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# Effects of acute trans-spinal neuromodulation on trunk posture and sacral motor output during gait in older adults

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ABSTRACT

*Background:* Age-related decline in trunk control during gait increases fall risk and limits mobility. *Trans*-Spinal direct current stimulation is a non-invasive technique that may modulate spinal motor output and improve neuromuscular function. This study investigated whether a single session of cathodal trans-spinal direct current stimulation alters trunk posture and sacral motor output in older adults during walking.
*Methods:* Nineteen older and twenty young adults participated in a double-blind, sham-controlled study. Participants received either twenty minutes of cathodal trans-spinal direct current stimulation or sham stimulation while seated. Before and after stimulation, gait data were collected on a treadmill, including full-body kinematics, ground reaction forces, and surface electromyography from multiple lower-limb and trunk muscles. Electromyography data were projected onto a spinal topographical map to estimate segmental motor output, particularly at sacral levels.
*Findings:* In older adults, trans-spinal direct current stimulation reduced the amplitude and shifted the timing of sacral motor output during walking, without significantly altering ground reaction forces. These neuromuscular changes were accompanied by a reduction in trunk flexion. No changes were observed in younger adults.
*Interpretation:* A single session of cathodal trans-spinal direct current stimulation can acutely modulate sacral motor output and trunk posture in older adults without affecting kinetic parameters. These findings suggest that trans-spinal direct current stimulation may support clinical interventions aiming to address age-related neuromuscular decline during locomotion.

## 1. Introduction

The ability to walk safely and independently is a key determinant of autonomy and quality of life in older adults (Freiberger et al., 2020). As life expectancy increases, preserving mobility becomes a central challenge in aging populations due to its close link with functional capacity, fall risk, and overall health outcomes (Fielding et al., 2011; Geirsdottir et al., 2022; Studenski, 2011). With aging, a redistribution of joint mechanics from distal to proximal segments occurs, where older adults rely less on the ankle and more on the hip to generate forward progression (Delabastita et al., 2021; Franz, 2016; Waanders et al., 2019). This shift also encompasses increased anterior trunk flexion, another hallmark of aging gait (Honda et al., 2023), which has been associated with mechanical alterations, specifically in double contact phase (Núñez-Lisboa et al., 2024).

Although biomechanical changes clearly influence gait with aging, these changes cannot be explained solely by a decline in propulsive power generation, suggesting that neural factors also play a critical role (Avaltroni et al., 2024; Boyer et al., 2017; Hortobagyi et al., 2011; Hortobágyi et al., 2009; Monaco et al., 2010; Peterson and Martin, 2010). In particular, consistent age-related differences in muscle activation patterns have been observed across a wide range of walking tasks in older adults despite differing biomechanical demands and propulsion requirements (Dewolf et al., 2021a, 2021b).

By mapping multi-muscle EMG activity onto the spinal cord in correspondence with the approximate rostro-caudal locations of motor neuron pools, it is possible to infer segmental spinal motor output during locomotion (Cappellini et al., 2010; Dewolf et al., 2019a; Ivanenko et al., 2008, 2013; La Scaleia et al., 2014; Yokoyama et al., 2017). Dewolf et al. (2021a & 2021b) demonstrated that older adults exhibit earlier and

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**Table 1**
Individual characteristics.

| | Young adults | | Older adults | | |
|---|---|---|---|---|---|
| *Variable* | sham | stim | sham | stim | |
| n | 10 | 10 | 9 | 10 | |
| Sex | ♂ = 8, ♀ = 2 | ♂ = 9,♀ = 1 | ♂ = 3,♀ = 6 | ♂ = 5,♀ = 5 | |
| Age (years) | 27.2 ± 4.9 | 27.3 ± 3.3 | 71.4 ± 4.1 | 71.6 ± 5 | * |
| Height (cm) | 177.7 ± 7.6 | 179.9 ± 8.3 | 166 ± 5.5 | 171.9 ± 12.2 | * |
| Weight (kg) | 76.3 ± 7.3 | 71.4 ± 10.4 | 66.7 ± 7.2 | 76.1 ± 14.9 | † |
| BMI (kg $m^{-2}$) | 24.2 ± 2.1 | 22 ± 2.4 | 24.2 ± 2.7 | 25.5 ± 2.6 | † * |
| Met-min/week | 3888 ± 2650.4 | 4968 ± 1614.7 | 4651.1 ± 6063.7 | 3926 ± 2852 | |

The table presents the characteristics of the young and older adult participants, grouped according to stimulation condition (sham or stim). The variables include age (years), height (cm), weight (kg), body mass index (BMI) (kg/$m^2$), and physical activity level expressed as MET-min/week. Data are reported as means with corresponding standard deviations (±). Significant main effects of age and the interaction between age and tsDCS are indicated with the symbols * and †, respectively.

broader temporal distribution and earlier activation of muscles innervated by sacral segments compared to younger individuals. These findings suggest a systematic shift in the spatiotemporal organization of spinal motor output with age. However, to our knowledge, whether and how this age-related segmental organization can be acutely modulated during walking using neuromodulation remains unknown. To date, studies using non-invasive spinal neuromodulation have primarily focused on reflex modulation or clinical populations, with limited examination of its impact on segmental spinal motor output during gait in healthy older adults.

While interventions such as exercise-based training improve strength and balance (Allen et al., 2021; Hepple and Rice, 2016), their effects on segmental spinal motor control during functional tasks such as walking are less well characterized (Beijersbergen et al., 2013; Boyer et al., 2012), highlighting the need for complementary neuromodulatory strategies. *Trans*-Spinal direct current stimulation (tsDCS) is a non-invasive technique that modulates afferent input and spinal network excitability (Song and Martin, 2017). Although cortical stimulation techniques such as transcranial direct current stimulation have been used to modulate motor performance, gait control largely relies on lumbosacral sensorimotor circuits integrating afferent feedback and descending input (Avaltroni et al., 2024; Di Russo et al., 2023; Rybak et al., 2015). The age-related changes previously observed in spinal motor maps specifically involve sacral segment activity, suggesting a segmental reorganization at the spinal level rather than a purely cortical alteration (Dewolf et al., 2021a, 2021b; Monaco et al., 2010). Therefore, targeting the spinal cord allows a more direct modulation of the neural structures implicated in locomotor rhythm generation and posture control during walking.

Evidence from clinical and healthy populations indicates that tsDCS can modify muscle activity and gait coordination by influencing spinal motor circuits (Hubli et al., 2013; Skiadopoulos and Knikou, 2024). Computational modeling also indicates that electrode montage strongly shapes current distribution within lumbar spinal structures (Pereira et al., 2022). However, its potential to mitigate age-related neuromuscular changes during walking remains unexplored.

From a clinical perspective, improving spinal motor coordination could contribute to better postural control and reduced fall risk in aging populations. Therefore, this study aimed to determine whether a single session of cathodal tsDCS applied over the lumbosacral region

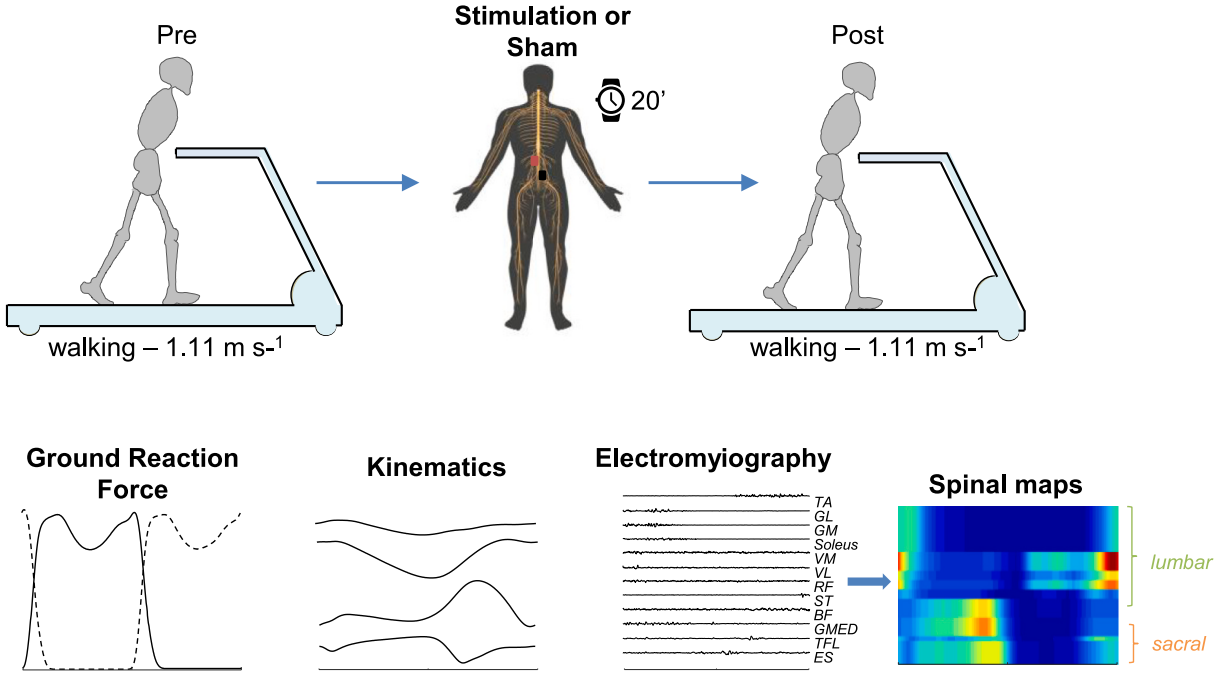


**Fig. 1.** Experimental design and data acquisition. (A) Participants performed treadmill walking before (Pre) and after (Post) a 20-min trans-spinal direct current stimulation (tsDCS) or sham session. The stimulation targeted the thoracolumbar spinal cord through surface electrodes positioned over T11 (anode) and the lumbosacral region (cathode). (B) Biomechanical and neurophysiological data collected included ground reaction forces (GRF), kinematics of the trunk and lower limbs, raw EMG from 12 lower-limb muscles, and segmental spinal motor output estimated from spinal mapping.

modulates spinal motor output and trunk posture during walking in older adults. Cathodal tsDCS has often been associated with inhibitory-like modulation of spinal excitability in humans, although polarity-specific effects at the spinal level do not strictly mirror those observed with cortical stimulation (Kuck et al., 2018; Powell et al., 2019; Winkler et al., 2010). Given the earlier and broader sacral-related motor output reported in older adults (Dewolf et al., 2021a; Nùñez-Lisboa et al., 2023a; Núñez-Lisboa and Dewolf, 2025), suggesting a relative over-activation or reduced temporal specificity of sacral segments, we selected a cathodal montage to test whether downregulating this sacral bias could rebalance segmental spinal motor output during walking. Our aim was therefore not to induce a global inhibition, but rather to restore a more temporally specific segmental organization. Based on previous literature, we first expected to replicate the age-related sacral motor output pattern previously described in older adults, to provide a reference against which tsDCS-induced modulation could be interpreted. We then hypothesized that active cathodal tsDCS, compared with sham, would attenuate the age-related sacral bias during walking, resulting in a later and reduced sacral-related motor output, shifting toward the young adult activation profile. We further hypothesized that this segmental modulation would be accompanied by measurable changes in gait biomechanics, particularly in older adults.

## 2. Methods

### 2.1. Participants

Twenty younger adults (27.2 ± 4.1 years old) and twenty older adults (71.5 ± 4.5 years old) were included in the study (see Table 1 for individual characteristics). One older adult was excluded due to voluntary dropout. Participants were randomly assigned to either the sham or stimulation group. Inclusion criteria included: (1) ability to walk 1 km, (2) no musculoskeletal injury, (3) no neurological disorders. All participants gave written informed consent. The study protocol was approved by the UCLouvain ethics committee, Brussels, Belgium (Belgian Registration Number: B403201524765) and adhered to the Declaration of Helsinki.

### 2.2. Experimental protocol

*Gait:* Participants walked at 1.11 m/s (4 km/h) on an instrumented treadmill (H/P Cosmos-Stellar, Germany) with four force transducers (Arsalis, Belgium) collecting 3D ground reaction forces (GRF) at 1000 Hz (Fig. 1). The selected walking speed was similar to the one used in our previous studies (Dewolf et al., 2019a; Dewolf et al., 2021a, 2021b, 2022) and was reported as a comfortable and economical average walking speed. Before starting data collection, participants familiarized themselves with treadmill walking through multiple trials with verbal feedback from the experimenter. Data acquisition started after the familiarization period and after at least 30 s of steady-state walking.

*trans-Spinal direct current stimulation (tsDCS):* Cathodal tsDCS was delivered at 2.5 mA for 20 min using a battery-driven stimulator (Soterix Medical, USA) with two 10 × 5 cm surface electrodes. For active stimulation, the cathode (active electrode) was positioned longitudinally over the lumbosacral region, aligned with the spinal axis, and the anode (return electrode) was positioned over T11, also aligned with the spinal axis. For sham, the current was ramped up for 30 s and then turned off. This longitudinal montage was selected to preferentially target lumbosacral circuitry relevant to gait; modeling work shows that tsDCS electrode montage strongly shapes the resulting electric field distribution within lumbar spinal structures (Pereira et al., 2022). Skin was shaved and cleaned to reduce impedance, and charge density remained within safety limits (~85.7 mC/cm$^2$). Participants remained seated and relaxed during stimulation. A seated position was used since maintaining an upright standing posture for 20 min could have induced postural fatigue or altered baseline neuromuscular activation, potentially confounding pre–post gait comparisons (especially in older adults). Instead, the seated position unsure comfort and stable electrode contact.

### 2.3. Data collection

During walking, ground reaction forces, kinematics and surface electromyographic activity were recorded. Considering both the pre- and post-stimulation trials, an average of 56.2 ± 5.8 strides were analyzed per participant.

#### 2.3.1. Ground reaction forces

The three components of the ground reaction forces (vertical ($F_v$), fore-aft ($F_f$), and mediolateral ($F_l$)) were collected at a sampling rate of 1000 Hz (Willems and Gosseye, 2013). The treadmill used for gait and balance analysis (H/P Cosmos-Stellar treadmill, Germany, belt surface: 1.6 × 0.65 m) was equipped with four force transducers (Arsalis®, Belgium).

#### 2.3.2. EMG

Surface electromyographic activity (global bi-polar EMG) of muscle was recorded from 12 right-sided muscles using a Delsys Trigno Wireless System (Delsys®, Boston, MA), at a sampling frequency of 2048 Hz. The muscles recorded included *erector spinae* (ES), *tensor fasciae latae* (TFL), *gluteus medius* (Gmed), *vastus medialis* (VM), *vastus lateralis* (VL), *rectus femoris* (RF), *tibialis anterior* (TA), *semitendinosus* (ST), *biceps femoris* (BF), *gastrocnemius lateralis* (GL), *gastrocnemius medialis* (GM), and *soleus* (SOL). Before placing the electrodes, the skin was prepared (shaved and cleaned) in line with SENIAM recommendations (www.seniam.org). Electrodes were placed parallel to muscle fibers after palpation, and signal quality was verified using standardized test contractions (plantarflexion; gastrocnemius co-activation expected). EMG signals were synchronized with kinetic and kinematic data using a Delsys Trigger Module.

#### 2.3.3. Kinematics

The three-dimensional full-body kinematic data were collected at 240 Hz using a Qualisys motion capture system (Gothenburg, Sweden), which included 14 Oqus 600+ and 4 Miqus M3 cameras positioned around the treadmill. A total of 20 reflective markers were attached bilaterally to anatomical landmarks including the neck, shoulders, elbows, wrists, anterior and posterior superior iliac spines, greater trochanters, external condyles of the knee, malleoli, and fifth metatarsal heads, based on reproducible palpation guidelines (Serge Van Sint Jan et al., 2007).

### 2.4. Data analysis

#### 2.4.1. General gait parameters

The first instant of foot contact (FC) and toe-off (TO) events were estimated from the displacement of the center of pressure (CoP) on the treadmill belt (Meurisse et al., 2016). A stride was delimited by two successive right FC and contact phases were measured as the time between foot contact (FC) and toe-off (TO) of the same leg.

#### 2.4.2. Kinetics

The vertical velocity of the CoM ($V_v$) was calculated by time-integration of the vertical acceleration of the CoM (Dewolf et al., 2016). The time of occurrence of the minimum vertical velocity of the CoM ($V_{v,min}$) at the beginning of the double contact phase (DC) was then detected. Additionally, the peak vertical forces under the front ($F_{front}$) and back ($F_{back}$) legs were identified at each step.

*Kinematics:* trunk, thigh, shank, and foot segment angles were calculated relative to the vertical (Borghese et al., 1996; Dewolf et al., 2018), with 0° indicating the vertical. Then, the hip, knee and ankle joint angles were then computed from the relative orientations of adjacent segments. The average angle and range of motion (ROM) were

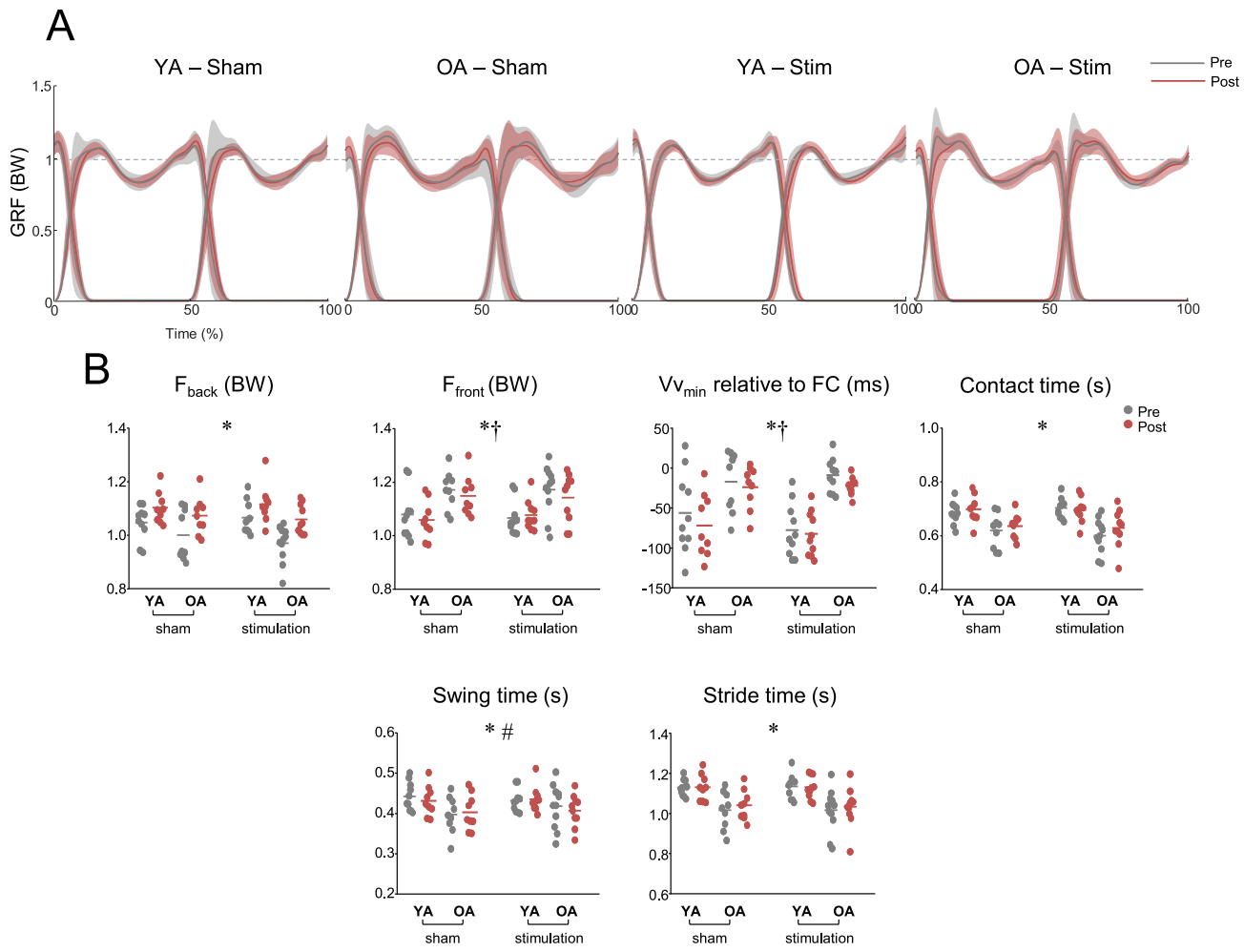


**Fig. 2.** Vertical ground reaction force (GRFv) patterns and summary metrics before (Pre) and after (Post) trans-spinal direct current stimulation (tsDCS) across age groups. (A) Time-normalized vertical GRF signals (mean ± SD) over five gait cycles, expressed relative to body weight, and separated by group and condition. (B) Individual and group-averaged results for GRFv metrics, including first and second peak forces, loading rate, and impulse, grouped by condition (Pre/Post), age (YA = young adults/OA = older adults), and stimulation (sham/stim). Gray and red denote sham and stimulation, respectively. *Symbols denote significant effects ($p < 0.05$): Age (YA vs OA), †stimulation condition (stim vs sham), ‡Age×stimulation, and #Age×time (Pre vs Post) × stimulation. Post hoc pairwise differences are indicated by different letters (a,b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

calculated for the hip, knee, and ankle joints, as well as for trunk elevation angle.

### 2.4.3. EMG

The 12 raw EMG signals were high-pass filtered at 30 Hz, then rectified, and subsequently, low-pass filtered using a zero-lag 4th-order Butterworth filter at 10 Hz. Gait cycles containing evident artefacts were manually excluded following visual inspection. The root mean square (RMS) of each EMG signal was then computed across the gait cycle. For each condition, the full width half maximum (FWHM) was determined as the time during which the EMG activity exceeded half of its maximum value (Martino et al., 2014; Santuz et al., 2020). The centre of activity (CoA) of each EMG signal was measured as an estimation of the timing of activation. The CoA during the gait cycle was calculated using circular statistics (Batschelet, 1981) and plotted in polar coordinates. In brief, the CoA of the EMG waveform was calculated as the angle of the resultant vector (i.e., the first trigonometric moment) pointing to the center of mass of the circular distribution of EMG activity relative to the gait cycle (Martino et al., 2014).

### 2.4.4. Spinal maps

The EMG activities were then mapped onto the rostro-caudal positions of the motoneuron (MN) pools in the human spinal cord, ranging from segments L2 to S2. This mapping followed the **myotomal charts of** Kendall et al. (2005), based on the approximate rostro-caudal location of MN pools innervating different muscles in the human spinal cord (Dewolf et al., 2019b; Mesquita et al., 2023). To compute the total motor output for each condition, the motor output patterns across the gait cycle were summed across the lumbar, sacral and all spinal segments. The mean activation of the lumbar (L2 to L5) and sacral (S1 to S2) segments was computed by averaging the motor output patterns for each region. Finally, the FWHM and the CoA were calculated for both lumbar and sacral segments.

## 2.5. Statistics

The sample size was estimated a priori using G*Power 3.1.9.7 based on effect sizes reported by Awosika et al. (Awosika et al., 2019a, 2019b). In the absence of prior data examining tsDCS effects on segmental spinal motor output during walking, a simplified two-sample comparison was used as an approximation (effect size = 2.21, α = 0.05, power = 0.95), yielding an estimated minimum of 8 participants per condition. Final statistical analyses were performed using linear mixed-effects models to account for the repeated-measures design. Given that mixed models incorporate within-subject variance and repeated observations, this analytical approach provides greater statistical efficiency than the

**Table 2**
Mixed-model results for kinetic gait variables.

| Variable | Age | tsDCS | Time | Interactions |
|---|---|---|---|---|
| Contact time (s) | $F_{1,36}$ = 22.85, $p$ < 0.001 | / | / | ns |
| Swing time (s) | $F_{1,36}$ = 6.41, $p$ = 0.016 | / | / | Age×Time×tsDCS: $F_{1,34}$ = 4.34, $p$ = 0.045 |
| Stride time (s) | $F_{1,36}$ = 13.37, p < 0.001 | / | / | / |
| $F_{back}$ (BW) | $F_{1,36}$ = 9.31, p = 0.043 | / | / | / |
| $F_{front}$ (BW) | $F_{1,36}$ = 23.96, p < 0.001 | / | / | / |
| $V_{v,min}$ relative to foot contact (ms) | $F_{1,36}$ = 29.66, p < 0.001 | $F_{1,34}$ = 6.63, p = 0.015 | / | / |

Results from linear mixed-effects models examining the effects of Age (young vs older adults), Stimulation (active tsDCS vs sham), Time (pre vs post), and their interactions. Reported values correspond to F statistics and associated p-values for fixed effects. Only significant interaction terms are displayed explicitly. BW = body weight. / = non-significant ($p \geq 0.05$).

independent test used for power estimation. However, to ensure adequate power and account for a potential dropout, we included 10 participants per group. For each dependent variable, the normality of residuals was visually assessed using Q–Q plots. When the assumption of normality was not met, a log10 transformation was applied, and normality was re-evaluated and confirmed. A linear mixed-effects model was conducted with age group (young vs. older adults) and tsDCS condition (stimulation vs. sham) as fixed factors, and time (pre vs. post) as a repeated measure. Interactions were included and post hoc pairwise comparisons were performed using Bonferroni test. Primary outcomes were defined as spinal motor output and trunk angle, while other variables were treated as secondary or exploratory. Therefore, interaction effects and secondary outcomes were interpreted cautiously given multiple testing. Additionally, Statistical Parametric Mapping (SPM) was used to assess the $F_v$ and the spinal motor output of lumbar and sacral segments. In this analysis, statistical significance was defined based on a critical threshold $t^* > 4.3$, which the SPM{t} statistic must exceed at any point in the gait cycle to detect a meaningful difference. In the *Results* section, *P*-values are reported for fixed effects (main effects and interactions) from the linear mixed-effects models, unless explicitly stated as post hoc pairwise comparisons or SPM results. All statistical analyses were conducted using GraphPad Prism 8.0.1, with an alpha level of 0.05. SPM analyses were performed in MATLAB R2023a using the open-source spm1d toolbox (v0.4.12).

## 3. Results

Some variability in participant characteristics was observed between groups (Table 1). Older adults were smaller compared to young adults ($F_{1,35} = 12.14$, $p = 0.001$). No main effect of age or tsDCS was found on body weight (all $p > 0.41$). However, BMI was higher in older adults than in young adults (age main effect: $F_{1,35} = 4.9$, $p = 0.032$), with a significant age × tsDCS interaction ($F_{1,35} = 4.9$, p = 0.032). No main effect of tsDCS was observed ($F(1,35) = 0.3$, $p = 0.570$).

### 3.1. Walking kinetics

As already documented, contact ($F_{1,36} = 22.85$, $p < 0.001$), swing ($F_{1,36} = 6.408$, $p = 0.015$) and stride time ($F_{1,36} = 13.37$, p < 0.001) were significantly shorter in older adults compared to young participants (Fig. 2B, Table 2). A significant three-way interaction was found for swing time (age × time × tsDCS; $F_{1,34} = 4.339$, $p = 0.044$). No other significant main or interaction effects were found (all $p > 0.22$).

In all participants, the $F_v$ curve over a gait cycle showed the characteristic double-peak so-called M-pattern during walking (Fig. 2A). As already documented, in older adults, $F_{back}$ was significantly lower ($F_{1,36} = 9.307$, $P = 0.043$) whereas $F_{front}$ was significantly greater ($F_{1,36} = 23.96$, $p < 0.001$), as compared to young adults. Notably, SPM{t} analysis revealed no significant pre–post differences in any group, with all test statistics remaining below the critical threshold ($t > 4.3$)*. No effects of tsDCS or interaction were observed on $F_{back}$ (all $p > 0.230$), but $F_{front}$ was higher in the stimulation condition ($F_{1,34} = 38.82$, $p < 0.001$), without interaction with age (all $p > 0.30$). Finally, $V_{v,min}$ occurred later in the gait cycle in older adults as compared to young ($F_{1,36} = 29.66$, p < 0.001), and later in the sham group ($F_{1,34} = 6.627$, $p = 0.014$), with no interaction effects (Fig. 2B).

### 3.2. Kinematics of walking

To assess time-resolved differences in joint kinematics, SPM{t} was applied across the gait cycle. In young and older adults with both sham and stimulation, no significant differences were found with time in any of the angle analyzed ($p > 0.05$). Still, an increased trunk elevation was significantly different between age-group ($F_{1,36} = 21.42$, $p < 0.001$) and between tsDCS condition ($F_{1,35} = 4.697$, $p = 0.037$), with an additional interaction between age and tsDCS ($F_{1,35} = 4.508$, $p = 0.040$) (Fig. 3A; Table 3). No other main effects or interactions reached significance for ankle, knee, or hip angles (all $p > 0.100$), except a main effect of tsDCS on hip angle ($F_{1,35} = 4.738$, $p = 0.036$) (Fig. A.2).

### 3.3. Muscle activation during walking

The EMG activation amplitudes across the gait cycle revealed group-specific differences in muscle activation amplitude (Fig. 4). An effect of age was found for VL, RF, TA, ST, BF and GM (all $P < 0.02$), whereas an effect of tsDCS was observed for VM, RF, TA, ST, BF, GL, GM, and SOL (all $p < 0.040$) (Fig. 5 & A.1).

When mapped onto the rostro-caudal motoneuron pool representation, spinal maps highlighted distinct stimulation-related changes (Fig. 5A). Mean activation was higher in older adults at both lumbar ($F_{1,34} = 21.6$, p < 0.001) and sacral levels ($F_{1,34} = 18.9$, p < 0.001). By comparing the spinal activation before and after stimulation, SPM{t} analysis showed that the tsDCS increased lumbar output in young adults during the loading phase (0–5% of the gait cycle, $p = 0.006$), and decreased sacral output in older adults at multiple time windows: 95–3%, 7–9%, and 32–36% of the gait cycle (all $p < 0.050$). Indeed, the tsDCS significantly increased activity at both levels (lumbar: $F_{1,31} = 17.2$, p < 0.001; sacral: $F_{1,31} = 14.5$, p < 0.001). A main effect of time was found in the sacral region ($F_{1,34} = 5.43$, $p = 0.026$). Maximum activation showed an age effect at lumbar level only ($F_{1,31} = 5.40$, $p = 0.027$). tsDCS increased sacral max activity ($F_{1,31} = 9.72$, p < 0.001), with an age × tsDCS interaction ($F_{1,31} = 4.47$, $p = 0.043$), indicating greater responsiveness in older adults.

Temporal structure of spinal output revealed earlier center of activity (CoA) in sacral segments in older adults ($F_{1,34} = 9.89$, $p = 0.003$), with no effect at lumbar level. Burst duration (FWHM) was longer in older adults at both lumbar ($F_{1,34} = 13.2$, p < 0.001) and sacral levels ($F_{1,34} = 4.24$, $p = 0.047$), with an age × time interaction in lumbar FWHM ($F_{1,34} = 6.04$, $p = 0.019$).

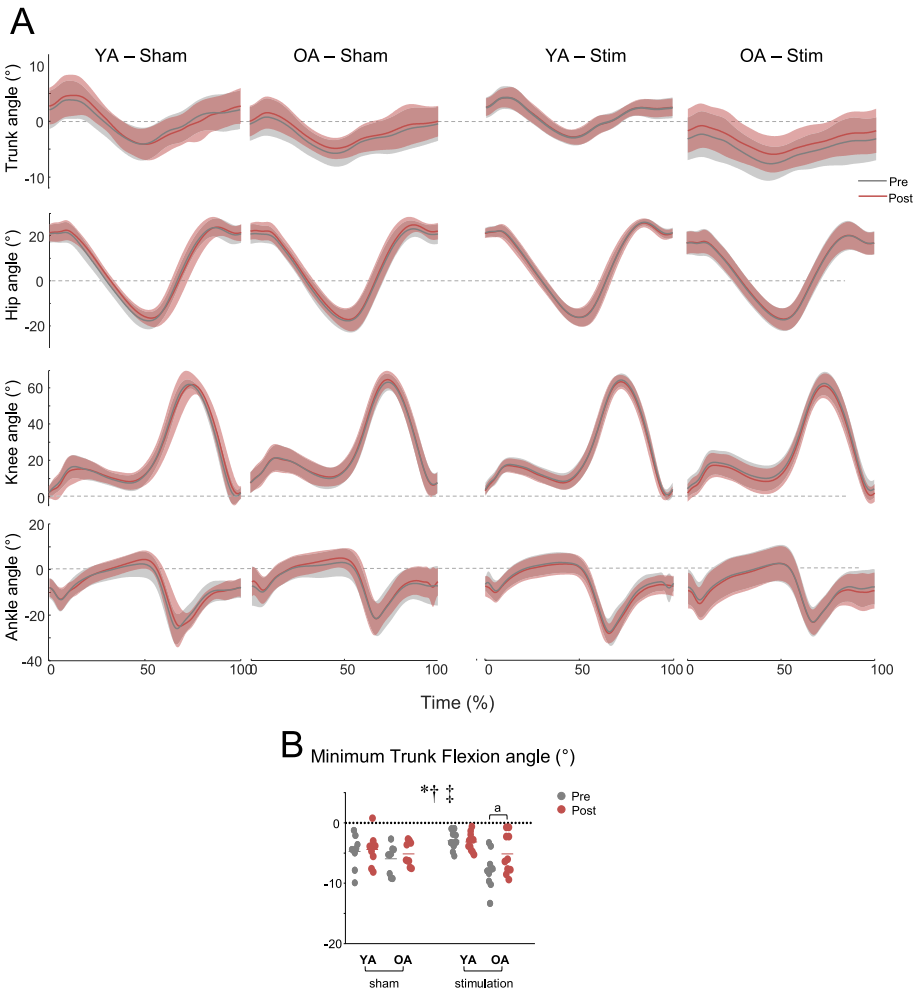


**Fig. 3.** Effects of tsDCS on trunk and lower limb kinematics during gait. (**A**) Time-normalized angular trajectories (Mean ± SD) of the trunk, hip, knee, and ankle across the gait cycle (%), shown for young adults (YA) and older adults (OA) under sham and stimulation (Stim) conditions, before (gray) and after (red) the intervention. Joint angles are represented in the sagittal plane, with extension (ext.) and flexion (flex.). Where 0° represents vertical alignment. (B) Minimum trunk flexion angle (°) pre - and post-intervention. Significance symbols are defined as in Fig. 2 ($p < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 3**
Mixed-model results for kinematic gait variables.

| Variable | Age | tsDCS | Time | Interactions |
|---|---|---|---|---|
| Trunk angle (°) | $F_{1,36} = 21.42$, $p < 0.001$ | $F_{1,35} = 4.70$, $p = 0.037$ | / | Age×tsDCS: $F_{1,35} = 4.51$, $p = 0.041$ |
| Trunk RoM Min (°) | $F_{1,35} = 11.55$, $p = 0.002$ | $F_{1,35} = 6.56$, $p = 0.015$ | / | Age×tsDCS: $F_{1,35} = 5.42$, $p = 0.026$ |
| Hip angle (°) | / | $F_{1,35} = 4.74$, $p = 0.036$ | / | / |
| Knee angle (°) | / | / | / | / |
| Ankle angle (°) | / | / | / | / |

Results from linear mixed-effects models examining the effects of Age (young vs older adults), Stimulation (active tsDCS vs sham), Time (pre vs post), and their interactions. Other information as in Table 3.

## 4. Discussion

This study aimed to evaluate whether a single session of cathodal tsDCS over the lumbosacral region could modulate gait patterns and spinal motor output in young and older adults. We hypothesized that tsDCS would reorganize the spinal motor output during walking, particularly in sacral segments, and induce changes in gait biomechanics in older participants. Our findings partially support this hypothesis. A single tsDCS session modulated sacral spinal motor output in older adults and induced subtle but significant changes in trunk posture, while kinetic and joint-level adaptations remained limited.

Baseline age-related differences in sacral spinal motor output and vertical force distribution (lower $F_{back}$ and higher $F_{front}$ in older adults) were consistent with prior work and are reported here only to contextualize the tsDCS effects (Dewolf et al., 2021a, 2021b; Ivanenko et al., 2013; Monaco et al., 2010; Nùñez-Lisboa et al., 2023b) (Fig. 2B). Against this baseline, the clearest stimulation-related effect was postural: tsDCS reduced trunk flexion in older adults (Fig. 3B). Given the link between trunk inclination, propulsion, and step-to-step coordination (Dewolf et al., 2022; Honda et al., 2023; Núñez-Lisboa et al., 2024), this postural adaptation may reflect an acute modulation of gait-related control. We therefore interpret this modest change as a shift in trunk alignment during walking, consistent with tsDCS influencing lumbosacral sensorimotor processing relevant to trunk control.

While the kinematic adaptations were limited, we observed a decrease in sacral output amplitude without changes in burst timing or duration, suggesting an acute modulation of the magnitude of segmental motor output rather than of its temporal organization (Fig. 5B). Indeed, after tsDCS, a reduction of the amplitude of sacral motor output is observed, particularly during early and late stance phases (Fig. 5A). While a modest decrease in sacral output is also observed in the sham

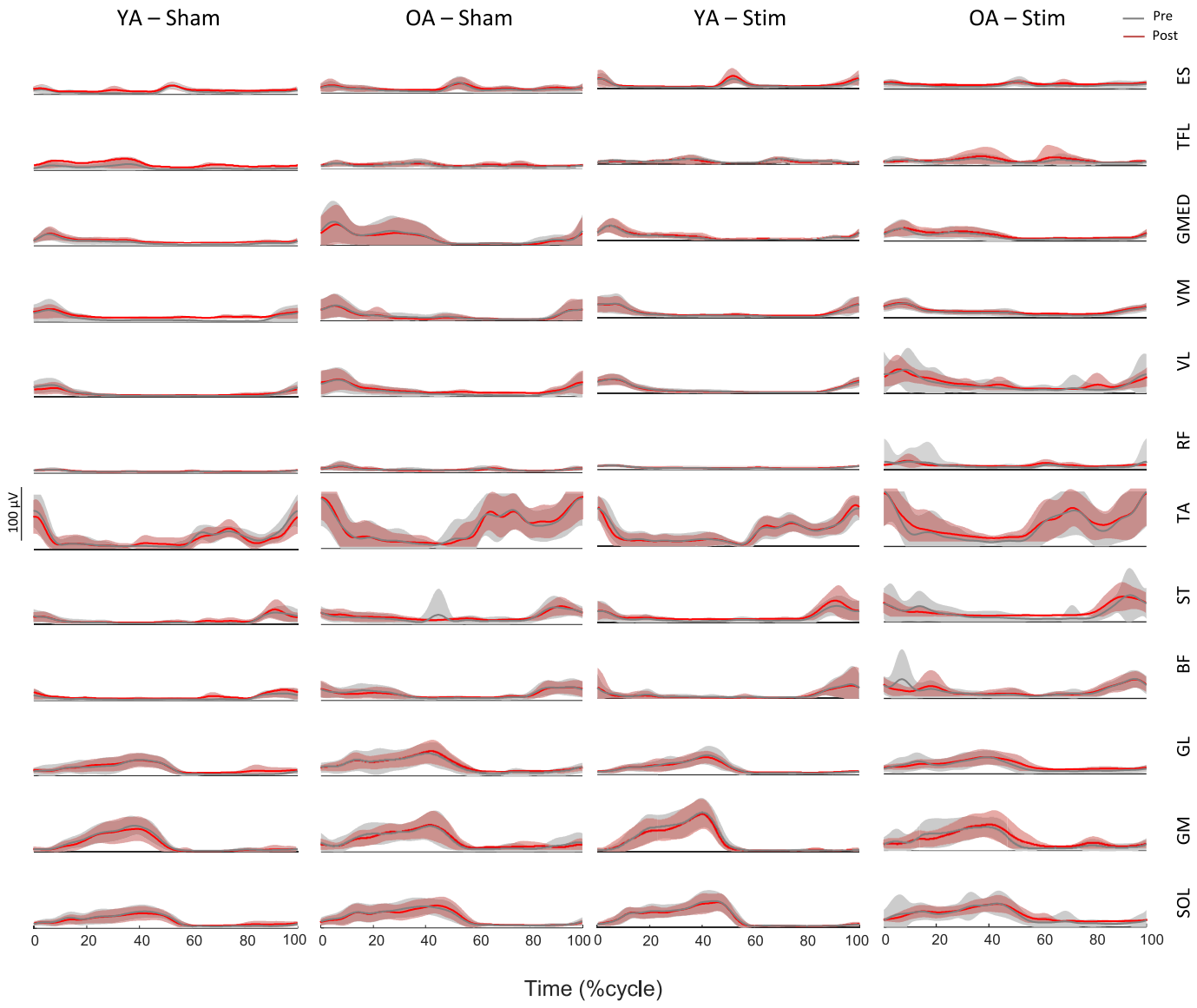


**Fig. 4.** Rectified EMG profiles of 12 lower limb muscles across the gait cycle for each experimental condition. Each subplot represents the average signal (mean ± SD) for a given muscle and condition, expressed over 100% of the gait cycle. Conditions are arranged by group and stimulation: YA-Sham, OA-Sham, YA-Stim, and OA-Stim (left to right). EMG activity is shown for both pre-intervention (black) and post-intervention (red) sessions. Shaded areas represent inter-subject variability (±1 SD). EMG amplitude is shown in arbitrary units, normalized to each subject's peak value. Significance symbols are defined as in Fig. 2 ($p < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

group near the end of the gait cycle, the reduction following tsDCS after stimulation is more robust, spanning both early and late stance (Fig. 5B). Given that sacral motor pools innervate distal muscles that contribute to forward propulsion (Kendall et al., 2005), this finding may reflect a re-weighting of segmental drive to distal musculature rather than a global change in gait strategy.

The absence of clear kinetic changes in the present study is not inconsistent with the broader literature, showing that tsDCS effects are highly variable across studies and outcome measures. Indeed, several investigations using comparable experimental protocols have reported limited or absent changes in gait parameters, spinal reflexes, or excitability indices (Bettmann et al., 2020; Fava De Lima et al., 2022; Kuck et al., 2018; Lamy et al., 2012). This variability likely reflects the state-dependent and task-dependent nature of neuromodulation, as well as differences in population characteristics and selected endpoints. In this context, the lack of significant tsDCS effects in young adults may reflect a ceiling or state-dependent phenomenon: in the absence of an age-related changes, there may be limited scope for further modulation. This interpretation aligns with prior reports of null findings in populations without baseline sensorimotor imbalance.

The precise mechanisms underlying tsDCS-induced modulation remain to be clarified. In line with polarity-dependent effects reported for tsDCS, cathodal stimulation may modulate afferent-driven transmission within spinal circuits, thereby influencing sensorimotor processing (Song and Martin, 2017). It is nevertheless important to emphasize that, although tsDCS is sometimes referred to as 'spinal stimulation', its effects are not best explained by direct polarization of motor axons; instead, evidence suggests that tsDCS modulates the processing of sensory input within spinal circuits (Lenoir et al., 2018). Indeed, current evidence suggests that tsDCS predominantly affects spinal sensorimotor processing by polarizing afferent fibers and their intraspinal terminals as they enter the gray matter, thereby modulating premotoneuronal interneuronal circuits rather than directly driving motoneuron output (Jankowska, 2017). Thus, the observed changes in sacral spinal motor output during walking may reflect altered integration of afferent feedback within lumbosacral networks, leading to

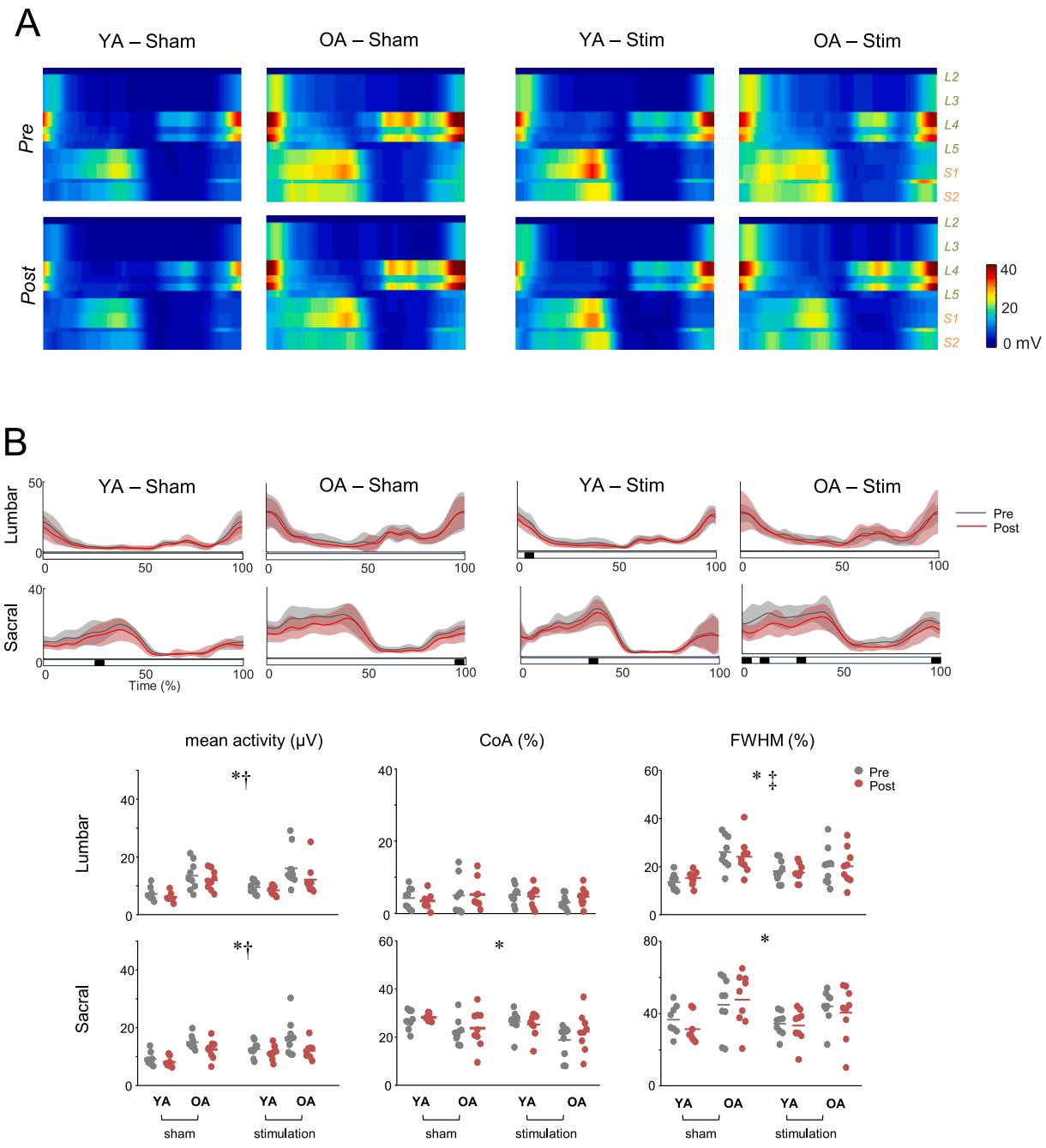


**Fig. 5.** Spinal motor output and summary parameters before and after tsDCS. (A) Interpolated colour maps of spinal motor output across lumbar (L2–L5) and sacral (S1–S2) segments over the normalized gait cycle (0–100%) for each group and condition (YA-Sham, OA-Sham, YA-Stim, OA-Stim). Colour intensity reflects relative segmental activation levels. (B) Ensemble-averaged time-series (mean ± SD) of lumbar and sacral segmental output, shown separately for pre (black) and post (red) stimulation conditions. Black rectangles in the lumbar and sacral activation time-series indicate regions of the gait cycle where significant differences between pre and post conditions were identified by statistical parametric mapping (SPM). (C) Summary parameters of spinal activation per participant, including maximum amplitude, mean amplitude, center of activity (CoA), and full width at half maximum (FWHM), expressed as a percentage of the gait cycle. Gray and red dots represent pre and post values, respectively; horizontal bars indicate the group mean respectively; horizontal bars indicate group means Significant main effects and interactions are indicated with symbols as in Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

secondary modulation of segmental motor organization. These neuromodulatory effects are thought to interact with spinal central pattern generators (CPGs), which orchestrate the rhythmic and phase-specific activation of motor pools during gait (Kiehn, 2006). Because stance phases involve strong proprioceptive inflow from ankle extensors and load-sensitive afferents, modulation of afferent transmission at this stage could preferentially influence sacral motor pools during early and late stance.

## 5. Limitations

A key limitation of the study is the absence of direct measures of spinal excitability, which would have provided more conclusive evidence of spinal involvement (Oluwole O. Awosika et al., 2019a, 2019b; Yamaguchi et al., 2020). These findings should be interpreted with caution, as the effects of a single session may not translate into lasting change in spinal cord excitability and functional benefits. Future studies

should evaluate repeated tsDCS sessions combined with task-specific gait training to determine whether cumulative adaptations occur. Another limitation of our study is the absence of direct measurements of subcutaneous tissue thickness at the stimulation site, and we assumed comparable fat distribution and thus similar depths of neural structures beneath the skin. However, differences in local adiposity could affect the proportion of current reaching deeper tissues, introducing variability in the neuromodulatory effects of tsDCS (Fernandes et al., 2018). Also, the relatively low stimulation intensity (2.5 mA), which, although within established safety thresholds, may have been insufficient to induce more pronounced or widespread neuromodulatory effects (Eberhardt et al., 2023).

## 6. Clinical implications and perspectives

The present findings demonstrate that lumbosacral spinal circuits in older adults are responsive to non-invasive neuromodulation, as reflected by modulation of sacral spinal motor output. In addition, a modest change of the trunk posture change was observed. The functional consequences of these changes were not directly assessed in the present study, and future research should determine whether repeated tsDCS sessions, alone or combined with gait training, can induce more durable and clinically meaningful adaptations, including potential effects on stability, fall risk, or gait efficiency.

## 7. Conclusion

A single session of cathodal tsDCS modulated sacral spinal motor output and was accompanied by a modest reduction in trunk flexion in older adults during walking, with limited effects on joint-level kinetics. These findings provide proof-of-mechanism that non-invasive spinal neuromodulation can acutely influence segmental motor output during gait. Further studies are needed to establish whether repeated stimulation leads to sustained or functionally relevant biomechanical adaptations.

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## CRediT authorship contribution statement

**Mario N Núñez-Lisboa:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Arthur H Dewolf:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

## Code availability

The code used for data processing and analysis in this study is available upon reasonable request from the corresponding author.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Data availability

The data that support the findings of this study are available from the corresponding author, AHD, upon reasonable request.

## References

Allen, M.D., Dalton, B.H., Gilmore, K.J., McNeil, C.J., Doherty, T.J., Rice, C.L., Power, G. A., 2021. Neuroprotective effects of exercise on the aging human neuromuscular system. Exp. Gerontol. 152, 111465. https://doi.org/10.1016/j.exger.2021.111465.

Avaltroni, P., Cappellini, G., Sylos-Labini, F., Ivanenko, Y., Lacquaniti, F., 2024. Spinal maps of motoneuron activity during human locomotion: Neuromechanical considerations. Front. Physiol. 15, 1389436. https://doi.org/10.3389/fphys.2024.1389436.

Awosika, O.O., Sandrini, M., Volochayev, R., Thompson, R.M., Fishman, N., Wu, T., Floeter, M.K., Hallett, M., Cohen, L.G., 2019. Transcutaneous spinal direct current stimulation improves locomotor learning in healthy humans. Brain Stimulat. 12, 628–634. https://doi.org/10.1016/j.brs.2019.01.017.

Batschelet, E., 1981. Circular Statistics in Biology. Academic Press.

Beijersbergen, C.M.I., Granacher, U., Vandervoort, A.A., DeVita, P., Hortobágyi, T., 2013. The biomechanical mechanism of how strength and power training improves walking speed in old adults remains unknown. Ageing Res. Rev. 12, 618–627. https://doi.org/10.1016/j.arr.2013.03.001.

Bettmann, J.H., Meyer-Frießem, C.H., Schweizer, L.M., Schlaffke, L., Zahn, P.K., Tegenthoff, M., Höffken, O., 2020. Transcutaneous spinal direct current stimulation shows no effect on paired stimulation suppression of the somatosensory cortex. Sci. Rep. 10, 22010. https://doi.org/10.1038/s41598-020-79131-2.

Borghese, N.A., Bianchi, L., Lacquaniti, F., 1996. Kinematic determinants of human locomotion. J. Physiol. 494, 863–879. https://doi.org/10.1113/jphysiol.1996.sp021539.

Boyer, K.A., Andriacchi, T.P., Beaupre, G.S., 2012. The role of physical activity in changes in walking mechanics with age. Gait Posture 36, 149–153. https://doi.org/10.1016/j.gaitpost.2012.02.007.

Boyer, K.A., Johnson, R.T., Banks, J.J., Jewell, C., Hafer, J.F., 2017. Systematic review and meta-analysis of gait mechanics in young and older adults. Exp. Gerontol. 95, 63–70. https://doi.org/10.1016/j.exger.2017.05.005.

Cappellini, G., Ivanenko, Y.P., Dominici, N., Poppele, R.E., Lacquaniti, F., 2010. Migration of motor pool activity in the spinal cord reflects body mechanics in human locomotion. J. Neurophysiol. 104, 3064–3073. https://doi.org/10.1152/jn.00318.2010.

Delabastita, T., Hollville, E., Catteau, A., Cortvriendt, P., De Groote, F., Vanwanseele, B., 2021. Distal-to-proximal joint mechanics redistribution is a main contributor to reduced walking economy in older adults. Scand. J. Med. Sci. Sports 31, 1036–1047. https://doi.org/10.1111/sms.13929.

Dewolf, A.H., Peñailillo, L.E., Willems, P.A., 2016. The rebound of the body during uphill and downhill running at different speeds. J. Exp. Biol., jeb.142976 https://doi.org/10.1242/jeb.142976.

Dewolf, A.H., Ivanenko, Y., Zelik, K.E., Lacquaniti, F., Willems, P.A., 2018. Kinematic patterns while walking on a slope at different speeds. J. Appl. Physiol. 125, 642–653. https://doi.org/10.1152/japplphysiol.01020.2017.

Dewolf, A.H., Meurisse, G.M., Schepens, B., Willems, P.A., 2019a. Effect of walking speed on the intersegmental coordination of lower-limb segments in elderly adults. Gait Posture 70, 156–161. https://doi.org/10.1016/j.gaitpost.2019.03.001.

Dewolf, A.H., Ivanenko, Y.P., Zelik, K.E., Lacquaniti, F., Willems, P.A., 2019b. Differential activation of lumbar and sacral motor pools during walking at different speeds and slopes. J. Neurophysiol. 122, 872–887. https://doi.org/10.1152/jn.00167.2019.

Dewolf, A., Sylos-Labini, F., Cappellini, G., Ivanenko, Y., Lacquaniti, F., 2021a. Age-related changes in the neuromuscular control of forward and backward locomotion. PLoS One 16, e0246372. https://doi.org/10.1371/journal.pone.0246372.

Dewolf, A., Sylos-Labini, F., Cappellini, G., Zhvansky, D., Willems, P.A., Ivanenko, Y., Lacquaniti, F., 2021b. Neuromuscular age-related adjustment of gait when moving upwards and downwards. Front. Hum. Neurosci. 15. https://doi.org/10.3389/fnhum.2021.749366.

Dewolf, A.H., Meurisse, G.M., Ivanenko, Y., Lacquaniti, F., Bastien, G.J., Schepens, B., 2022. Relation between step-to-step transition strategies and walking pattern in older adults. Appl. Sci. 12, 5055. https://doi.org/10.3390/app12105055.

Di Russo, A., Stanev, D., Sabnis, A., Danner, S.M., Ausborn, J., Armand, S., Ijspeert, A., 2023. Investigating the roles of reflexes and central pattern generators in the control and modulation of human locomotion using a physiologically plausible neuromechanical model. J. Neural Eng. 20. https://doi.org/10.1088/1741-2552/acfdcc.

Eberhardt, F., Enax-Krumova, E., Tegenthoff, M., Höffken, O., Özgül, Ö.S., 2023. Anodal transcutaneous spinal direct current stimulation influences the amplitude of pain-related evoked potentials in healthy subjects. Sci. Rep. 13. https://doi.org/10.1038/s41598-023-47408-x.

Fava De Lima, F., Silva, C.R., Kohn, A.F., 2022. Transcutaneous spinal direct current stimulation (tsDCS) does not affect postural sway of young and healthy subjects during quiet upright standing. PLoS One 17, e0267718. https://doi.org/10.1371/journal.pone.0267718.

Fernandes, S.R., Salvador, R., Wenger, C., De Carvalho, M., Miranda, P.C., 2018. Transcutaneous spinal direct current stimulation of the lumbar and sacral spinal cord: a modelling study. J. Neural Eng. 15, 036008. https://doi.org/10.1088/1741-2552/aaac38.

Fielding, R.A., Vellas, B., Evans, W.J., Bhasin, S., Morley, J.E., Newman, A.B., Abellan Van Kan, G., Andrieu, S., Bauer, J., Breuille, D., Cederholm, T., Chandler, J., De Meynard, C., Donini, L., Harris, T., Kannt, A., Keime Guibert, F., Onder, G., Papanicolaou, D., Rolland, Y., Rooks, D., Sieber, C., Souhami, E., Verlaan, S., Zamboni, M., 2011. Sarcopenia: an undiagnosed condition in older adults. Current consensus definition: prevalence, etiology, and consequences. International working group on sarcopenia. J. Am. Med. Dir. Assoc. 12, 249–256. https://doi.org/10.1016/j.jamda.2011.01.003.

Franz, J.R., 2016. The age-associated reduction in propulsive power generation in walking. Exerc. Sport Sci. Rev. 44, 129–136. https://doi.org/10.1249/JES.0000000000000086.

Freiberger, E., Sieber, C.C., Kob, R., 2020. Mobility in older community-dwelling persons: a narrative review. Front. Physiol. 11, 881. https://doi.org/10.3389/fphys.2020.00881.

Geirsdottir, O.G., Chang, M., Briem, K., Jonsson, P.V., Thorsdottir, I., Ramel, A., 2022. Determinants of physical function in community dwelling old people. J. Gerontol. Geriatr. 70, 9–16. https://doi.org/10.36150/2499-6564-N261.

Hepple, R.T., Rice, C.L., 2016. Innervation and neuromuscular control in ageing skeletal muscle. J. Physiol. 594, 1965–1978. https://doi.org/10.1113/JP270561.

Honda, K., Sekiguchi, Y., Izumi, S.-I., 2023. Effect of aging on the trunk and lower limb kinematics during gait on a compliant surface in healthy individuals. Biomechanics 3, 103–114. https://doi.org/10.3390/biomechanics3010010.

Hortobágyi, T., Solnik, S., Gruber, A., Rider, P., Steinweg, K., Helseth, J., DeVita, P., 2009. Interaction between age and gait velocity in the amplitude and timing of antagonist muscle coactivation. Gait Posture 29, 558–564. https://doi.org/10.1016/j.gaitpost.2008.12.007.

Hortobagyi, T., Finch, A., Solnik, S., Rider, P., DeVita, P., 2011. Association between muscle activation and metabolic cost of walking in young and old adults. J. Gerontol. A Biol. Sci. Med. Sci. 66A, 541–547. https://doi.org/10.1093/gerona/glr008.

Hubli, M., Dietz, V., Schrafl-Altermatt, M., Bolliger, M., 2013. Modulation of spinal neuronal excitability by spinal direct currents and locomotion after spinal cord injury. Clin. Neurophysiol. 124, 1187–1195. https://doi.org/10.1016/j.clinph.2012.11.021.

Ivanenko, Y.P., Cappellini, G., Poppele, R.E., Lacquaniti, F., 2008. Spatiotemporal organization of α-motoneuron activity in the human spinal cord during different gaits and gait transitions. Eur. J. Neurosci. 27, 3351–3368. https://doi.org/10.1111/j.1460-9568.2008.06289.x.

Ivanenko, Y.P., Dominici, N., Cappellini, G., Di Paolo, A., Giannini, C., Poppele, R.E., Lacquaniti, F., 2013. Changes in the spinal segmental motor output for stepping during development from infant to adult. J. Neurosci. 33, 3025–3036. https://doi.org/10.1523/JNEUROSCI.2722-12.2013.

Jankowska, E., 2017. Spinal control of motor outputs by intrinsic and externally induced electric field potentials. J. Neurophysiol. 118, 1221–1234. https://doi.org/10.1152/jn.00169.2017.

Kendall, F., McCreary, E., Provance, P., Rodgers, M., Romani, W., 2005. Muscles. Testing and Function with Posture and Pain. Lippincott Williams and Wilkins, Baltimore.

Kiehn, O., 2006. Locomotor circuits in the mammalian spinal cord. Annu. Rev. Neurosci. 29, 279–306.

Kuck, A., Stegeman, D.F., Van Der Kooij, H., Van Asseldonk, E.H.F., 2018. Changes in H-reflex recruitment after trans-spinal direct current stimulation with multiple electrode configurations. Front. Neurosci. 12, 151. https://doi.org/10.3389/fnins.2018.00151.

La Scaleia, V., Ivanenko, Y.P., Zelik, K.E., Lacquaniti, F., 2014. Spinal motor outputs during step-to-step transitions of diverse human gaits. Front. Hum. Neurosci. 8. https://doi.org/10.3389/fnhum.2014.00305.

Lamy, J.-C., Ho, C., Badel, A., Arrigo, R.T., Boakye, M., 2012. Modulation of soleus h reflex by spinal DC stimulation in humans. J. Neurophysiol. 108, 906–914. https://doi.org/10.1152/jn.10898.2011.

Lenoir, C., Jankovski, A., Mouraux, A., 2018. Anodal transcutaneous spinal direct current stimulation (tsDCS) selectively inhibits the synaptic efficacy of nociceptive transmission at spinal cord level. Neuroscience 393, 150–163. https://doi.org/10.1016/j.neuroscience.2018.10.007.

Martino, G., Ivanenko, Y.P., Serrao, M., Ranavolo, A., d'Avella, A., Draicchio, F., Conte, C., Casali, C., Lacquaniti, F., 2014. Locomotor patterns in cerebellar ataxia. J. Neurophysiol. 112, 2810–2821. https://doi.org/10.1152/jn.00275.2014.

Mesquita, R.M., Catavitello, G., Willems, P.A., Dewolf, A.H., 2023. Modification of the locomotor pattern when deviating from the characteristic heel-to-toe rolling pattern during walking. Eur. J. Appl. Physiol. https://doi.org/10.1007/s00421-023-05169-5.

Meurisse, G.M., Dierick, F., Schepens, B., Bastien, G.J., 2016. Determination of the vertical ground reaction forces acting upon individual limbs during healthy and clinical gait. Gait Posture 43, 245–250. https://doi.org/10.1016/j.gaitpost.2015.10.005.

Monaco, V., Ghionzoli, A., Micera, S., 2010. Age-related modifications of muscle synergies and spinal cord activity during locomotion. J. Neurophysiol. 104, 2092–2102. https://doi.org/10.1152/jn.00525.2009.

Núñez-Lisboa, M.N., Dewolf, A.H., 2025. The role of physical activity in mitigating age-related changes in the neuromuscular control of gait. Npj Aging 11, 49. https://doi.org/10.1038/s41514-025-00239-8.

Nùñez-Lisboa, M., Valero-Breton, M., Dewolf, A.H., 2023. Unraveling age-related impairment of the neuromuscular system: exploring biomechanical and neurophysiological perspectives. Front. Physiol. 14, 1194889. https://doi.org/10.3389/fphys.2023.1194889.

Núñez-Lisboa, M., Echeverría, K., Willems, P.A., Ivanenko, Y., Lacquaniti, F., Dewolf, A. H., 2024. Understanding gait alterations: trunk flexion and its effects on walking neuromechanics. J. Exp. Biol. 227, jeb249307. https://doi.org/10.1242/jeb.249307.

Pereira, M., Fernandes, S.R., Miranda, P.C., De Carvalho, M., 2022. Lumbar trans-spinal direct current stimulation: a modeling-experimental approach to dorsal root ganglia stimulation. Front. Neurosci. 16, 1041932. https://doi.org/10.3389/fnins.2022.1041932.

Peterson, D.S., Martin, P.E., 2010. Effects of age and walking speed on coactivation and cost of walking in healthy adults. Gait Posture 31, 355–359. https://doi.org/10.1016/j.gaitpost.2009.12.005.

Powell, E.S., Korupolu, R., Westgate, P.M., Carrico, C., Reddy, L., Sawaki, L., 2019. Dose-response relationship of transcutaneous spinal direct current stimulation in healthy humans: a proof of concept study. NeuroRehabilitation 43, 369–376. https://doi.org/10.3233/NRE-182469.

Rybak, I.A., Dougherty, K.J., Shevtsova, N.A., 2015. Organization of the mammalian locomotor CPG: review of computational model and circuit architectures based on genetically identified spinal interneurons(1,2,3). eNeuro 2. https://doi.org/10.1523/ENEURO.0069-15.2015.

Santuz, A., Brüll, L., Ekizos, A., Schroll, A., Eckardt, N., Kibele, A., Schwenk, M., Arampatzis, A., 2020. Neuromotor dynamics of human locomotion in challenging settings. iScience 23, 100796. https://doi.org/10.1016/j.isci.2019.100796.

Serge Van Sint Jan, Allard, Paul, Wu, Ge, 2007. Color Atlas of Skeletal Landmark Definitions. Guidelines for Reproducible Manual and Virtual Palpations. Churchill Livingstone/Elsevier, Edinburgh; New York.

Skiadopoulos, A., Knikou, M., 2024. Tapping into the human spinal locomotor centres with transspinal stimulation. Sci. Rep. 14, 5990. https://doi.org/10.1038/s41598-024-56579-0.

Song, W., Martin, J.H., 2017. Spinal cord direct current stimulation differentially modulates neuronal activity in the dorsal and ventral spinal cord. J. Neurophysiol. 117, 1143–1155. https://doi.org/10.1152/jn.00584.2016.

Studenski, S., 2011. Gait speed and survival in older adults. JAMA 305, 50. https://doi.org/10.1001/jama.2010.1923.

Waanders, J.B., Hortobágyi, T., Murgia, A., Devita, P., Franz, J.R., 2019. Advanced age redistributes positive but not negative leg joint work during walking. Med. Sci. Sports Exerc. 51, 615–623. https://doi.org/10.1249/MSS.0000000000001828.

Willems, P.A., Gosseye, T.P., 2013. Does an instrumented treadmill correctly measure the ground reaction forces? Biol. Open 2, 1421–1424. https://doi.org/10.1242/bio.20136379.

Winkler, T., Hering, P., Straube, A., 2010. Spinal DC stimulation in humans modulates post-activation depression of the h-reflex depending on current polarity. Clin. Neurophysiol. 121, 957–961. https://doi.org/10.1016/j.clinph.2010.01.014.

Yamaguchi, T., Beck, M.M., Therkildsen, E.R., Svane, C., Forman, C., Lorentzen, J., Conway, B.A., Lundbye-Jensen, J., Geertsen, S.S., Nielsen, J.B., 2020. Transcutaneous spinal direct current stimulation increases corticospinal transmission and enhances voluntary motor output in humans. Phys. Rep. 8. https://doi.org/10.14814/phy2.14531.

Yokoyama, H., Ogawa, T., Shinya, M., Kawashima, N., Nakazawa, K., 2017. Speed dependency in α-motoneuron activity and locomotor modules in human locomotion: indirect evidence for phylogenetically conserved spinal circuits. Proc. R. Soc. B Biol. Sci. 284, 20170290. https://doi.org/10.1098/rspb.2017.0290.