has also been validated by a simulation study (Dhawale et al., 2019). In agreement with a previous study (Qiao and Jindrich, 2012), our findings demonstrate that the human locomotion employs task-level strategies to account for either or both external and internal perturbations. Characterizing the mechanical behaviour governed by feed-forward control strategies could help better understanding of sensory-motor mechanisms underlying the stabilisation of human perturbed locomotion. By illustrating adjustments in the global leg-spring stiffness specific to alterations in the posture and ground configurations, our findings further support the notion of dependency of the stability of the spring-mass running through the global leg stiffness on the local joint elasticities, and on the leg geometry at TD (Arampatzis et al., 1999; Farley et al., 1998; Farley and Morgenroth, 1999; Günther and Blickhan, 2002; Mauroy et al., 2014). These findings may improve understanding of the role of posture in human perturbed locomotion relevant for design and development of exoskeleton or humanoid bipedal robots.

Competing interests

The authors declare no competing or financial interests.

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Data availability

Data are available from the authors on request.

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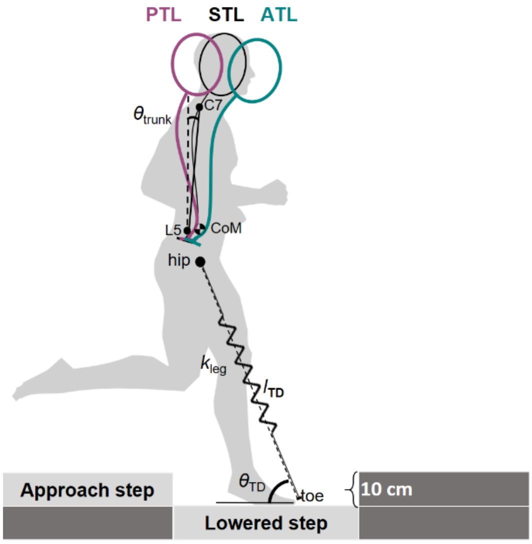

Fig. 1. **Schematic illustration of drop-negotiation during running with altered trunk postures.** The illustration depicts the definition of the trunk angle (θ_{trunk}) and the spring–mass model properties as used in this study. A visible drop was created by lowering the the second force plate (stepdown; step↓) by 10 cm. Approach step ($\overrightarrow{step}$); STL, self-selected trunk lean; ATL, anterior trunk lean; PTL, posterior trunk lean; CoM, centre of mass; k_{leg}, leg stiffness; l_{TD}; leg length at touchdown; θ_{TD}, leg angle at touchdown.

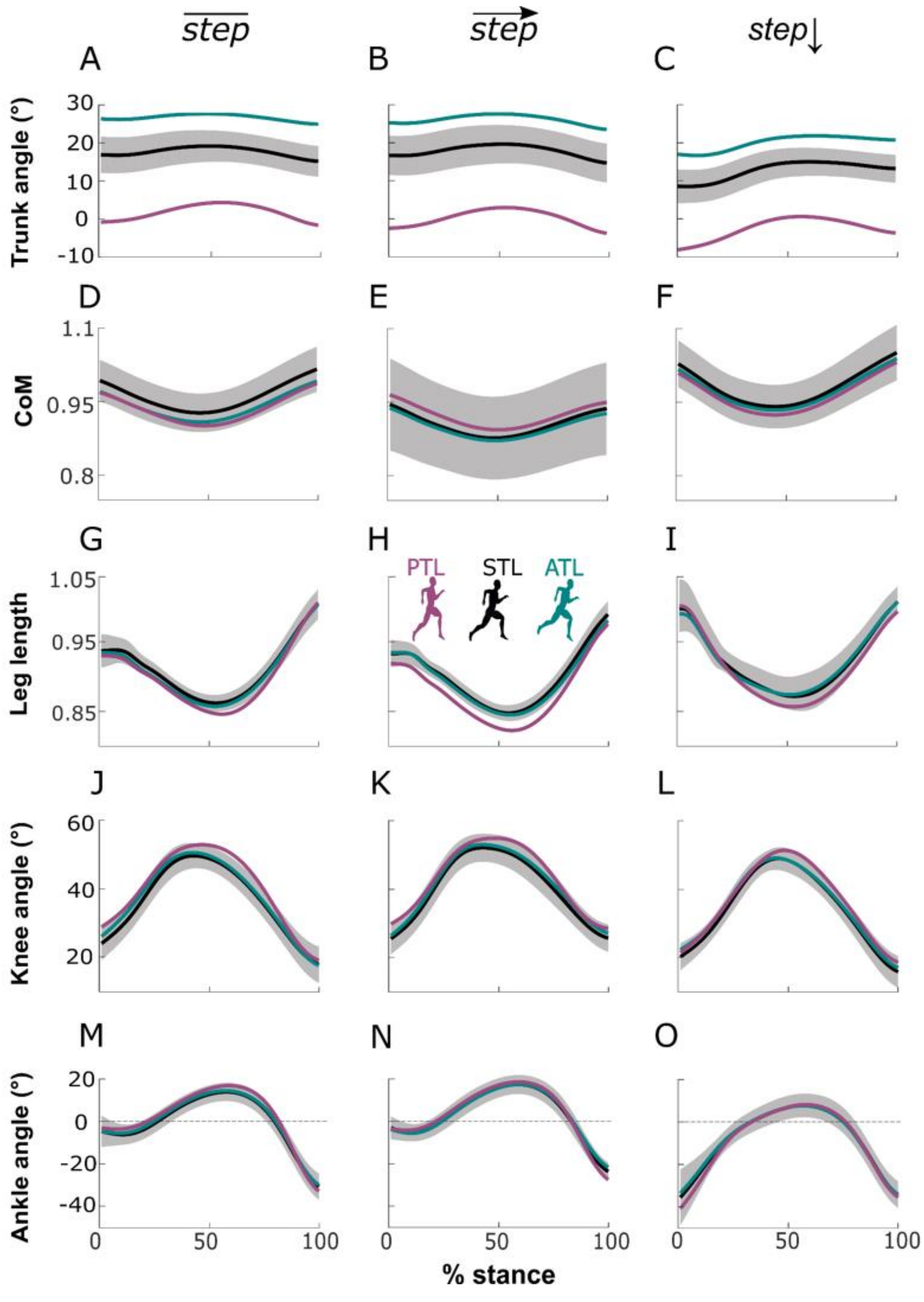

Fig. 2. Global and local sagittal plane kinematic waveforms. Shown are ensemble-averaged trunk angular displacement (A:C), normalized body centre of mass (D:F), normalized leg length (G:I), knee angular displacement (J:L), and ankle angular displacement (M:O) for STL (self-selected trunk lean), ATL (anterior trunk lean), and PTL (posterior trunk lean) running conditions across the stance phase of $\overline{step}$ (control step), step↓ (approach step) and step↓(stepdown) (N=12). The contact time is normalized to 100%. The grey shaded area represents the corresponding S.D for the STL condition.

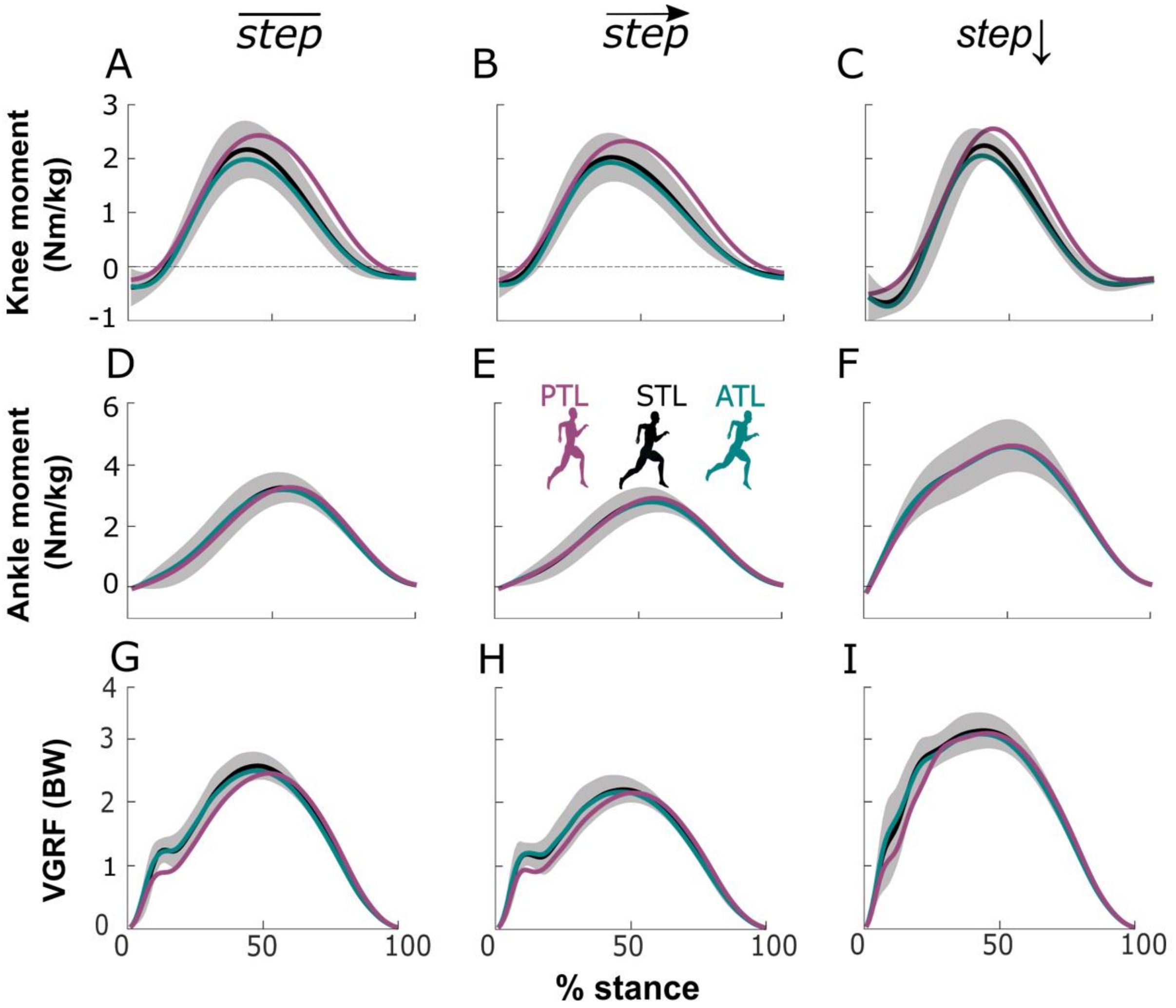

Fig. 3. Joint moment and vertical ground reaction force (GRF) waveforms. Shown are ensemble-averaged normalized knee extensor moments (A:C), ankle extensor moments (D:F), and normalized vertical GRF (G:I) for STL (self-selected trunk lean), ATL (anterior trunk lean), and PTL (posterior trunk lean) running conditions across the stance phase of $\overline{step}$ (control step), step↓ (approach step) and step↓(stepdown) (N=12). The contact time is normalized to 100%. The grey shaded area represents the corresponding S.D for the STL condition.

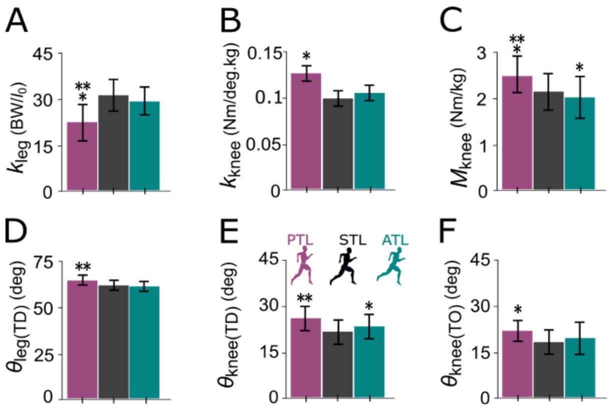

Fig. 4. Main effects of *Posture*. The main effect of *Posture* (mean ± S.D.) on variables for whom two-way repeated-measurement ANOVAs revealed no *Step* × *Posture* interaction (N=12). Significant differences from STL and ATL are indicated by '*' and '**', respectively (p<0.05; Bonferroni post-hoc test). Error bars denote standard deviation. STL, self-selected trunk lean; ATL, anterior trunk lean; PTL, posterior trunk lean; *k*, stiffness; *M*, peak net joint moment; *θ*, angle; TD, touchdown; TO, toe-off.

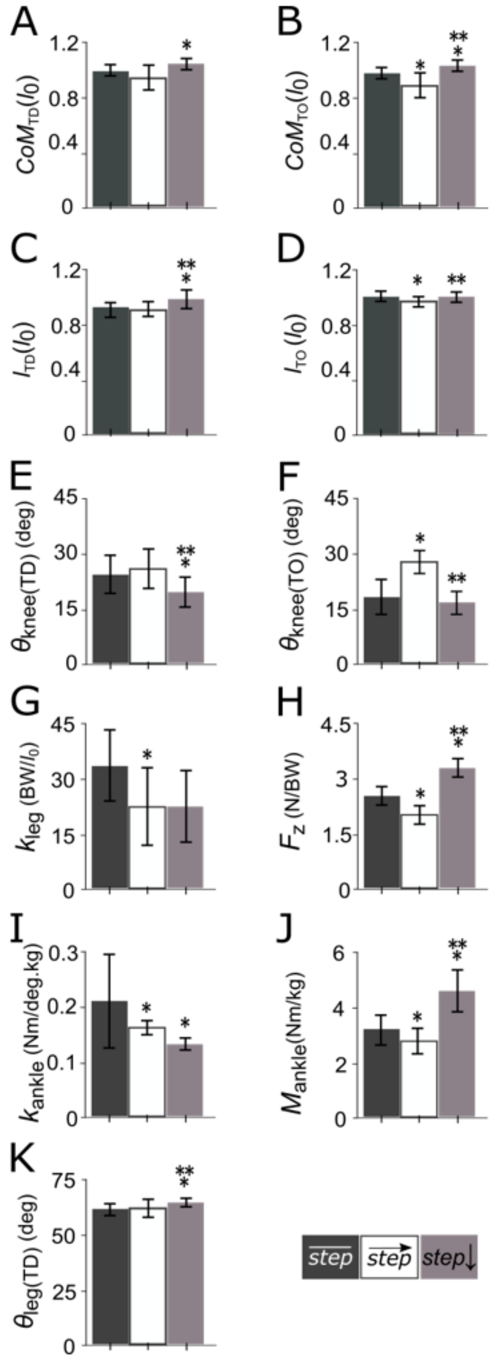

Fig. 5. Main effects of *Step*. The main effect of *Step* (mean ± S.D.) on variables for whom two-way repeated-measurement ANOVAs revealed no *Step* × *Posture* interaction (N=12). Significant differences from $\overline{step}$ and $\overrightarrow{step}$ are indicated by '*' and '**', respectively (p<0.05; Bonferroni post-hoc test). Error bars denote standard deviation. $\overline{step}$, control step; $\overrightarrow{step}$, approach step; *step*↓, stepdown; *CoM*, centre of mass; *k*, stiffness; *l*; leg length; *θ*, angle; *M*, peak net joint moment; F_z; peak vertical ground reaction force; *k*, stiffness; *M*, peak net joint moment; *θ*, angle; TD, touchdown; TO, toe-off.