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Understanding Gait Alterations: Trunk Flexion and Its Effects on Walking Neuromechanics

--Manuscript Draft--

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Additional Information:	
Question	**Response**
Editor Suggestions You may request that your submission is assigned to a specific editor. Please suggest no more than three editor names in order of preference. Although you may suggest an editor for your submission, the journal will make the final assignment. If you do not request an editor, your submission will be assigned to the most appropriate editor as determined by the editorial staff.	Monica Daley
Companion Paper	No

Is your paper a companion paper (part of a group of papers being submitted)?	
Special Issue	No, this article is not part of a special themed issue
Open Access Please check your funder requirements carefully and select the appropriate Open Access publication route below. A quote for your Open Access publication charges will be available to view on the final submission page, revealing any institutional discounts and providing you with another chance to select Open Access. See **Instructions** for further information.	**Green Open Access**
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Response to Reviewers:	Dear Editor, Thanks for your feedbacks, and support in the revision process, that helped us to greatly improve the quality of our work. Please find hereunder the point-by-point answer to the reviewer comments. Best Regards, Arthur D. Reviewer 1: Thank you for addressing all my comments. I have only some minor comments: 1) In the abstract (line 38) the authors write "4 km/h-1". It should say "4 km/h" here. Please check this throughout the entire manuscript. Changed accordingly. 2) In the introduction (line 67-69) the authors write "For instance, Müller et al. (2017) demonstrated that during walking with a flexed trunk, the CoM is displaced forward and slightly downward, with repercussions on stability (Aminiaghdam et al., 2017a)." Please add a second reference of AminiAghdam at the end of the sentence (AminiAghdam, S., Müller, R., & Blickhan, R. (2018). Locomotor stability in able-bodied trunk-flexed gait across uneven ground. Human Movement Science, 62, 176-183). We have added the reference as suggested. 3) In this study, participants were asked to walk wearing their shoes on an instrumented treadmill. This is in contrast to AminiAghdam et al. and Hora et al., in which participants walked on level ground (with shoes or barefoot) at their self-selected speed. This difference should be added to the manuscript. We have added the following sentence: the fixed speed imposed in our study allows us to isolate the effect of trunk inclination, as previous research has shown that preferred walking speed can be influenced by trunk inclination AminiAghdam et al. 4) Participants were instructed to bend the hips to achieve the target trunk flexion instead of rounding at the lower or upper back (line 123-124). However, it is unclear whether there were restrictions on arm movements. Please explain. Now it reads: “no instruction were done regarding arm movements” 5) The EMG time scale was normalized by interpolating individual gait cycles over 400 points. However, it is unclear to what extent the authors also normalized the EMG amplitudes. Please explain. No, we did not normalize the EMG amplitude because our statistical comparisons were conducted per muscle, within the same participants

	across different walking conditions. Therefore, the (absence of) amplitude normalization does not impact the statistical results. 6) The results read like a figure legend. For example, "Figure 1A-B illustrates… Figure 3A illustrates…". Please revise the results section and try to condense the results a little more to the essentials. We have decided to keep it as it is; but we will keep it in mind for our future work. 7) A punctuation mark is missing in line 345. Done. Thanks.

UCLouvain
Institute Of NeuroScience (IoNS)

Louvain-la-Neuve, Le 19/07/ 2024

Journal of Experimental Biology

Dear Pr. Daley,
Dear Monica,

We are grateful for the opportunity to resubmit our manuscript titled " Understanding Gait Alterations: Trunk Flexion and Its Effects on Walking Neuromechanics" (Manuscript ID: JEXBIO/2024/247683) to the Journal of Experimental Biology. We put effort to meet the requirements outlined by the reviewers and yourself. We have carefully addressed all the comments and concerns raised by the reviewers and made substantial revisions to the manuscript. The most important one concerned the inclusion of female participants: We acknowledge the reviewer's concern regarding the exclusion of females from the initial sample; this is indeed a significant issue. Although sex was not a specific inclusion criterion in our initial study, our recruitment was limited to individuals in the immediate vicinity of the lab, which unfortunately resulted in a predominantly male sample. We recognize the importance of a more balanced sample for generalizing results. To address this concern, we conducted additional experiments that included ten young female participants, thereby doubling our sample size and ensuring a more balanced representation. These new experiments were led by a young scientist who we have now included in the author list, further balancing the list of male coauthors. We hope this step contributes to better inclusion in science, particularly in Chile.

Also, other changes were made, like a better contextualization and Literature Integration, clarification of methological details, figure updated, etc.

The attached document includes a detailed point-by-point response to each reviewer's comments. It outlines how each comment was addressed, and the specific changes made to the manuscript.

We are convinced these revisions have significantly improved the quality and clarity of our manuscript. We thank the reviewers and you for the valuable feedback and hope that the revised manuscript meets the high standards of the Journal of Experimental Biology. We look forward to your feedback and are prepared to make any further revisions necessary.

Thank you for considering our resubmission.

Sincerely,

Arthur Dewolf;

LOUVAIN-LA-NEUVE | BRUXELLES WOLUWE | MONS | TOURNAI | BRUXELLES SAINT-GILLES | CHARLEROI
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Dear Editor,

Thanks for your feedbacks, and support in the revision process, that helped us to greatly improve the quality of our work. Please find hereunder the point-by-point answer to the reviewer comments.

Best Regards,

Arthur D.

Reviewer 1: Thank you for addressing all my comments. I have only some minor comments:
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Manuscript

Understanding Gait Alterations: Trunk Flexion and Its Effects on Walking Neuromechanics

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Summary statement

This study explores the impact of trunk flexion on walking patterns, revealing specific adjustments in muscle activity related to mechanics. Gaining insights into the relation between posture and gait has implications for the understanding of motor control in gait disorders.

Abstract

Evolutionary and functional adaptations of morphology and postural tone of the spine and trunk are intrinsically shaped by the field of gravity in which humans move. Gravity also significantly impacts the timing and levels of neuromuscular activation, particularly in foot-support interactions. During step-to-step transitions, the centre of mass velocity must be redirected from downwards to upwards. When walking upright, this redirection is initiated by the trailing leg, propelling the body forward and upward before the foot contact of the leading leg**,** defined as an anticipated transition. In this study, we investigate the neuromechanical adjustments when walking with a bent posture. Twenty adults walked on an instrumented treadmill at 4 km/h under normal (upright) conditions and with varying degrees of anterior trunk flexion (10, 20, 30, and 40°). We recorded lower-limb kinematics, ground reaction forces under each foot, and the electromyography activity of five lower-limb muscles. Our findings indicate that with increasing trunk flexion, there is a lack of these anticipatory step-to-step transitions, and the leading limb performs the redirection after the ground collision. Surprisingly, attenuating distal extensor muscle activity at the end of stance is one of the main impacts of trunk flexion. Our observations may help to understand the physiological mechanisms and biomechanical regulations underlying our tendency toward an upright posture, as well as possible motor control disturbances in some diseases associated with trunk orientation problems.

Keywords: step-to-step transition; bipedal gait mechanics; trunk inclination

Introduction

Upright bipedal walking is one of the most highly automated motor acts that humans perform and distinguish humans from other mammals. It necessitates several specific adaptations of the locomotor apparatus (Huw Crompton et al., 1998; Spoor et al., 1994), including the erect posture of the trunk and head. Such an erect posture makes walking gait mechanically efficient because the centre of mass of the body (CoM) vaults over the supporting relatively straight limb like an inverted pendulum (Cavagna et al., 1977; Willems et al., 1995). This mechanism limits energy expenditure by means of a transduction between the kinetic (E_k) and potential (E_p) energies of the CoM (Cavagna et al., 1977; Dewolf et al., 2017; Willems et al., 1995). A major part of the muscular work is used to redirect the CoM from one pendulum arc to the next during walking (Kuo et al., 2005; Ruina et al., 2005a). To do so, the propulsion of the trailing limb at the end of stance and the weight acceptance of the leading limb at the beginning of the stance are coordinated to avoid collisional loss at foot contact (Dewolf et al., 2022; Dewolf and Willems, 2019; Donelan et al., 2002; Hiebert et al., 1996; Meurisse et al., 2019a). As a result, the lower-limb muscle activation pattern is pulsatile, with muscle activity occurring briefly at specific phases of the cycle to re-excite the intrinsic oscillations of the system when energy is lost (Ivanenko et al., 2004; Lacquaniti et al., 2012).

The head and trunk segments represent up to 65% of the body's mass (Dempster, 1955). Therefore, deviations from the erect posture, even small ones, have inevitable mechanical consequences. For instance, Müller et al. (2017) demonstrated that during walking with a flexed trunk, the CoM is displaced forward and slightly downward, with repercussions on stability (Aminiaghdam et al., 2017a, 2018). Also, the associated posterior shift of the hip relative to the centre of mass leads to a flatter angle at foot contact of the leading leg and a steeper trailing leg angle at toe-off and induces a modification of the two peaks of vertical ground reaction force (Aminiaghdam et al., 2017) and a modification of joint moments of the lower limbs (Leteneur et al., 2009), suggesting a modification of the step-to-step transition. These biomechanical modifications lead to alterations in the muscle activation patterns of the lower limb (Alghamdi and Preece, 2020; Grasso et al., 2000), with more crouched postures resulting in greater activation of both proximal and distal muscles, but with a stronger effect on the activation of the thigh and gluteal muscles compared to shank muscles (Hora et al., 2024). Although these studies provided valuable insights, they did not explore the modification of the step-to-step strategy during the double support phase of walking. Understanding trunk control and its impact on gait is important for clinicians and scientists, as various pathological and aging-related conditions tend to increase trunk inclination during walking. For example, there is a substantial body of research demonstrating increased trunk flexion during gait with aging (Dewolf et al., 2021a, 2019b) and with pathologies such as Parkinson's disease (Pongmala et al., 2022) or knee osteoarthritis (Preece and Alghamdi, 2021). In older adults, there is a reduction in mechanical power generated by the plantar flexor muscles during the push-off phase of walking (Delabastita et al., 2021; Winter et al., 1990), an unanticipated step-to-step transition (the redirection of the CoM occurring after foot contact) (Dewolf et al., 2022; Meurisse et al., 2019a, 2019b), and a widening of distal muscle activations (Dewolf et al., 2021a, 2021b).

While the inter-relationship between posture and locomotion is well recognized, the isolated effects of trunk flexion on the neuromuscular control of gait are not well understood. In particular, it is not clear whether or not the trunk flexion and the associated modification of lower-limb kinematics affect the step-to-step transition of walking and, with it, the activation pattern of lower limb muscles observed in able-bodied human gait. To answer this question, we studied the effects of small (from 10°) and large (up to 40°) changes in upper body inclination in twenty young and healthy participants. The ground reaction forces, the activity of five lower-limb muscles, and the joint angles of lower limb segments were recorded. We hypothesized that trunk flexion would result in a more flexed limb posture during stance, a greater peak of force by the leading limb (and a smaller peak under the trailing one), and an anticipated activation of the distal extensors, consistent with the compensations observed in older adults.

Methods

Participants

Twenty healthy young adults (10 males and 10 females, age: 29.4 ± 4.6 years, mass: 69.3 ± 11.5 kg, height: 1.69 ± 0.11 m, mean ± SD) volunteered to participate in this study. The sample size was estimated a priori based on the difference of 75% of the rate of F_{back}/F_{front} (η^2= 1.51) (Dewolf et al., 2022). Considering a power analysis of 0.85 (1-beta) and one-way ANOVA with an alpha level of 0.05, 7 participants would be sufficient. The software used for the sample size was G-Power (version 3.1.9.7, Germany). All participants had no history of gait pathologies, neurological disease, or orthopedic problems that would affect how they walked. Informed consent was obtained from all participants, and the procedures used for this study were approved by the ethics committee of Finis Terrae University, Chile (Ref. No. 22-114). The study followed the guidelines of the Declaration of Helsinki. Preliminary results have already been published in a conference paper (Nunez-Lisboa and Dewolf, 2023).

Experimental procedure and data collection

Participants were asked to walk wearing their shoes on an instrumented treadmill at 4 km/h. The fixed speed imposed in our study allows us to isolate the effect of trunk inclination, as previous research has shown that preferred walking speed can be influenced by trunk inclination (Aminiaghdam et al., 2018). The selected walking speed was reported as the comfortable and economical average walking speed based on the net energy consumption (Cavagna and Kaneko, 1977). Five different gait conditions were tested. Participants were first asked to walk normally, with a natural trunk orientation (called 'normal walking'). Then, they were asked to walk with an anterior trunk flexion of 10, 20, 30, and 40 degrees relative to the vertical. The motion capture system used was FreeMoCap v1.0.25 (https://freemocap.org/) to track the estimated vertical and anteroposterior coordinates of the acromial apex, greater trochanter, lateral femoral condyle, lateral malleolus and fifth metatarsophalangeal joint at 60 Hz. The participants were filmed in the sagittal plane, and the trunk flexion, defined as the orientation of the line crossing the acromial apex and greater trochanter relative to the vertical axis, during the different gait conditions was controlled by a mobile app (OnForm, version 2.03.0). Before starting the data collection, participants took several trials with oral feedback from the experimenter until they adopted the correct position. Participants were instructed to bend the hips to achieve the target trunk flexion instead of rounding at the lower or upper back, following the methodology described by Kluger et al., (2014). No instruction was given regarding arm movements. The participants walked then for at least one minute per condition, with two minutes of rest between each trial to avoid muscular fatigue. Data were recorded for 10 seconds once steady walking was reached, and on average, 7.3 ± 0.5 (mean ± SD) strides were analysed for each participant.

The treadmill (H/P/ Cosmos-Stellar, Germany; belt surface: 1.6 x 0.65 m; mass: ~240 kg;) was instrumented with four force transducers (Arsalis®, Belgium). Since the transducers were placed under the body of the treadmill, the force transducers measured the three components of ground reaction force (GRF) exerted by the treadmill belt under the foot (Willems and Gosseye, 2013): F_v, F_f and F_l are respectively the vertical, fore aft, and lateral component of the GRF. Data were sampled at a frequency of 500 Hz. Two algorithms were used to reconstruct the 3 components of the force under the left and right foot (Bastien et al., 2019; Meurisse et al., 2016).

Electromyographic (EMG) activities from five muscles of the right lower-limb were recorded at 2 kHz using a Delsys Trigno Wireless System (Boston, MA): vastus medialis (VM), vasto lateral (VL), tibial anterior (TA), medial gastrocnemius (MG) and lateral gastrocnemius (LG). We selected these muscles to have a good comparison of activity between proximal and distal muscles of the lower limbs. The EMG activity of other relevant muscles, such as biceps femoris, rectus femoris and gluteus maximus has previously been reported in a similar task (Grasso et al., 2000). Furthermore, our focus was specifically on step-to-step transitions, where extensor muscles have been shown to significantly contribute to COM propulsion and where the recorded muscles are particularly active (Dewolf et al., 2019a; Ivanenko et al., 2008). The location of the electrode was based on suggestions from SENIAM (the European project of surface EMG-seniam.org). The signal quality was verified visually by checking the EMG signals during voluntary contractions before walking. Acquisition of the EMG and GRF were synchronized with a trigger module from Delsys.

Data analysis

Division of the stride: The foot contact (FC) and toe-off (TO) events were estimated from the displacement of the centre of pressure on the belt (Meurisse et al., 2016). A stride was defined as two successive right FCs. Stance phases were measured as the time between TO and FC of the same leg. The double contact phase (DC) started from the front leg FC to the back leg TO.

Kinematics: The vertical and antero-posterior coordinates of the head of the fifth metatarsal, the external malleolus, the lateral condyle of the knee, the greater trochanter, and the apex of the shoulder of the right side of the body were recorded. The coordinates were filtered with the 4th order of the Butterworth filter, with a 7 Hz cut-off frequency. The angle of each segment (trunk, thigh, shank, and foot) relative to the vertical (elevation angles) were computed in the sagittal plane. From these angles, the hip, knee, and ankle joint angles were calculated. The hip, knee and ankle joint angle during standing were subtracted from the joint measured during walking tasks. Each stride of each participant was interpolated over 100 points. For the three joint angles and the trunk elevation angle, the range of motions (ROM) and the mean values were measured. Joint angles were measured relative to the subject's standing position, with 0° indicating this posture.

Kinetics: The fore-aft and vertical velocity of the CoM was determined from the fore-aft and vertical components of the GRF using the procedure described in detail in Dewolf et al. (2017). In short, the fore-aft acceleration of the CoM was calculated as $a_f = F_f/m$, where m is the participant's body mass. The vertical acceleration of the CoM was calculated as $a_v = (F_v - m\,g)/m$, where g is the acceleration of gravity. The vertical (V_v) and the forward velocity (V_f) of the CoM were calculated by time-integration of a_v and a_f, respectively, plus an integration constant, which was computed so that the average velocity over a stride was equal to zero. The vertical and forward displacements of the CoM (S_v and S_f, respectively) were then computed by time-integration of V_v and V_f.

The time of occurrence of the minimum of forward ($V_{f\,min}$) and vertical velocities of the CoM ($V_{v\,min}$) at the beginning of the double contact phase were detected. The step-to-step transition strategy was defined as follows: the transition was considered as *anticipated* when $V_{v\,min}$ occurred before FC and *unanticipated* when $V_{v\,min}$ occurred after FC. Also, the peaks of vertical force under the front leg (F_{front}) and the back leg (F_{back}) were measured during the DC. In addition, the negative ($F_{f,brake}$) and positive ($F_{f,propulsion}$) peak of the left and right fore-aft force were measured.

The energy of the CoM (E_{com}) was computed as the algebraic sum at each instant of its gravitational potential energy ($E_p = m\,g\,S_v$) and its kinetic energy ($E_k = ½\,m\,(V_f + V_v)^2$). The work done to move the CoM relative to the surroundings (W_{com}) was then computed as the sum of the positive increments of E_{com} (Cavagna et al., 1976). The energy transduction between E_p and E_k was estimated from the relative amount of energy saved over a step (%R):

$$\%\boldsymbol{R} = \frac{\boldsymbol{W_k} + \boldsymbol{W_p} - \boldsymbol{W_{com}}}{\boldsymbol{W_k} + \boldsymbol{W_p}} * \mathbf{100}$$

EMG: The raw EMG signals were high-pass filtered (30 Hz), rectified and low-pass filtered with a zero-lag 3th-order Butterworth filter (10 Hz). The time scale was normalized by interpolating individual gait cycles over 400 points. For each condition and each stride, the full width at half maximum (FWHM) was calculated as the period during the EMG activity exceeded half of its maximum (Martino et al., 2014). Each EMG waveform's centre of activity (CoA) was calculated as the vector's angle that points to the centre mass of the circular distribution (Martino et al., 2014). Also, the mean activation was calculated.

Statistics

For each dependent variable, the normality of residuals was visually assessed using QQ plots. A mixed-effects model with a post-hoc Fisher LSD test was performed to evaluate differences between normal and the 10°, 20°, 30°, and 40° conditions. Both numerator and denominator degrees of freedom (DF) were reported; the numerator degrees of freedom reflect the number of comparisons, and the denominator degrees of freedom adjust for the sample size and variability. In cases where sphericity was violated, the Greenhouse-Geisser correction was applied to adjust both DF (Wright and Wolfinger, 1997). Furthermore, the Friedman test with post-hoc Dunn's test was used for dependent variables that did not meet the normality assumption. Cohen's d-effect size (ES) was calculated for each comparison, interpreted as 0.2 (small), 0.5 (medium), and 0.8 or greater (large). All statistical analyses were conducted using GraphPad Prism 9 software (GraphPad Software, California, USA) with an alpha level set at 0.05.

Results

Figure 1A-B illustrates the digital joint identification at the sagittal plane, the typical curves of the vertical force and forward of the back and front leg, and raw EMG data during one stride in all conditions. Figure 2 demonstrates the average comparison of walking conditions with trunk flexion. The anterior trunk flexion during walking differed between conditions ($F_{2.857, 50.72} = 252.1$, $p < 0.0001$, Fig. 2). Specifically, compared to normal walking, the degrees of anterior trunk flexion was higher at 10°, 20°, 30° and 40° (post-hoc: $p < 0.0001$, ES = 4.31; $p < 0.0001$, ES = 7.61; $p < 0.0001$, ES = 6.44, $p < 0.0001$, ES = 8.55, respectively), and the average trunk elevation angle was close to (but smaller than) the angle requested to the participants (normal = -1.55° ± 1.92; 10° = 7.5° ± 2.2; 20° = 18.3° ± 3.1; 30° = 24.5° ± 5.3; 40° = 33.3° ± 5.3). The stride duration was affected by the trunk flexion ($F_{1.644, 31.24} = 17.40$, $p < 0.0001$, Fig. 2). Specifically, compared to normal walking, the stride duration was lower at 10°, 20°, 30° and 40° (post-hoc: $p = 0.045$, ES = 0.26; $p = 0.005$, ES = 0.30; $p = 0.001$, ES = 0.83; $p < 0.0001$, ES = 1.25, respectively). However, no difference was observed in the stance duration ($F_{2.439, 45.72} = 1.865$, $p = 0.158$) (Fig. 2). Specifically, compared to normal walking, the stance duration did not change at 10°, 20°, 30° and 40° (post-hoc: $p = 0.938$, ES = 0.14; $p = 0.778$, ES = 0.12; $p = 0.734$, ES = 0.32; $p = 0.247$, ES = 0.59, respectively).

Figure 3A illustrates the average waveform of the hip, knee, and ankle joint angles during normal and flexed conditions over a stride. Notably, the joint angle's time course changed significantly as trunk flexion increased during the stride. Trunk inclination significantly affected the average angles of all lower-limb joints (hip: $F_{1.200, 118.8} = 4404$, $p < 0.0001$; knee: $F_{1.058, 104.8} = 124.6$, $p < 0.0001$; ankle: $F_{1.588, 157.2} = 404.3$, $p < 0.0001$) (Fig. 3B). Furthermore, trunk inclination had a significant impact on the mean range of motion (ROM) of the hip, knee, and ankle joint (hip: $F_{3.180, 56.44} = 165.7$, $p < 0.0001$; knee: $F_{2.816, 49.99} = 28.60$, $p < 0.0001$; ankle: $F_{2.776, 49.27} = 15.48$, $p < 0.0001$) (Fig. 3B). Compared to the normal condition, the average joint angles of the hip were higher at 10°, 20°, 30°, and 40° of trunk flexion (post-hoc: $p < 0.0001$, ES = 2.05; $p < 0.0001$, ES = 4.17; $p < 0.0001$, ES = 5.36; $p < 0.0001$, ES = 7.34, respectively), while the average joint angle of the ankle and knee was higher at 20°, 30°, and 40° of trunk flexion (ankle post-hoc: $p = 0.204$, ES = 0.37; $p < 0.0001$, ES = 1.14; $p < 0.0001$, ES = 1.68; $p < 0.0001$, ES = 2.21, respectively) (knee post-hoc: $p = 0.080$, ES = 0.59; $p < 0.0001$, ES = 1.75; $p < 0.0001$, ES = 2.40; $p < 0.0001$, ES = 3.09, respectively).

Figure 4A presents typical traces of V_v (bottom) and V_f (below) during one stride in all walking conditions. The black dots represent the min ($V_{v\,min}$) and max of V_v, which define the step-to-step transition. The black dots also indicate the min ($V_{f\,min}$) and max of V_f. With increasing trunk flexion angle, $V_{v\,min}$ occurred later in the stride ($\chi^2 = 68.98$, df = 4, $p < 0.0001$). This indicates that the step-to-step transition was *anticipated* during normal walking and walking with a 10° flexion (V_v min occurred before FC) and *unanticipated* at higher trunk flexion angles (V_v min occurred after FC) (post-hoc: 20°: $p < 0.0001$, ES = 1.64; 30°: $p < 0.0001$, ES = 2.47; 40°: $p < 0.0001$, ES = 2.88) (Fig. 4B). In a parallel observation, as the trunk flexion angle increased, $V_{f\ min}$ was noted to occur before heel strike ($F_{1.534,\ 28.77} = 3.139$, $p = 0.0703$), coinciding with a monotonic change in the peak of vertical and fore-aft forces exerted by the back leg and by the front leg (Fig. 4C). With increasing trunk flexion, F_{back} decreased ($F_{2.165,\ 41.13} = 84.31$, $p < 0.0001$). Compared to normal walking, the mean F_{back} decreased at 10°, 20°, 30°, and 40° (post-hoc: $p < 0.0001$, ES = 1.03; $p < 0.0001$, ES = 1.85; $p<0.0001$, ES = 2.54; $p<0.0001$, ES = 2.72, respectively). In contrast, F_{front} increased by the increase of trunk flexion ($F_{2.021,\ 38.40} = 16.04$, $p < 0.0001$). The mean F_{front} increased at 20°, 30°, and 40° compared to normal walking (post-hoc: $p = 0.002$, ES = 0.67; $p < 0.0001$, ES = 1.09; $p = 0.0004$, ES = 0.99, respectively) (Fig. 4C). Additionally, $F_{f,propulsive}$ decreased with the increased trunk flexion ($F_{2.351,\ 44.08} = 32.64$, $p < 0.0001$). Specifically, compared to normal walking, the mean $F_{f,propulsive}$ decreased at 10°, 20°, 30°, and 40° (post-hoc: $p = 0.037$, ES = 0.42; $p = 0.001$, ES = 0.95; $p < 0.0001$, ES = 1.61; $p < 0.0001$, ES = 2.10, respectively). Conversely, $F_{f,brake}$ was unaffected by trunk inclination ($F_{2.023,\ 37.94} = 0.4022$, $p = 0.674$). Specifically, there were no significant changes in mean $F_{f,brake}$ decreased at 10°, 20°, 30°, and 40° (post-hoc: $p = 0.192$, ES = 0.21; $p = 0.278$, ES = 0.22; $p = 0.787$, ES = 0.07; $p = 0.609$, ES = 0.13, respectively) (Fig. 4C).

Figure 5 demonstrates the typical traces of the pendulum mechanism variables. Specifically, figure 5A illustrates a typical E_k, E_p, and E_{com} trace during one stride at each condition. The CoM work (W_{com}) significantly differs between conditions ($F_{1.292,\ 24.55} = 7.572$, $p = 0.007$, Fig. 5B). Compared to normal walking, W_{com} was lower at 10° and 20° (post-hoc: $p = 0.0004$, ES = 0.91 and $p = 0.006$, ES = 0.84, respectively) (Fig. 5B). Additionally, W_{com} didn't change at 30° and 40° (respectively $p = 0.415$, ES = 0.26; $p = 0.096$, ES = 0.58). The modification of W_{com} may partly be explained by the change of pendulum-like energy exchange (Fig. 5B). Indeed, the inclination of the trunk affects the %R ($F_{1.387,\ 26.35} = 11.82$, $p = 0.0008$). As compared to normal walking, the %R was higher at 10° and 20° (post-hoc: $p = 0.0004$, ES = 0.87 and $p = 0.015$, ES = 0.81, respectively), with no changes at 30° ($p = 0.405$, ES = 0.39) and significantly lower at 40° (post-hoc: $p = 0.025$, ES = 0.84).

Figure 6 presents the average (across strides and participants) rectified muscle activity of lower limb muscles (VM, VL, TA, GM, and GL) during one stride in each condition. The angle of trunk flexion significantly influenced the mean activation of most muscles (VM: $F_{1.563,\ 19.15} = 12.99$, $p = 0.0006$; VL: $F_{3.018,\ 46.03} = 4.153$, $p = 0.010$; TA: $F_{1.530,\ 16.06} = 8.180$, $p = 0.0058$; GL: $F_{1.619,\ 23.87} = 5.733$, $p = 0.013$), except for GM, which was not significantly affected ($F_{1.787,\ 22.79} = 1.583$, $p = 0.227$, Fig. 6B). Specifically, compared to normal walking, the mean GM did not change at 10°, 20°, 30°, and 40° (post-hoc: $p = 0.335$, ES = 0.41; $p = 0.432$, ES = 0.33; $p = 0.954$, ES = 0.23; $p = 0.904$, ES = 0.21, respectively). Furthermore, compared to normal walking, the mean VM muscle activity increased at 10°, 30°, and 40° (post-hoc: $p = 0.035$, ES = 0.16; $p = 0.005$, ES = 0.65; $p < 0.0001$, ES = 1.20, respectively). However, VM did not change at 20° of trunk flexion (post-hoc: $p = 0.263$, ES = 0.24). Additionally, the mean VL muscle activity increased at 10° and 40° (post-hoc: $p = 0.020$, ES = 0.31; $p = 0.031$, ES = 0.65, respectively) and did not change at 20° and 30° (post-hoc: $p = 0.118$, ES = 0.40; $p = 0.189$, ES = 0.51, respectively). The mean TA activity was higher at 40° (post-hoc: $p = 0.0174$) and did not change at 10°, 20°, and 30° (post-hoc: $p = 0.686$, ES = 0.05; $p = 0.352$, ES = 0.15; $p = 0.091$, ES = 0.38, respectively). Lastly, the mean activation of GL was higher at 30° and 40° (post-hoc: $p = 0.039$, ES = 0.51 and $p =$

0.008, ES=0.65, respectively), and did not change at 10° and 20° of trunk flexion (post-hoc: $p = 0.353$, ES = 0.10; $p = 0.114$, ES = 0.35).

In most muscles, the duration of muscle activation also varies with trunk flexion (Middle graphs on Fig. 6B). The trunk inclination affected the FWHM of VM, VL, GM, and GL (VM: $F_{2.510, 30.12} = 12.46$, $p < 0.0001$; VL: $F_{2.288, 37.76} = 4.604$, $p = 0.0129$; GM: $F_{3.108, 52.06} = 3.217$, $p = 0.028$; GL: $F_{2.991, 56.07} = 5.515$, $p = 0.002$). In contrast, the FWHM of TA was not significantly affected by trunk angle ($F_{2.170, 40.69} = 0.2317$, $p = 0.811$). Specifically, compared to normal walking, the mean TA did not change at 10°, 20°, 30° and 40° of trunk flexion (post-hoc: $p = 0.976$, ES = 0.0; $p = 0.993$, ES = 0.0; $p = 0.636$, ES = 0.11; $p = 0.670$, ES = 0.11, respectively). Furthermore, compared to normal walking, the FWHM of VM was higher at 10°, 20°, 30°, and 40° of trunk flexion (post-hoc: $p = 0.005$, ES = 0.47; $p = 0.004$, ES = 0.93; $p = 0.0007$, ES = 1.43, $p = 0.0001$, ES= 1.57, respectively); the FWHM of VL was higher at 40° of trunk flexion (post-hoc: $p = 0.021$, ES = 0.89), and did not change at 10°, 20°, and 30° of trunk flexion (post-hoc: $p = 0.656$, ES = 0.12; $p = 0.928$, ES = 0.03; $p = 0.361$, ES = 0.27, respectively); the FWHM of GM was higher at 20°, 30°, and 40° (post-hoc: $p = 0.015$, ES = 0.95; $p = 0.017$, ES = 0.84; $p = 0.014$, ES = 0.81, respectively), and did not change at 10°(post-hoc: $p = 0.147$, ES = 0.47); the FWHM of GL was higher at 20°, 30°, and 40° of trunk flexion (post hoc: $p = 0.016$, ES = 0.47; $p = 0.0004$, ES = 0.76; $p = 0.045$, ES = 0.44, respectively), and did not change al 10° of trunk flexion (post-hoc: $p = 0.071$, ES = 0.23).

The trunk flexion also influenced the timing of extensor muscle activation (VM: $F_{2.800, 30.80} = 16.09$, $p < 0.0001$; VL: $F_{2.158, 38.31} = 12.95$, $p < 0.0001$; GM: $\chi^2 = 40.6$, df = 4, $p < 0.0001$; GL: $F_{2.272, 30.67} = 19.07$ $p < 0.0001$) but not of flexor muscles (TA: $F_{2.881, 54.01} = 0.3533$, $p = 0.778$) (Bottom graphs on Fig. 6B). Compared to normal walking, the activation of VM occurred earlier at 30° and 40° of flexion (post-hoc: $p = 0.0003$, ES = 1.19; $p = 0.0008$, ES = 1.55) and did not change at 10° and 20° of flexion (post hoc: $p = 392$, ES = 0.11; $p = 0.889$, ES = 0.03, respectively). Furthermore, the activation of VL occurred later at 30° and 40° of flexion (post-hoc: $p = 0.0006$, ES = 1.29; $p = 0.0031$, ES = 1.41, respectively) and did not change at 10° and 20° of trunk flexion (post-hoc: $p = 0.392$, ES = 0.05; $p = 0.344$, ES = 0.67, respectively). For distal extensors, the changes were much larger: compared to normal walking, the CoA of GM and GL occurred earlier at all trunk flexion angles (GM: 10°: $p = 0.021$, ES = 65; 20°: $p = 0.0001$, ES = 1.15; 30°: $p < 0.0001$, ES = 1,30; 40°: $p < 0.0001$, ES =1.69; GL: 10°: $p = 0.0002$, ES = 0.88; 20°: $p = 0.0002$, ES = 1.29; 30°: $p = 0.0003$, ES = 2.25; 40°: $p < 0.0001$, ES = 2.20).

Figure 7A presents the mean activation of the extensor muscles (VM, GM, and GL) during the initial and final 20% of the stance phase. The initial 20% of the stance phase was influenced by trunk flexion in most muscles (VM; $F_{2.646, 28.44} = 18.70$, $p < 0.0001$; GM: $F_{2.586, 34.27} = 4.714$, $p = 0.009$; GL: $F_{2.900, 52.92} = 4.928$, $p = 0.004$). Compared to the normal condition, the mean activation of VM during this phase was higher at 10°, 30°, and 40° of trunk flexion (post-hoc: $p = 0.040$, ES = 1.21; $p = 0.0006$; ES = 4.15; $p = 0.0003$, ES = 5.52, respectively) and did not change at 10° of trunk flexion (post-hoc: $p = 0.096$, ES = 0.99). In contrast, VL was not significantly affected ($F_{1.878, 26.30} = 1.150$, $p = 0.329$). Compared to normal walking, VL did not change at 10°, 20°, 30°, and 40° of trunk flexion (post-hoc: $p = 0.921$, ES = 0.02; $p = 0.095$, ES = 0.32; $p = 0.301$, ES = 0.15; $p = 0.195$, ES = 0.21, respectively). The mean activation of GM was higher at 20° and 30° (post-hoc: $p = 0.032$, ES = 0.86; $p = 0.016$, ES = 0.91, respectively) and did not change at 10° and 40° of trunk flexion (post-hoc: p = 0.188, ES = 0.48; p = 0.127, ES = 0.73, respectively). The mean activation of GL was higher at 30° and 40° (post-hoc: p = 0.047, ES = 0.65; p = 0.016, ES = 0.77, respectively) and did not change at 10° and 20° (post-hoc: p = 0.412, ES = 0.19; p = 0.084, ES = 0.54, respectively).

Regarding the final 20% of the stance phase, discernible alterations were observed in VM ($F_{2.630, 32.21}$ = 3.016, p = 0.0501). Specifically, VM remained significantly unaltered at 10°, 20°, 30°, and 40° of trunk flexion (post-hoc: p = 0.622, ES = 0.19; p = 0.695, ES = 0.17; p = 0.114, ES = 0.81; p = 0.061, ES = 0.86, respectively) (Fig. 7A). Similarly, VL did not show significant changes ($F_{0.06431, 0.9325}$ = 1.210, p = 0.1214). Compared to normal walking, VL didn't report significant changes (post-hoc: p = 0.884, ES = 0.03; p = 0.756, ES = 0.06; p = 0.142, ES = 0.42; p = 0.161, ES = 0.39, respectively). Furthermore, the mean activation of GM did not present significant changes (χ^2 = 0.5, df = 4, p = 0.969). Specifically, GM did not change at 10°, 20°, 30° and 40° of trunk flexion (post-hoc: p = 0.932, ES = 0.06; p = 0.682, ES = 0.01; p = 0.969, ES = 0.14; p = 0.622, ES = 0.14, respectively). In contrast, GL showed significant changes (χ^2: 12.33, df = 4, p = 0.015), increasing at 40° of trunk flexion (post-hoc: p = 0.017, ES = 0.64) and did not change at 10°, 20° and 30° of trunk flexion (post-hoc: p = 0.656, ES = 0.14; p = 0.806, ES = 0.08; p = 0.066, ES = 0.55, respectively).

Discussion

This study aimed to determine the effect of trunk flexion on the neuromuscular control of gait. Specifically, we analysed the effect of trunk flexion on lower-limb kinematics, the step-to-step transition of walking, and, with it, its impact on lower-limb muscle activation patterns during walking. The results are discussed in the context of the biomechanical principles underlying foot-support interactions during step-to-step transitions in bipedal upright walking.

Given that the trunk and head segment constitute approximately 65% of the body mass (Dempster, 1955), walking with the trunk anteriorly flexed modifies the position of the CoM, which is displaced forward and slightly downward (Müller et al., 2017). As a result, even a small change in trunk orientation can influence the mechanical demands of walking (Figs. 3 & 4; Aminiaghdam et al., 2017b; Hora et al., 2024; Müller et al., 2017), in turn affecting the neuromechanical control of locomotion. As illustrated in Fig. 7B, trunk flexion alters the spatial relationship between the CoM and the foot contact point of the back leg at the end of the single stance (Warrener et al., 2021), resulting in different leg orientation (Aminiaghdam et al., 2017b). This results in a reduction of the vertical and fore-aft forces under the back leg during propulsion (Fig. 4C & 7B; Aminiaghdam et al., 2017b; Grasso et al., 2000). Additionally, the GRF is more vertical at foot contact since F_{front} increases at weight acceptance without changes in $F_{f, brake}$ (Fig. 4C). Similar modifications of vertical impulses have been observed in older adults (Delabastita et al., 2021; Dewolf et al., 2022, 2019b) and in trunk flexion-induced gait analysis (Müller et al., 2017). We documented here that it has a clear impact on step-to-step transition: an unanticipated transition was revealed at 20°, 30°, and 40° of trunk flexion (Figs. 1B, 4B & 7B), accompanied by a reduction in the mechanical recovery of walking at 40° of trunk flexion (Fig. 5B). The unanticipated transition occurs when $V_{v\ min}$ appears after foot contact (FC). This absence of modification of transition at 10° (and in turn of mechanical work; Fig. 5B) may be due to the minimal changes in the energy fluctuations (Fig. 5A).

Instead, with a greater trunk inclination, the vertical displacement of the CoM starts to increase and the modification of ratio between W_k and W_p induces a reduction of recovery between energies (Cavagna et al., 1976). The detailed results of W_p /W_k are shown in Fig. S1 (see supplementary materials).

As for the modification of muscle activation during the stride (Figs. 1, 6), it's noteworthy that with increasing trunk flexion, the activation of extensor muscles generally increases, except for GL and GM (Fig. 6B). Similar result has also been described recently in crouched walking (Hora et al., 2024), showing lower increases of activation in the lower leg muscles with trunk inclination compared to the thigh muscles. As suggested by Hora et al. (2024), the lower increase in activation of ankle muscles might reflect the smaller changes in ankle joint kinematics compared to the hip and knee joints (Fig. 3A&B). When specifically examining the activation of the extensor muscles in the front leg, VM increases its activity mainly during the initial 20% of the stance phase (Fig. 7A), confirming the greater contribution of VM during weight acceptance. However, during the initial 20% of stance, GM and GL also increase with increased trunk flexion, suggesting an antigravitational role (Hamner et al., 2010; Honeine et al., 2013) when the collision with the ground of the front leg becomes more important. This increase in distal extensor activation is related to their earlier activation (CoA; Fig. 6B) during the walking cycle. In addition, we noticed a change in the period during which muscle activity remains consistently above half of its maximum level (Fig. 6B). Here, we evidenced a higher FWHM with an increasing trunk inclination (Fig. 6B middle graphs) in proximal (VM and VL) and distal muscles (GM and GL). These prolonged activations likely suggest the need for enhanced stability and control as the body adapts to the forward trunk inclination. Similar compensatory mechanisms are observed in the gait pattern of patients with balance deficit, such as cerebellar ataxia (Martino et al., 2014). In summary, when the lower limbs are more flexed and the CoM is shifted forward and downward, increased muscle activity is required to generate the necessary joint torque to accomplish the walking task. This is also related to the more flexed lower-limb joint during stance (Fig. 3A&B; Aminiaghdam et al., 2017b). Indeed, as trunk flexion increases the participants exhibit a linear increase in hip, knee, and ankle (dorsi-) flexion, while the range of motion (ROM) of these joints remains consistent throughout the step (Fig. 3 A&B). This most likely induces muscle compensation reminiscent of crouched walking (Grasso et al., 2000). Indeed, Grasso et al. (2000) observed that imposing greater knee flexion during stance leads to a higher muscle activation of lower-limb muscle. As for walking with a flexed trunk, the increment of muscle activity can be related, among others, to the lower mechanical energy recovery through the pendular energy exchange (see Fig. 7 InLi Y. et al., 1996). Additionally, Grasso et al. (2000) also observed that the time sequence of activation of different muscles varied substantially as a function of imposed posture. In particular, as in the present study, a greater activation of the knee extensor (VL) was observed at the end of the stance, and a greater activation of ankle extensors (GM) at the beginning of the stance phase, consistent with our findings. In contrast, our study found greater activation of the knee extensor (VM) at the beginning of the stance phase (Fig. 7A).

This suggests that trunk inclination and the lower-limb kinematics change in parallel and cannot be studied separately. Similar observations were already made by Grasso et al. (1999) who showed that in Parkinson’s disease patients in the apomorphine OFF condition, the flexion of the trunk is paralleled by the flexion of the legs. In ON condition the trunk and the limbs extend together. These authors proposed that the basal-ganglia circuitry may provide a spatiotemporal framework for the control of both posture and movement in a gravity-based frame.

Also, a recent study (Mesquita et al., 2023) suggests that altering the foot interaction with the ground affects the walking pattern similarly to trunk flexion. By imposing different foot positions during stance (e.g., maintaining a flat-foot during all the stance phase), the authors described that deviating from the classical heel-to-toe pattern of walking leads to a higher F_{front}, a smaller F_{back}, an anticipated activation of distal extensors muscles, and a higher activation of proximal muscles. They argued that the specific use of heel-to-toe rolling pattern allows to delay the activation of distal extensor relative to proximal extensors, ensuring a smooth step-to-step transition. This is a specific adaptation of the locomotor apparatus to bipedalism. Indeed, in quadrupeds, the step-to-step transition is not as crucial as in biped since the mechanical cost of the redirection is reduced in proportion to the number of contacts used to achieve a given redirection of the CoM (Ruina et al., 2005b). In addition, the change of the hindlimb configuration at the end of stance (knee flexed) may allow them to propel themselves forward using primarily the proximal extensors. Interestingly, deviating from the erect posture of the trunk, another specific adaptation of the locomotor apparatus to bipedalism, results in similar modifications of walking pattern.

These indications provide arguments to the fact that the erect posture has evolved to optimize gait, allowing the CoM vaulting over the supporting straight limb. Indeed, based on the fluctuation of the mechanical energy of the CoM, normal walking is often compared to an inverted pendulum model based on the fluctuation of the mechanical energy of the CoM (Cavagna and Kaneko, 1977; Willems et al., 1995). Maintaining a flexed trunk during walking potentially affects this pendulum-like mechanism since it modifies the position of the CoM and the limb posture during stance. Here, when comparing normal walking and walking with a 40° trunk inclination, we found a significant decrease of the energy transduction between E_p and E_k (%R) and with it, a medium effect (ES = 0.56) on the mechanical work done to move the CoM (W_{com}) (Fig. 5B). Furthermore, the pattern of walking with imposed trunk flexion is more similar to that of bipedal chimpanzee gait than to normal walking. Indeed, the kinematics and mechanics of walking with imposed trunk flexion overlap widely with the gait pattern of chimpanzee bipedal walking. Chimpanzees walk with a crouched posture with flexed limb (Johnson et al., 2022) and similar COM mechanics and recovery rates can be observed for chimpanzee bipedal walking (Demes et al., 2015). Understanding the link between posture and gait mechanics across different species may help researchers better interpret the effects of evolution on bipedal walking.

More surprisingly, the opposite was observed when comparing normal with walking with a 10° and 20° flexed trunk i.e., an increase in the %R and a decrease in W_{com}. This last result suggests that the recovery of energy only gives partial information concerning the metabolic cost of walking since the collisional loss occurring at contact is more likely to be a better determinant of the cost of locomotion. Nevertheless, it allows a better understanding of the mechanical-bioenergetic interaction of walking. In general, humans tend to prefer economical walking patterns. However, Hunter et al. (2010) showed that in shallow downhill slope, their participants do not take optimal advantage of the propulsion provided by gravity to decrease energetic cost, but instead prefer a more stable and costlier gait pattern. Here, it could be possible that, due to the shift in the hip relative to the foot, a 10° and 20° trunk flexed allowed the participant to take advantage of the propulsion provided by gravity and thus to reduced mechanical cost of walking at the expense of stability. When the trunk becomes more flexed, one may observe that E_k and E_p become more in phase after foot contact (Fig. 5A). This suggest that the pendulum-like exchange is progressively reduced, and other mechanisms as elastic energy storage potentially come into play (Dewolf et al., 2016).

In conclusion, this research sheds light on the impact of trunk flexion on gait dynamics and its neuromuscular control. The study reveals that even subtle changes in trunk orientation, as observed in older adults (Dewolf et al., 2022, 2021a) lead to adjustments in lower limb kinematics, step-to-step transitions, ground reaction forces, and lower-limb muscle activation patterns (Fig. 6B). Notably, increased trunk flexion introduces mechanical challenges due to the modification of CoM position (Müller et al., 2017). These findings underline the complex interplay between mechanics and neural control of gait, enhancing our understanding of human bipedal walking and its biomechanical underpinnings.

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Competing interests

The authors declare no competing or financial interests.

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Data availability

All data and custom software related to this paper are available from Zenodo: https://doi.org/10.5281/zenodo.12763511

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630

Figure Legends

Figure 1 Typical traces of one representative stride in each condition showing the ground reaction force and the raw signals of muscle activity. (**A**) The stickman illustrates the contact of the leading limb during walking with a 10° inclined trunk. Three joint angles were measured (ankle, knee and hip) as well as the orientation of the trunk relative to the vertical. The trunk was defined as the segment connecting the greater trochanter to the apex of the acromion. The pictures illustrate one participant in each condition during the double contact phase of walking. (**B**) The curves represent (top) the vertical and (bottom) forward ground reaction force normalized by body weight (F_v and F_f, respectively), acting upon each leg separately (continuous line: front leg; dotted line: back leg). The vertical continuous and dotted lines are the foot contact (FC) and the toe-off (TO), respectively. The peak of vertical force under the back leg (F_{back}) and the front leg (F_{front}), and the peak of negative ($F_{f,brake}$) and positive ($F_{f,propulsive}$) fore-aft force are indicated in the graph. (**C**) Typical raw EMG signal of the vastus medialis and lateralis (VM and VL), anterior tibialis (TA), and medial and lateral gastrocnemius (GM and GL), at each trunk inclination.

Figure 2 Spatio-temporal parameters of walking. Left: Mean and individual data point of the anterior trunk flexion during walking. Middle: Mean and individual data point of the percentage of stride duration relative to the cycle duration with increasing trunk flexion. Right: Mean and individual data point of stance duration relative to increasing trunk flexion. The bars represent the average, and the circles represent the mean values for each condition participant. The asterisks (*) denote post hoc comparisons between the normal condition and the other conditions (*$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$).

Figure 3. Joint angles of the lower limbs during walking. (**A**) The joint angle of the hip (bottom), knee (middle), and ankle (below) relative to the percentage of the stride at 4 km h^{-1} in each condition. All the curves of each participant walking at a given trunk inclination condition were first averaged (mean curve). The dashed black curve represents the average joint angle of normal walking. The black curve and the grey zone represent the average joint angle and the standard deviation, respectively, of 10°, 20°, 30° and 40° degrees of trunk inclination. The 0° corresponds to the standing posture, the positive values represent a more flexed joint than during standing. (**B**) The average range of motion of the hip, knee, and foot over one stride at 4 km h^{-1}. Each participant's strides walking a given trunk inclination condition were first averaged. The rectangles represent the grand mean of each condition at the hip, knee, and ankle joints. Thin bars represent the standard deviation. In panels A and B, an angle of 0° corresponds to a standing position.

Figure 4. Step-to-step transition strategy. (**A**) The upper and lower graphs represent the vertical (V_v) and forward (V_f) velocity of the CoM, respectively, as each trunk inclination. The

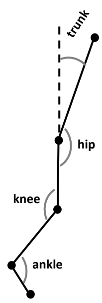
black dots indicate the minimal ($V_{v\ min}$ and $V_{f\ min}$) and maximal ($V_{v\ max}$ and $V_{f\ max}$) velocity of the CoM. (**B**) Occurrence of the $V_{v\ min}$ (left graph) and $V_{f\ min}$ (right graph) of the CoM relative to FC with increasing trunk flexion during walking. (**C**) Vertical and forward peak forces normalized to body weight for the back leg (F_{back} and $F_{f,propulsive}$) and front leg (F_{front} and $F_{f,\ brake}$) as a function of trunk flexion. Other indication as in Fig. 2.

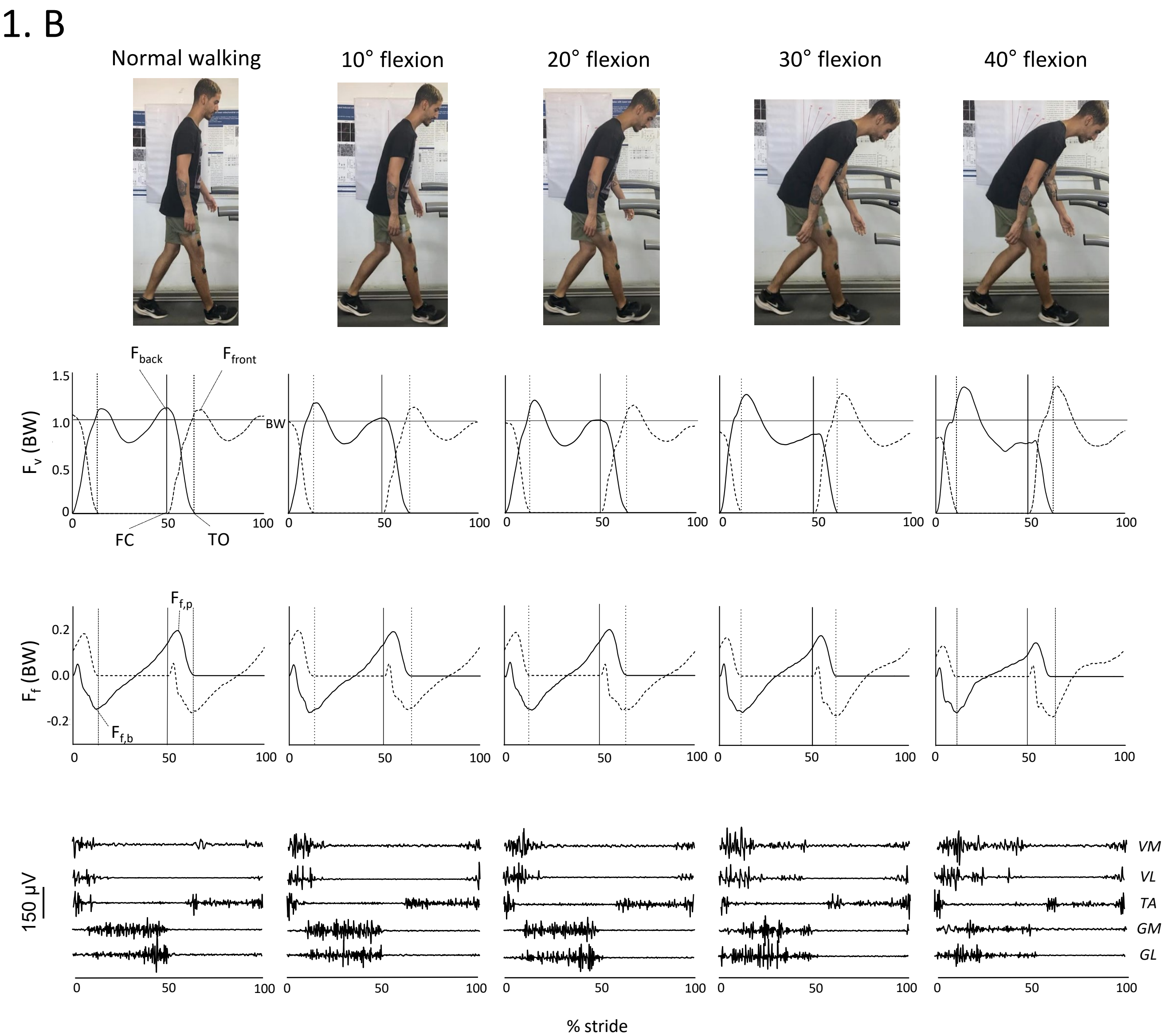
Figure 5. Pendulum mechanism of walking. (**A**) Typical traces of one representative stride of one participant (same as Fig. 1) in each condition illustrating kinetic (E_k), potential (E_p) and centre of mass energy (E_{com}) with the different trunk flexion. Other indication as in Fig. 1. (**B**) Positive external work to move the CoM relative to the surroundings over one stride (W_{com}) and average recovery during the stride (in %) with increasing trunk flexion. Other indication as in Fig. 2.

Figure 6. Muscular activity during walking. (A) Typical traces of the filtered and rectified EMG amplitude (in µv) of one representative stride of one participant (Same as Fig. 1) in each condition. The black horizontal line represents the duration of the stance phase, whereas the white one represents the duration of the swing phase. The y-axis indicates the amplitude of the EMG activity, with a vertical bar representing 4 µV as a reference. (**B**) Top: Mean activation (top), Full Width Half Maximum (FWHM, middle), and centre of activity (CoA, bottom) of the 6 lower-limb muscles as a function of trunk flexion. Other indication as in Fig. 2.

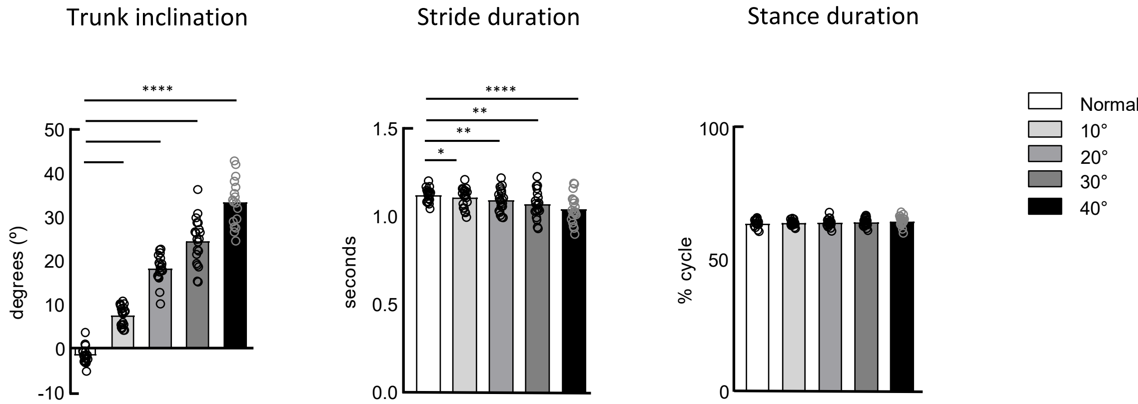
Figure 7. Initial and final muscular activity and schematic summary of the study results. (**A**)Top: Typical traces of the amplitude of the activation of the medial gastrocnemius at each condition. The grey areas indicate the initial and final 20% of the stance phase during a stride. Bottom: Mean activation of VM, VL, GM, and GL during the initial (left) and the final (right) 20% of the stance phase. Other indication as in Fig. 2. (**B**) Left: Schematic representation of the anticipated and unanticipated transition, defined by the time of the redirection velocity of the CoM relative to foot contact (FC), during normal walking and with a 40° flexion. The arrows represent the vertical velocity vector of the CoM. At the bottom, the corresponding vertical forces of the front legs during the double contact phase are represented, as well as the delay between foot contact of the front leg and the minimum vertical velocity (red brackets). Right: Schematic representation of the muscle activation at the FC and toe off (TO) with normal and 40° trunk flexion. The + indicate a greater muscular activation than during normal walking.

Figure


1. A
trunk
hip
knee
ankle

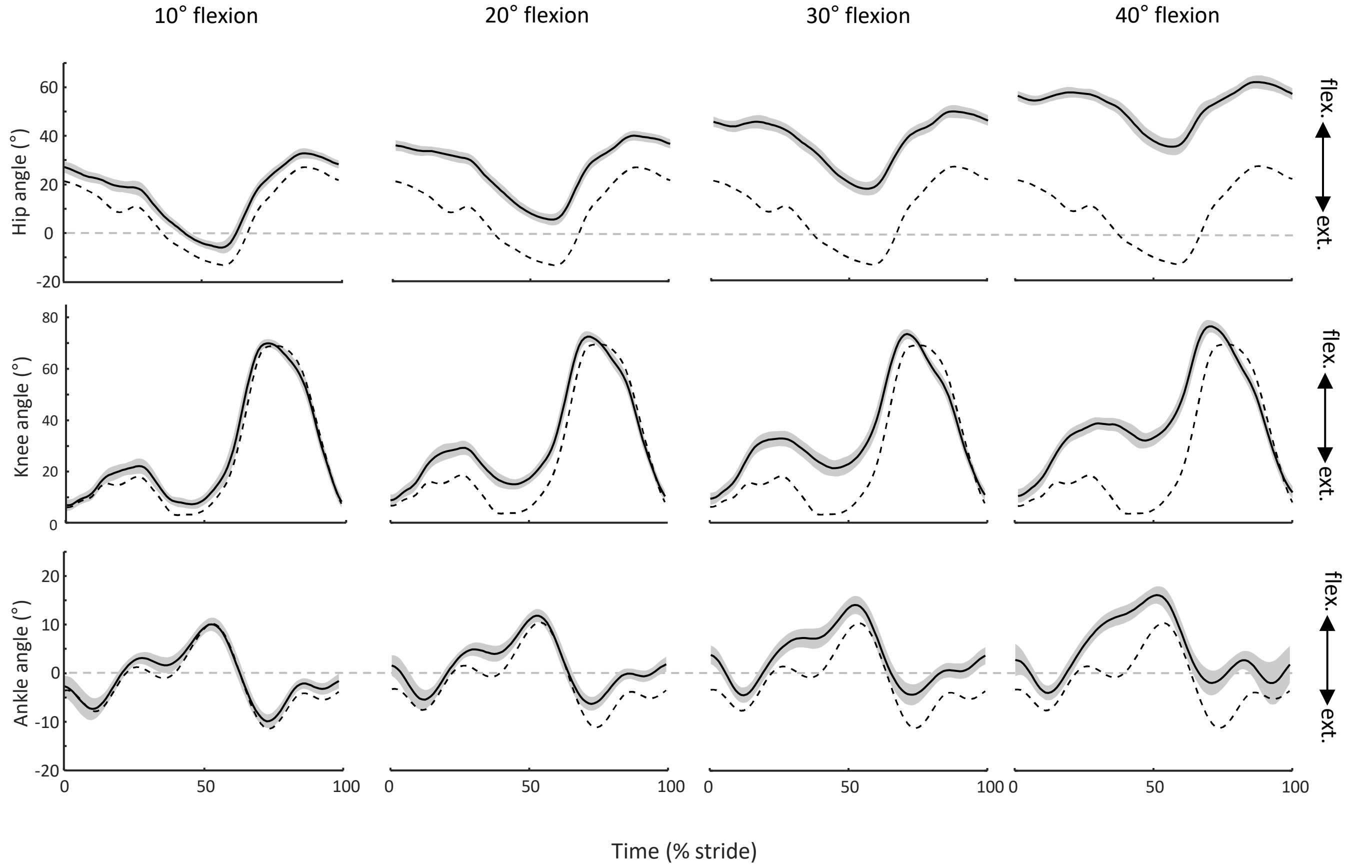

1. B
Normal walking
10° flexion
20° flexion
30° flexion
40° flexion
F back
F front
BW
Fv (BW)
FC
TO
Ff (BW)
Ff,p
Ff,b
150 µV
VM
VL
TA
GM
GL
% stride

2.



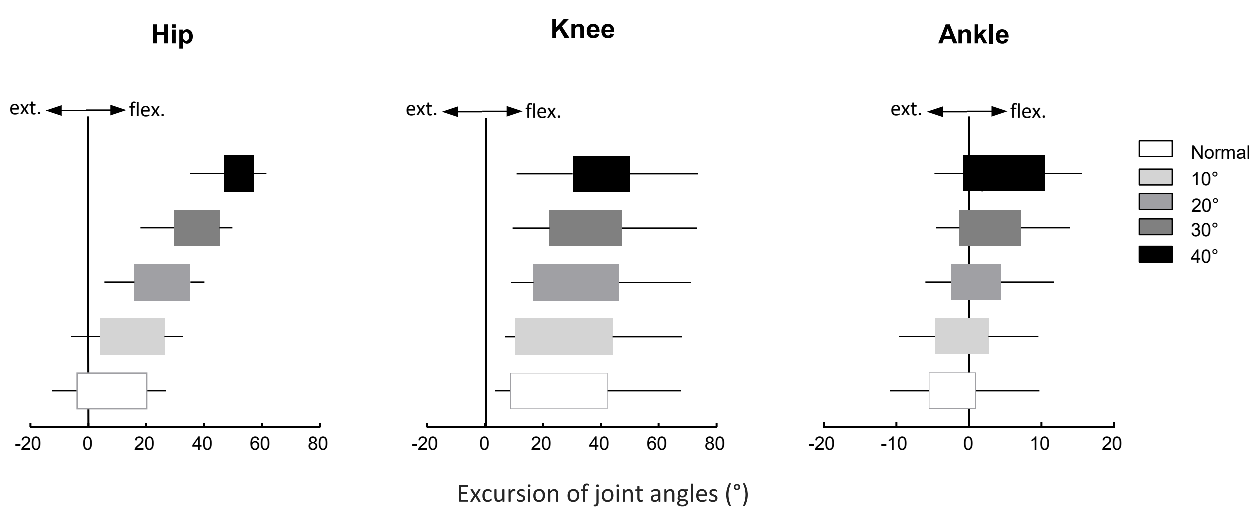
Trunk inclination
Stride duration
Stance duration
****
50
40
30
20
10
0
-10
degrees (°)
****
**
**
*
1.5
1.0
0.5
0.0
seconds
100
50
0
% cycle
Normal
10°
20°
30°
40°

3. A



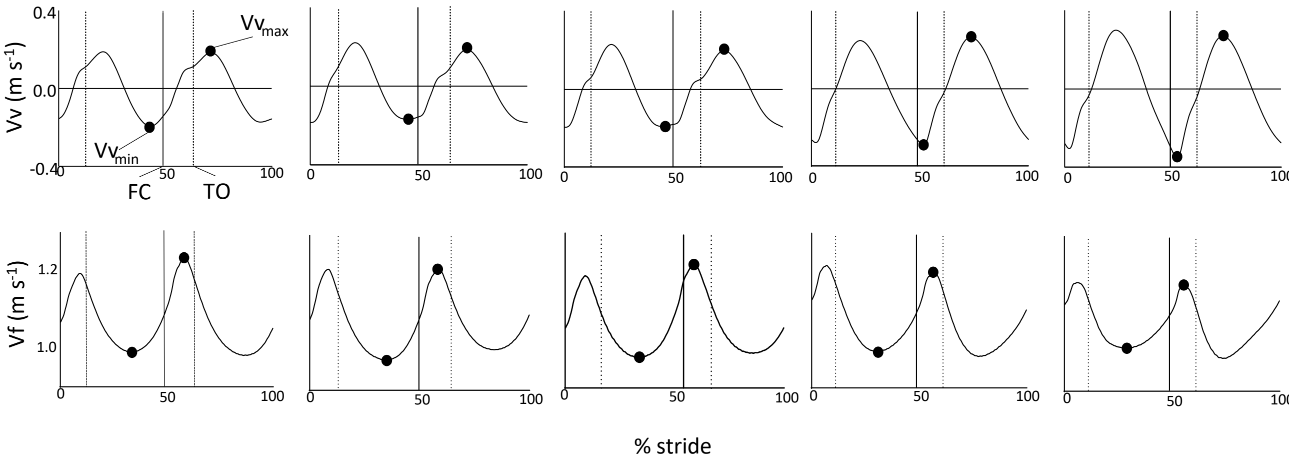
10° flexion
20° flexion
30° flexion
40° flexion
Hip angle (°)
Knee angle (°)
Ankle angle (°)
flex.
ext.
60
40
20
0
-20
80
10
-10
50
100
Time (% stride)

3. B



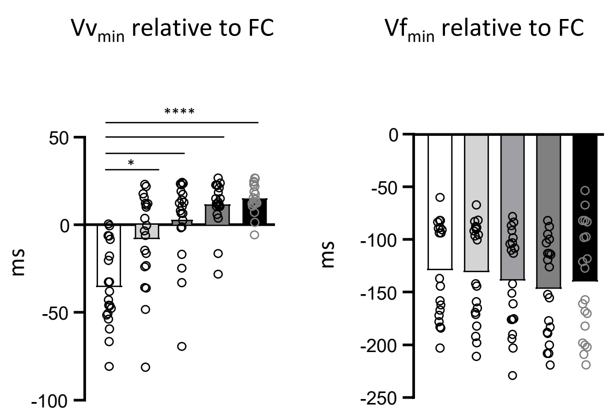
Hip
Knee
Ankle
ext.
flex.
Normal
10°
20°
30°
40°
-20
0
20
40
60
80
-10
10
Excursion of joint angles (°)

4.A



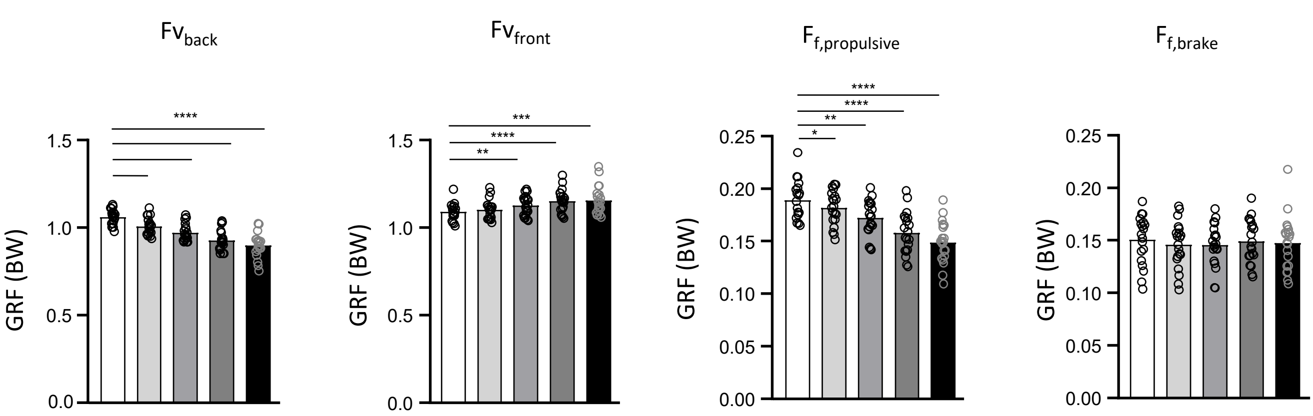
Vv (m s-1)
0.4
0.0
-0.4
Vvmax
Vvmin
FC
TO
Vf (m s-1)
1.2
1.0
0
50
100
% stride

4.B



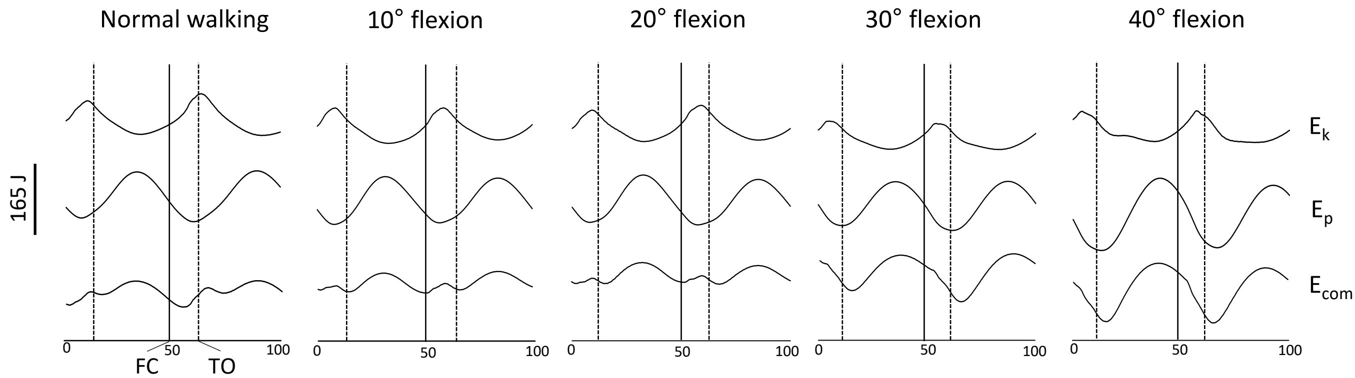
Vvmin relative to FC
Vfmin relative to FC
ms
50
0
-50
-100
-150
-200
-250
****
*

4.C



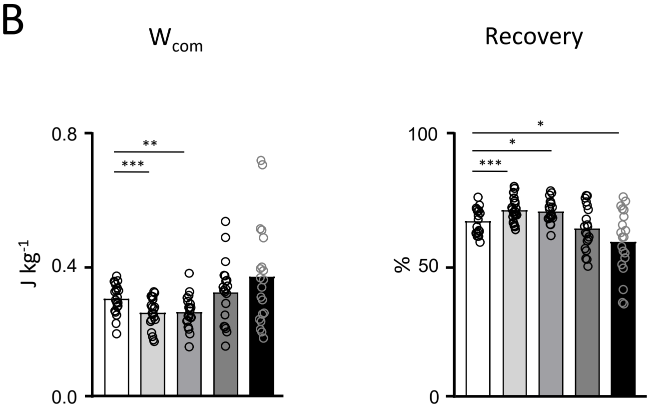
Fvback
Fvfront
Ff,propulsive
Ff,brake
GRF (BW)
1.5
1.0
0.5
0.0
0.25
0.20
0.15
0.10
0.05
0.00
****
***
**
*

5.A



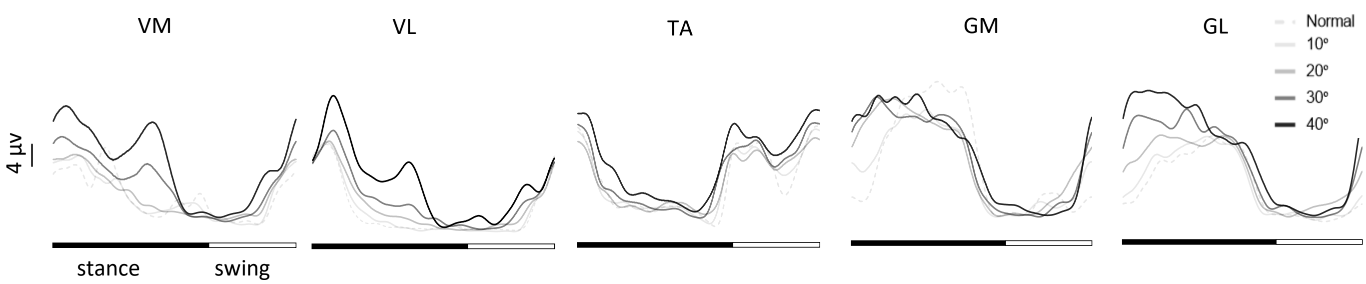
Normal walking
10° flexion
20° flexion
30° flexion
40° flexion
165 J
Ek
Ep
Ecom
0
50
100
FC
TO

5.B

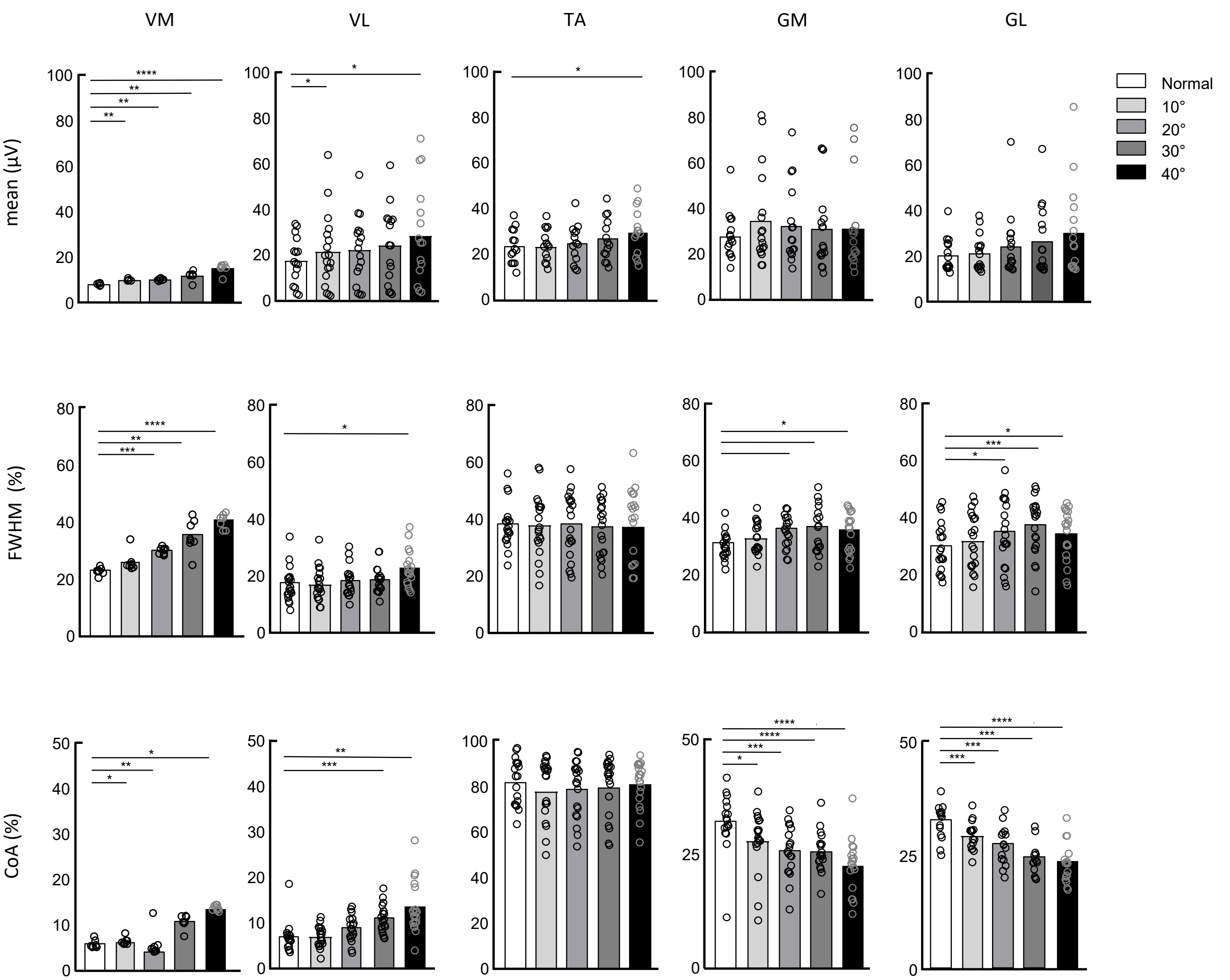


Wcom
Recovery
J kg-1
0.8
0.4
0.0
%
100
50
0
**
***
*
*
***

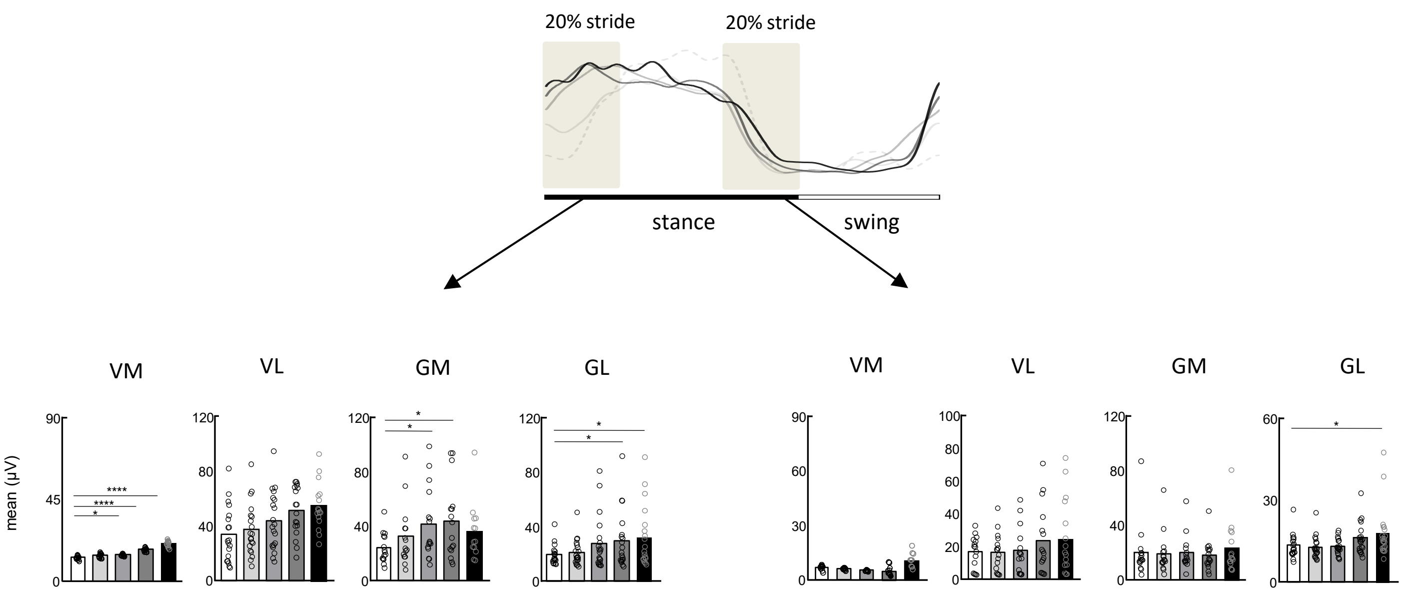
6.A


VM
VL
TA
GM
GL
Normal
10º
20º
30º
40º
4 µv
stance
swing

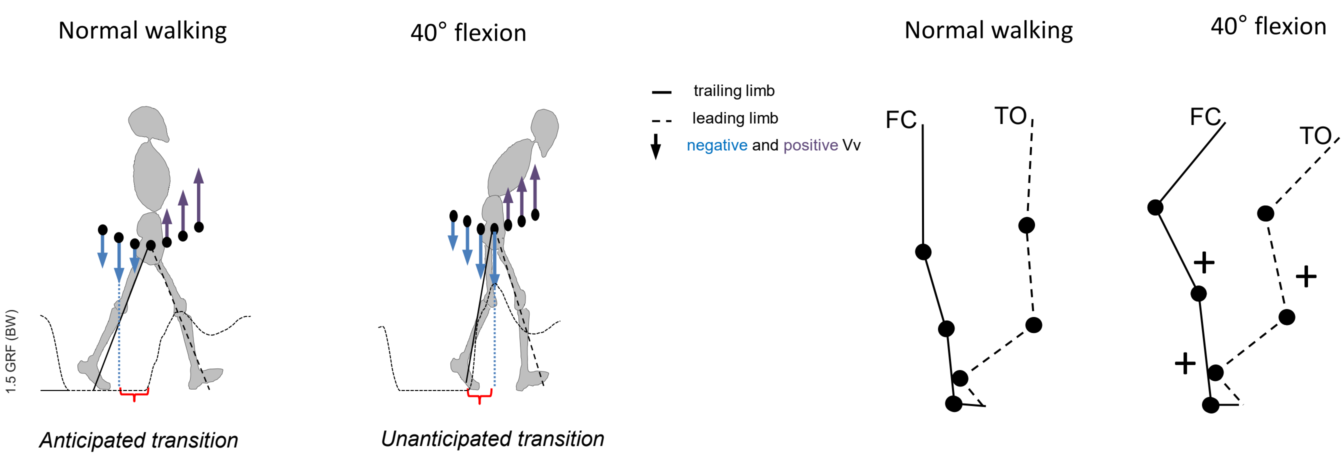
6.B


VM
VL
TA
GM
GL
Normal
10°
20°
30°
40°
mean (µV)
FWHM (%)
CoA (%)

7.A


20% stride
20% stride
stance
swing
VM
VL
GM
GL
VM
VL
GM
GL
mean (µV)

7.B


Normal walking
40° flexion
Normal walking
40° flexion
trailing limb
leading limb
negative and positive Vv
1.5 GRF (BW)
FC
TO
FC
TO
Anticipated transition
Unanticipated transition

S1

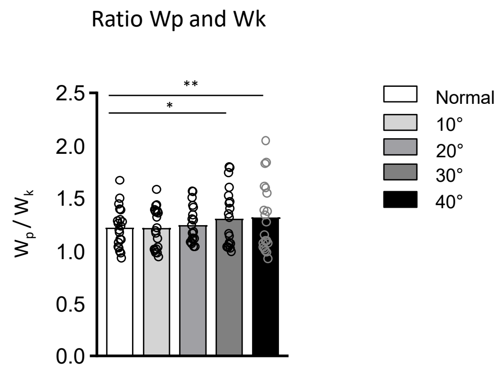


Figure S1. Average comparison of walking conditions with trunk flexion: the ratio of potential and kinetic work over one stride (W_p/W_k) with increasing trunk flexion. The bars represent the average, and the circles represent the mean values for each condition participant. The asterisks (*) denote post hoc comparisons between the normal condition and the other conditions (*p < 0.05, ** p < 0.01, *** p < 0.001, **** p < 0.0001). The statistical significance of the differences between conditions was assessed using a mixed-effects model ($F_{4,76}$ = 3.48, p = 0.011). Post hoc analysis results: normal vs. 10°, p = 0.9050, ES = 0.1198; normal vs. 20°, p = 0.5350, ES = 0.6232; normal vs. 30°, p = 0.0208, ES = 2.361; normal vs. 40°, p = 0.0094, ES = 2.665.