Different stabilizing mechanisms but a common task-level stabilization aim in standing and walking

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Abstract

Intrinsic mechanisms and feedback control work together to stabilize the body in upright tasks, such as standing and walking. Yet if, and how lumped parameters characterizing stabilization change across tasks is unclear. To answer this question, we applied a stabilization model, relating delayed center of mass position and velocity information to current ground reaction forces (corrected for effects of gravity) in unperturbed standing and walking, to estimate and compare the stabilization between tasks.

15 healthy young participants (21± 4 yrs, 63 ± 9 kg, 1.70 ± 0.10 m, 13 females, 2 males) participated in this study, they walked at 1.25 m/s for 5 minutes, and performed 3 different standing tasks: normal standing, unipedal standing, and step posture for 1 minute, repeated 5 times. Whole-body kinematics and ground reaction forces were collected and used to fit the stabilization model and estimate the effective delay and lumped gains. Results showed good model fits for both walking and standing with mean R^2 values higher than 0.69. The effective delay was significantly longer in walking than in standing. While the lumped position and velocity gains varied significantly across tasks and directions, the lumped position gains were mostly above critical stiffness and lumped velocity gains all at under-damped level, with an only exception that lumped position gains in the AP

direction in walking, which were slightly below critical stiffness. The ratio of lumped position to velocity gains in all tasks remained consistently close to human body's eigenfrequency ($\sqrt{g/l}$) as predicted by the extrapolated center of mass concept.

Our findings suggest that stabilization is organized at the task level, with lumped effects of all stabilizing mechanisms acting to preserve a consistent weighting between position and velocity contributions across tasks, effectively regulating the CoM motion to follow a pendulum-like trajectory.

1. Introduction

Standing and walking are two fundamental motor behaviors in human daily life. Both require sophisticated neuromuscular control to maintain an upright body orientation against the effects of unpredictable perturbations which are amplified by gravity. Such stabilization is achieved through the coordination of intrinsic mechanics and feedback control [1-3]. Intrinsic mechanisms provide immediate resistance to perturbations based on segmental inertia and passive tissue proprieties (i.e., stiffness and damping). In contrast, feedback control is adaptive and generates corrective responses selectively based on delayed sensory information [3-7]. While identifying these two stabilizing mechanisms separately is methodologically challenging [8], their combined effects determine the performance and robustness

of these motor tasks[1, 3]. While studying intrinsic mechanisms and feedback control separately provides insight into the contribution of both mechanisms, characterizing their lumped effects offers an overarching and functional view of how stability is controlled [9].

Given the different temporal and biomechanical characteristics of standing and walking, we expect that stabilizing mechanisms to be different in these tasks. Standing is a quasi-static behavior, during which stability can rely on constant intrinsic proprieties and time-invariant feedback control to maintain a 'fixed' body orientation. Walking is a dynamic, cyclic motion, during which the body experiences a phase-dependent instability. While the intrinsic mechanisms might provide some instantaneous and basic stability during the stance phase, feedback control must be dynamically modulated to deal with the time-varying stability requirements throughout the gait cycle [9, 10]. These fundamental differences suggest that the relative contributions of intrinsic and feedback mechanisms and the resulting global stabilizing effects may differ between standing and walking.

Compared to the relatively time-invariant intrinsic mechanisms, feedback control is context-dependent and adaptive. Many studies have addressed the neural mechanisms [5, 6, 9-14]. These studies commonly assume that sensory estimates of the task-level variable kinematics, i.e., center of mass (CoM), are used to modulate corrective responses (e.g., EMG, ankle torque, foot placement) to

achieve stabilization[5, 10, 11, 13]. While these models provide valuable insight into the neural mechanisms in stability control, they have two limitations. First, these models are generally derived under specific tasks, i.e., either in standing [5, 11, 13] or walking [10, 14, 15], making it difficult to directly compare different motor behaviors. Second, identification of feedback parameters usually requires perturbations and the measurements of physiological signals (e.g., EMG), which limits their application in studying natural, unperturbed behavior. Furthermore, focusing solely on feedback control fails to provide a comprehensive understanding about how global stability is maintained and changes across tasks, specifically for those with fundamentally different dynamics.

Since all corrective actions will ultimately be reflected by the ground reaction forces [16, 17], the lumped stabilizing mechanisms can be represented by the relationship between current ground reaction forces and delayed CoM deviations. Based on this, van Dieen et al. [18] proposed a model to assess stabilizing control in unperturbed walking by fitting a linear relationship between the delayed center of mass kinematics and horizontal ground reaction forces. More recently, we refined this model by using the CoM position (PCoM) and velocity (VCoM) information as separate predictors instead of combined into a single predictor, which enabled us to estimate the position- and velocity-related contributions. We now have a framework to evaluate and compare overall stabilization between

standing and walking without external perturbations or physiological measurements[1]. The method can provide a better understanding of how the control system regulates global stabilization based on preceding CoM kinematics, and how the parameters characterizing stabilization change across tasks.

The extrapolated center of mass (XCoM) concept, which equals the PCoM plus VCoM divided by the eigenfrequency ($\sqrt{g/l}$) of the body modeled as an inverted pendulum [19], couples the CoM position and velocity into a single metric. According to this concept, stability is achieved by keeping the XCoM within the base of support (BoS) [19, 20]. This suggests that stabilization relies on coordinated control of CoM position and velocity, with the relative control gain equal to the body's eigenfrequency. While the absolute values of lumped position and velocity gains are expected to differ to meet specific stability requirements, their relative contribution, expressed as the ratio of position to velocity gains, may remain consistent across tasks if a common pendulum-like stabilization aim exists. Especially for walking, a phase-dependent task, whether the overall effect (i.e., averaged control over the gait cycle) can be described by pendulum-like stabilization remains an open question.

[1] Here, it should be mentioned that in the past we have referred to these models as "feedback models", while also acknowledging that they also capture intrinsic mechanics. Here, we explicitly try to refrain from such language, as we feel it may create confusion. Thus, instead, we will use the term "stabilization models".

To address the above questions, we applied a model to quantify stabilization ('stabilization model') to unperturbed walking and typical standing postures (normal standing, unipedal, and step postures). Unipedal standing and step posture were selected as they are commonly observed during walking, while they provide a different base of support (BoS) and different structural stiffness compared with normal standing. Comparing these postures allows us to determine whether a consistent position-to-velocity control ratio exists across different biomechanical contexts. Based on our previous findings[18, 21], we hypothesized that: 1) effective delays are longer in walking than in standing, because stabilizing effects become effective mainly after ground contact of the leading leg; 2) lumped gains are larger in walking than in standing postures, to compensate for larger delays (c.f. Foulger, Liu et al. [22];) 3) directional differences exist, with larger gains in the ML than in the AP direction during walking, while in standing this would depend on the specific standing posture; 4) the ratio of lumped position to velocity gains in both walking and standing is constant and close to the eigen frequency of the body modeled as an inverted pendulum.

2. Methods

2.1 Experimental design & data collection

15 healthy young participants (21± 4 yrs, 63 ± 9 kg, 1.70 ± 0.10 m, 13 females, 2 males) participated in the experiment. The experimental procedure was approved by the ethics committee of the Faculty of Behavioural and Movement Sciences, Vrije Universiteit Amsterdam (number: VCWE-2023-170). The data collection started on September 24, 2024, and ended on November 11, 2024. All participants received oral and written explanations of the procedures and signed written consent before the experiment.

In this study, participants performed one walking trial and three different standing tasks. For walking, participants walked on the instrumented dual-belt treadmill (Motek-Force-link, Amsterdam, Netherlands) with belt speed set at 1.25 m/s (4.5 km/h) until a steady gait was achieved, followed by an additional 5 min walking trial. All participants reported that this speed felt natural without requiring excessive effort or causing fatigue. For standing tasks, participants stood on the instrumented dual-belt treadmill and were asked to perform: 1) Normal standing: stand upright with feet together. 2) Unipedal standing: stand on the preferred leg with the other leg in a position in which the participants could maintain stability. We tested the preferred leg only, because previously no differences were observed between standing on the dominant and non-dominant leg [23]. 3) Step posture: participants took a natural step as if walking normally at least three times until they confirmed to have reached the most comfortable step length and width, then

maintained that position with body weight evenly distributed between both feet. This even distribution was selected as our pilot study showed no consistent differences between different weight-distributions. Foot positions were marked for consistency across trials. All standing tasks were kept for 1 min and repeated 5 times in random order. For each standing trial, participants faced forward and kept their arms naturally at their sides, trying to keep as still as possible. Sufficient rest time was given between tasks to avoid fatigue. Trials with stability loss (e.g., ground contact with the non-stance leg in unipedal standing, excessive arm movement) were discarded and repeated.

2.2 Data processing

Data collection and processing followed procedures from our previous study [21]. In short, we collected whole-body 3D kinematic data using Optotrak cameras (Northern Digital Inc., Waterloo, Ontario, Canada) and ground reaction forces with force plates embedded in the treadmill (Motek-Force-link, Amsterdam, Netherlands), and processed these data using MATLAB (2024a, The MathWorks, Natick, US). Both kinematic and force data were low-pass filtered using a second-order Butterworth filter with a cut-off frequency of 10 Hz, then high-pass filtered at 0.1 Hz to remove noise associated with low-frequency postural adjustments and drift in position on the treadmill. The force data were down-sampled to 50 Hz to

match the kinematics sampling frequency. The whole-body center of mass position (PCoM) was calculated using a 3D linked segment model developed by Kingma, deLooze (24), and the center of mass velocity (VCoM) was calculated as the time derivative of PCoM. These variables were further processed differently for standing and walking.

For standing tasks, the mean PCoM was defined as the referenced upright position, accordingly, PCoM was calculated as the deviation from this reference. The stabilization effort, represented by the corrected ground reaction forces (F_{corr}), was obtained by removing the gravitational acceleration component from the total ground reaction forces (F_{gr}), assuming the whole body moved as a single inverted pendulum (IP), in both ML and AP directions. The removal process is illustrated in **Fig 1**, with further details in [21]. For model fitting, we analyzed experimental data from seconds 6 to 50 of each trial. This interval was selected to exclude initial postural adjustments at the start and increased body sway at the end of the task, particularly in unipedal standing.

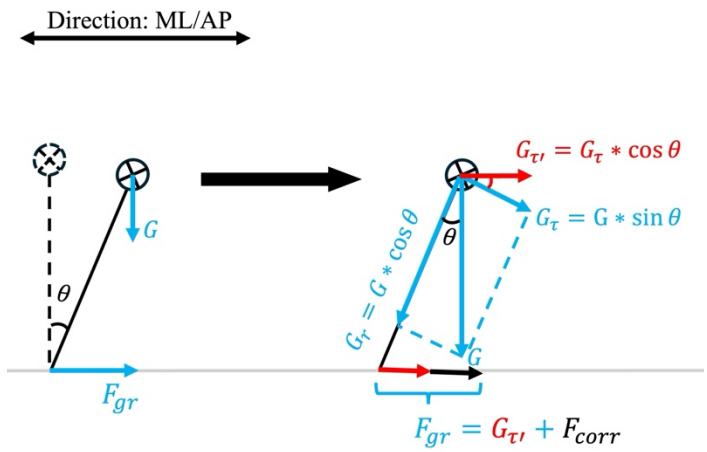

Fig 1. Removal of the gravity component. In this figure, the human body is modelled as a single inverted pendulum (IP). The left plot represents the IP states, with the dashed line indicating the reference upright state, while the solid line shows a representative IP state with a sway angle θ. In this representative state, the IP experiences the gravitational force (G) and generates a ground reaction force (F_{gr}) in the ML/AP direction. Due to the inclination, the horizontal F_{gr} includes a passive force resulting from gravity in addition to the ground reaction force generated by muscle activity (F_{corr}). The right plot further explains how we calculated the corrected ground reaction force F_{corr}. Gravity can be decomposed into two components: a centripetal force (G_r), which equals $G * cos\,\theta$, and a tangential force (G_τ), which equals $G * sin\,\theta$. The effect of G_τ in both horizontal directions ($G_{\tau\prime}$) can be calculated as $G_\tau * cos\,\theta$. Finally, F_{corr} is obtained by $F_{corr} = F_{gr} - G_{\tau\prime}$.

For walking, PCoM, VCoM and forces were time-normalized to the gait cycle, yielding 100 samples per stride (from left heel strike to subsequent left heel strike) and the PCoM was re-referenced to the mean foot position during the mid-stance phase of each stride. Compared to standing, removing the gravitational component

from total ground reaction forces (F_{gr}) during walking is more challenging as the inverted pendulum (IP) model is too simple to fully represent the complex characteristics of walking [25], particularly during the double-stance phase. Nevertheless, we applied the same removal method as used in standing, as failing to remove the gravity components might mask the actual stabilization effects and lead to an underestimation of the stabilizing parameters. To address this, we used both F_{gr} and F_{corr} to fit the stabilization model. Results supported the use of corrected ground reaction forces (F_{corr}) as the model fit was significantly improved when using this over F_{gr} (**Fig 3**). Thus, for all reported analyses, we used F_{corr}. The whole 300s walking data were used to fit the model.

2.3 Stabilization model

We fitted the stabilization model for standing and walking separately given their time-invariant and phase-dependent control.

For standing, equation (1) was used:

$$\boldsymbol{F_{corr_i} = \widehat{K} * PCOM_{i-\hat{\tau}} + \widehat{B} * VCOM_{i-\hat{\tau}} + \epsilon_i} \qquad (\mathbf{1})$$

where $\widehat{K}$ and $\widehat{B}$ are the lumped position and velocity gains, $\boldsymbol{\epsilon_i}$ represents the residual error, i represents the current time point, $\hat{\tau}$ represents the effective delay ranging from 100 to 1000ms [11].

We evaluated the model's goodness of fit using the coefficient of determination (R^2), and estimated the lumped gains using ordinary least square regression, fitting F_{corr_i} to the linear model specified in equation (1) for each delay ($\hat{\tau}$). The effective delay was selected based on the model fit (maximum R^2), which is a common goodness of fit criterion in model fitting and regression analysis. The corresponding $\widehat{K}$ and $\widehat{B}$ were considered as the lumped position and velocity gains.

For walking, equation (2) was applied to estimate the stabilizing parameters:

$$\boldsymbol{F_{corr_j} = \widehat{K_j} * PCOM_{j-\hat{\tau}} + \widehat{B_j} * VCOM_{j-\hat{\tau}} + \epsilon_j} \qquad (\mathbf{2})$$

where $\boldsymbol{\widehat{K_j}}$ and $\boldsymbol{\widehat{B_j}}$ represents the phase-dependent lumped position and velocity gains, $\boldsymbol{\epsilon_j}$ represents the residual error, j represents the current phase (from 51% to 100% gait cycle), $\hat{\tau}$ represents the effective delay ranging from 1% to 50% gait cycle. Model fit in walking was estimated using the same method as in standing. However, the effective delay could not be determined as the delay at which the best model fit was obtained. During walking, the center of mass signal exhibits relatively low variance during certain phases. As a result, the numerically optimal fit in these phases does not reflect stabilization (e.g., the effective delay in the ML direction selected based on the best fit was less than 50ms, which is physiologically implausible). Thus, we selected the time lag that yielded the most negative weighted sum of position and velocity gains averaged over the stance

phase as the effective delay. For this selected effective delay, the lumped position and velocity gains that produced the largest negative weighted gains were used as the peak gains. Because peak parameters represent control at a specific phase and do not reflect the overall stabilizing efforts during the whole stance phase, we additionally calculated the mean model fit and mean gains across the whole stance phase. These mean values were used to allow direct comparison with standing. For clarity, the peak and mean parameters are referred to as walking peak and walking, respectively.

The effective delay ($\hat{\tau}$), and lumped gains ($\widehat{K}$ and $\widehat{B}$) were estimated for all trials and subsequently averaged for statistical analysis. We further performed normalization of lumped position and velocity gains based on their critical values, i.e., critical stiffness and critical damping. The critical stiffness (K_{cr}) refers to the minimal stiffness required to stabilize the system which was calculated by equation (3). The critical damping refers to the damping value under which the system returns to the target position without overshoot and was calculated by equation (4):

$$K_{cr} = m * g * l \tag{3}$$

$$B_{cr} = 2 * \sqrt{\widehat{K} * m} \tag{4}$$

Where the m is body mass, g is the gravitational acceleration (9.81 m/s^2), l is the center of mass height, $\widehat{K}$ is the current stiffness.

For the lumped position gain, the estimated linear form ($\widehat{K}$) was first converted into its angular form by multiplying by l^2, then normalized by dividing by the critical stiffness (K_{cr}), yielding the normalized position gain ($\widehat{K_n}$). Similarly, for the lumped velocity gain, the estimated linear gain ($\hat{B}$) was first converted to rotational damping by multiplying by l^2 and then normalized by dividing by the critical damping (B_{cr}), yielding the normalized velocity gain ($\widehat{B_n}$). These normalized gains are unitless and describe how many times greater their rotational values are compared to their corresponding critical values, providing information about how the body was controlled.

To figure out whether the CNS modulates the lumped position and velocity gains based on a specific relationship as indicated by the concept of the extrapolated center of mass (i.e., based on the (angular) eigenfrequency), we calculated the ratio between the raw, unnormalized lumped position and velocity gains ($\widehat{K}/\hat{B}$), and further normalized this ratio relative to the IP eigenfrequency by dividing by $\sqrt{g/l}$, represented as $\widehat{R_n}$. If indeed lumped position and velocity gains are modulated according to the extrapolated center of mass concept, we expect that $\widehat{R_n} \approx 1$.

Simulations showed that, for standing, the identified stabilizing parameters are primarily determined by feedback control [21]. While intrinsic stabilization leads to systematic biases: under realistic combination of intrinsic and feedback

parameters, increased intrinsic parameters lead to a shorter delay but increased position and velocity gains compared to the input feedback values. These biases should be taken into account when comparing the lumped values across tasks.

3. Statistical analysis

We examined the effects of Task and Direction on model fit and stabilizing model parameter using a two-way repeated measures ANOVA with Task (walking peak and/or walking, normal standing, unipedal standing, and step posture) and Direction (ML, AP) as within-participant factors to compare stabilizing parameters.

Post-hoc pairwise comparisons with Bonferroni correction were conducted when a significant main effect of Task, Direction or an interaction was found. All statistical analyses were performed in MATLAB (2024a, The MathWorks, Natick, US). Statistical significance was set at $\alpha = 0.05$. Results are presented as mean ± standard deviation (mean ± SD). Effect size was evaluated using partial eta squared ($\eta^2{}_p$), with values of 0.01, 0.06, and 0.14 considered as small, medium, and large effects, respectively[26].

4. Results

Similar to our previous study[21], we considered F_{corr} to be sufficiently reconstructed when $R^2 \geq 0.70$. Our stabilization model showed overall good performance with most mean R^2 values ranging from 0.72 to 0.95 across tasks and directions. The exceptions were walking in the ML direction and step posture in the AP direction (both R^2 = 0.69), as well as walking peak in the ML direction (R^2 = 0.54) and AP direction (R^2 = 0.68). All stabilizing parameters ($\hat{\tau}$, $\widehat{K_n}$, $\widehat{B_n}$) exhibited significant main effects of Task and Direction, as well as significant Task $*$ Direction interactions, except the ratio of stabilizing position to velocity gains ($\widehat{R_n}$), which showed only main effects of Task and Direction (**Fig 2, Table 1**). Furthermore, all observed effects exhibited large effect sizes ($\eta^2{}_p$>0.4) with the exception of the Task $*$ Direction interaction for $\widehat{R_n}$, ($\eta^2{}_p$=0.11). These results showed that the stabilizing parameters differed across tasks and directions.

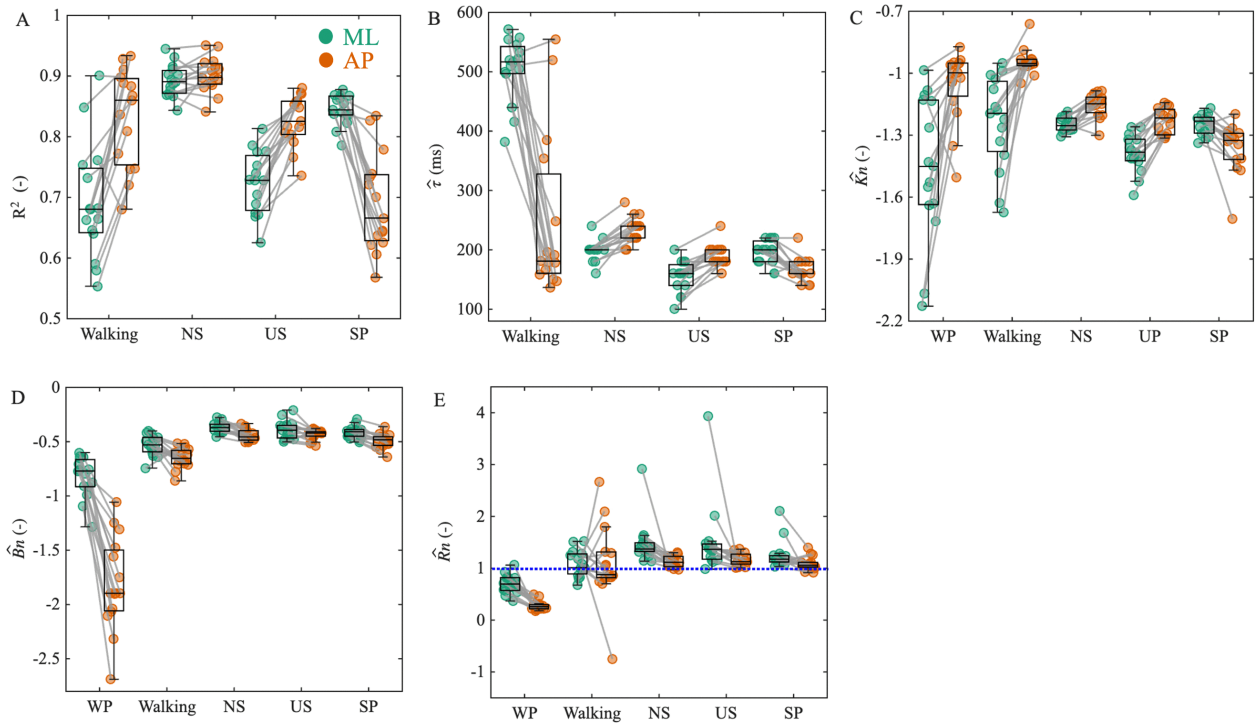

Fig 2. Model fit and estimated stabilizing parameters of all tasks. A) model fit, B) effective delay, C) normalized position gain, D) normalized velocity gain, E) normalized position to velocity ratio. Box-plot shows estimated values across all participants, with central line indicating the median, box edges showing the interquartile range, and whiskers representing the non-outlier range. Dots represent individual participant's data, with green for ML and orange for the AP direction, grey lines connect the data from same participant. The blue dot line in panel E represent y=1. X-axis labels donate: WP: walking peak; Walking: walking mean; NS: normal standing; US: unipedal standing; SP: step posture.

Table 1. Statistical results across tasks.

Variables	Factor	df	F	p	η^2_p
R^2	Task	3,42	21.16	<0.001**	0.60
	Direction	1,14	7.17	0.018*	0.34
	Task * Direction	3,42	59.92	<0.001**	0.81
$\hat{\tau}$	Task	3,42	78.23	<0.001**	0.85
	Direction	1,14	29.30	<0.001**	0.68

	Task * Direction	3,42	54.81	<0.001**	0.80
$\widehat{K_n}$	Task	4,56	10.92	<0.001**	0.44
	Direction	1,14	27.84	<0.001**	0.67
	Task * Direction	4,56	20.00	<0.001**	0.59
$\widehat{B_n}$	Task	4,56	179.74	<0.001**	0.93
	Direction	1,14	64.71	<0.001**	0.82
	Task * Direction	4,56	65.31	<0.001**	0.82
$\widehat{R_n}$	Task	4,56	26.89	<0.001**	0.66
	Direction	1,14	10.73	0.006*	0.43
	Task * Direction	4,56	1.70	0.16	0.11

The asterisks indicating levels of significance, where * indicates $p < 0.05$ and ** indicates $p<0.001$.

From the results (**Fig 3**), it was evident that walking peak gains differed significantly from that in walking and standing, whereas the walking gains were more comparable to standing. Considering that the peak gains represent a strategy at a specific moment within the stance phase, we deemed it less appropriate for direct comparison with standing, therefore, we report the results in two sections. In the first section, we focus on the results in walking, including the comparisons between using total ground reaction forces and corrected ground reaction forces as model outputs, and examining the differences between peak and mean gains across the stance phase. In the second section, we focus on the results between walking

(mean gains) and standing postures, to evaluate the similarities and differences between dynamic and static conditions.

4.1 Walking

4.1.1 Fitting model using total forces vs. corrected forces

The model fit (R^2) significantly improved when using corrected ground reaction forces compared to total ground reaction forces in both the ML and AP direction (**Fig 3**, **S1 Table**). In both directions, peak gains occurred in the early stance phase (~60% gait cycle), regardless of using the total ground reaction forces or corrected forces. Notably, using the corrected ground reaction forces indicated continuous stabilization for position, which was masked when using total forces (**Fig 3**).

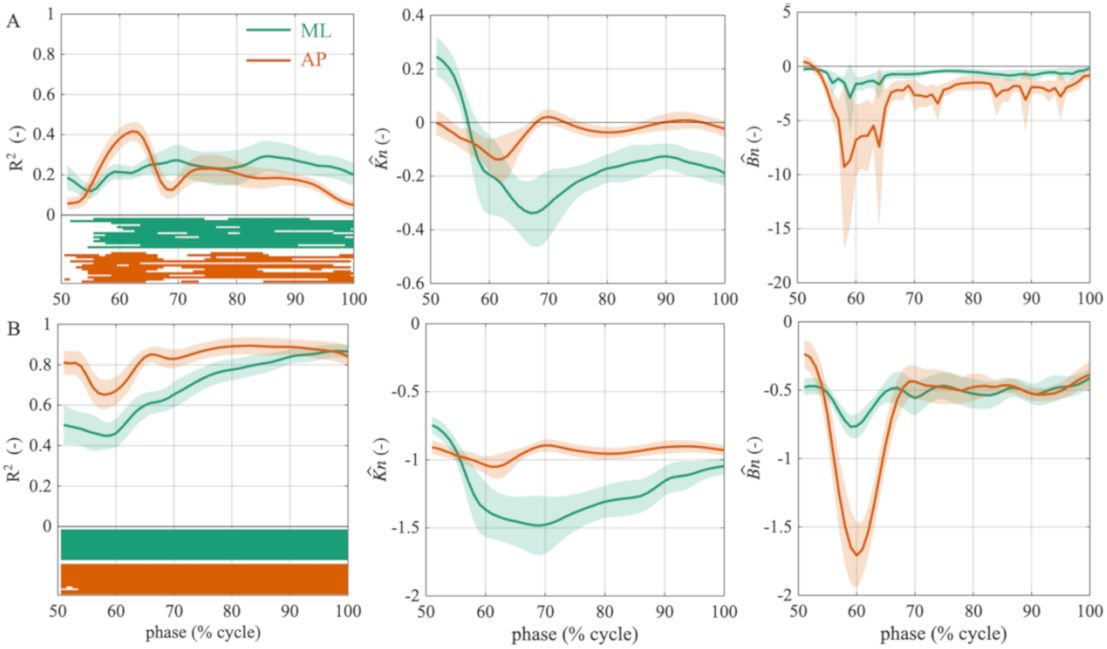

Fig 3. stabilization models identified in walking with the total (panel A) and corrected ground reaction forces (panel B) as predicted variables. From left to right: model fit (R^2), normalized position gains ($\widehat{K_n}$) and velocity gains ($\widehat{B_n}$) across the gait cycle. The green and orange lines represent the averaged results (over participants) in ML and AP direction, respectively. The dashed areas indicate the 95% confidence intervals. The horizontal lines in the left panels indicate when the model fit was significant for each individual participant (p<0.05).

4.1.2 Peak gains vs. mean gains

Based on the results using corrected ground reaction forces, the effective delays in walking were 46±5% and 23±13% of the gait cycle in the ML and AP directions, corresponding to 504±54ms and 250±137ms. The effective delay in the ML direction was significantly longer than in the AP direction (p<0.001) (**Table 1**, **Fig 3**).

For the position gains ($\widehat{K_n}$), the peak value was significantly larger than the mean value in the ML direction (p=0.001), while no significant difference was observed

in the AP direction (p=0.14). Moreover, both peak and mean position gains showed larger values in the ML direction than the AP direction (p<0.001). The peak velocity gains ($\widehat{B_n}$) were consistently larger than the mean values in both directions (p<0.001), and both peak (p=0.009) and mean (p<0.001) values were significantly larger in the AP direction than in the ML direction. Consistent with the concept of extrapolated center of mass, the ratio of the mean position to velocity gains ($\widehat{R_n}$) was not significantly different from 1. However, $\widehat{R_n}$ of the peak gains was significantly smaller than 1 and significantly smaller than of the mean gains in both ML direction (p<0.001) and AP direction (p=0.009). $\widehat{R_n}$ of mean gains in the ML direction was significantly larger than in the AP direction (p<0.001), whereas no significant directional differences were observed for $\widehat{R_n}$ of the peak gains (p=0.98).

4.2 Comparison between tasks

In the comparison of standing and walking we report, for walking, values based on averages over the stance phase only.

4.2.1 Model fit

Post-hoc simple effects showed that, in the ML direction, normal standing had a significantly better model fit than all the other tasks (p<0.001), followed by the step posture for which model fit was significantly better than for walking and unipedal standing (p<0.001). No differences were found between walking and

unipedal standing in this direction ($p=1$). In the AP direction, the model fit for step posture was significantly lower than for all the other tasks ($p<0.05$). Moreover, unipedal standing yielded a significantly lower model fit than normal standing ($p<0.001$), but comparable to walking ($p=1$). No significant differences were observed between walking and normal standing ($p=0.07$).

When comparing directions within the same task, walking and unipedal standing showed a significantly better model fit in the AP direction than in the ML direction ($p<0.001$). In contrast, in the step posture, the model fit was better in the ML direction than in the AP direction ($p<0.001$). No directional differences were observed in normal standing ($p=0.18$).

4.2.2 Effective delay

In line with our hypothesis, the post-hoc simple effects showed that the effective delay was significantly longer in walking than in standing postures in both directions ($p<0.001$). Among standing postures, in the ML direction, unipedal standing had a significantly shorter delay than normal standing($p<0.001$) and step posture ($p<0.001$), while there were no differences between normal standing and step posture ($p=1$). In the AP direction, normal standing had a significantly longer effective delay than in unipedal standing ($p<0.001$) and step posture ($p<0.001$),

while no differences were observed between unipedal standing and step posture (p=0.06).

Comparing directions, significantly longer effective delays in the ML than in the AP direction were found in walking ($p<0.001$) and step posture ($p<0.001$), while the opposite was found in normal standing ($p<0.001$) and unipedal standing ($p<0.001$).

4.2.3 Position gain

In the ML direction, the lumped position gains in all tasks exceeded their critical values with $\widehat{K_n} < -1$, and no significant differences were observed between walking and all standing postures ($p>0.05$). Within standing postures, unipedal standing showed significantly larger position gains than both normal standing ($p<0.001$) and step posture ($p<0.001$). In the AP direction, the lumped position gain in walking was slightly below its critical value and was significantly smaller than that of all the standing postures ($p<0.001$), and the lumped position gains of all standing tasks exceeded their critical values. Among standing tasks, the step posture had the largest position gain, followed by unipedal standing, with normal standing exhibiting a significantly smaller position gain.

The step posture showed significantly larger position gains in the AP than in the ML direction ($p<.001$), whereas the opposite pattern was found in the other tasks ($p<.001$).

4.2.4 Velocity gain

In contrast to the position gain, the velocity gains were all below critical damping ($\widehat{B_n} > -1$), and the velocity gain in walking was significantly larger than in standing postures in both directions ($p<.001$). No significant differences were observed among standing postures ($p>.05$).

The directional differences within task were consistent, with velocity gains larger in the AP direction than in the ML direction ($p<.05$).

4.2.5 Ratio of position to velocity gains

All standing tasks showed a normalized ratio ($\widehat{R_n}$) significantly larger than 1, whereas in walking it was not significantly different from 1. No significant task differences were observed ($p>.05$), but the ratio was consistently larger in the ML direction than in the AP direction ($p = .005$).

5. Discussion

In the present study, we applied a stabilization model to investigate and compare the lumped stabilizing effects of intrinsic mechanics and feedback control across tasks. We found task-dependent differences in stabilizing parameters, with larger velocity gains in walking and lower position gains in the AP direction in walking than in standing. Despite these differences, most tasks exhibited a lumped stiffness which was above critical stiffness, as well as under-damped control. The only exceptions were lumped position gains in the AP direction in walking, which were slightly below critical stiffness. Notably, the ratio between position and velocity gains remained relatively constant across tasks and was close to the body's eigenfrequency predicted by the extrapolated center of mass (XCoM) concept. Our findings suggest that, while individual stabilizing parameters are modulated to meet task-dependent demands, the overall stabilization preserved a similar relationship between position- and velocity-related contributions. In other words, different tasks might apply task-dependent stabilizing mechanisms while aiming to achieve the same task-level stabilization: maintaining the CoM movement a pendulum-like trajectory.

5.1 Stabilizing mechanisms in walking

The significantly improved model fit (**Fig 3**), as well as the observed continuous control in both directions suggest that correcting for gravitational effects allows for more accurate estimation of stabilizing mechanisms in walking.

Afschrift et al. described phase-dependent characteristics of feedback responses to perturbations of walking at different speeds [10]. Our results, at a speed of 1.2m/s, were similar to theirs. Specifically, we found that the lumped stabilizing gains were modulated across the gait cycle, with velocity gains being more phase-dependent than position gains in the AP direction, this suggests that task-level stability is achieved by dynamically modulating feedback control. However, a timing difference was observed. Our results showed peak gains occurred during early stance, while the feedback responses to perturbations were most pronounced at mid-stance[10]. This timing difference can be attributed to fact that we estimated the lumped effects, while the effects of the intrinsic mechanisms are likely to be most pronounced in early stance. Furthermore, methodological differences may also have affected the timing of the peak gains, because we used corrected ground reaction forces as the model output and selected the effective delay based on the variation of gains across the gait cycle, whereas Afschrift, De Groote (10) used the EMG and ankle torque as model output and used a constant feedback delay.

We found that the effective delay during walking was significantly longer in the ML direction than in the AP direction, which may suggest different stability demands and stabilizing strategies between directions. In the ML direction, stabilization has been shown to be more challenging [27-30] and to rely more on foot placement [28, 31], while in the AP direction, stabilization has been suggested

to rely more on the ankle strategy [9, 32], which can take effect during the stance phase and hence at a shorter delay.

We also found that both mean and peak lumped gains in walking were larger in the ML direction, while in the AP direction velocity gains were higher. These directional differences are consistent with the foot placement model [33], which demonstrated that ML foot placement control relies more on CoM position, whereas AP foot placement relies more on CoM velocity. Peak gains around early stance were expected, as this phase would impose high demands, especially to control AP velocity, where over-damped control appears to be used to avoid overshoot and oscillations to allow smooth and stable forward progression. The mean gains reflect control over the whole stance phase. Since velocity fluctuations in the remainder of the stance phase are smaller, an overall under-damped control may suffice.

5.2 Comparison of stabilizing mechanisms across tasks

5.2.1 Effective delay

As hypothesized, the estimated effective delay was significantly longer in walking than in standing. This was expected as in walking, as corrections are mainly applied after foot contact, while in standing stability control is continuous [30].

The differences in effective delays between standing postures can be attributed to different biomechanical and neurophysiological characteristics. As noted in the methods section [21], increased intrinsic stiffness leads to a negative bias in effective delays. The observed shorter delays in unipedal standing may thus be explained by an increased intrinsic stiffness due to the higher co-contraction levels [2, 34-38]. In the step posture, its non-neutral ankle angles coincide with higher intrinsic stiffness compared to normal standing, due to the non-linear relationship between ankle angle and elastic parameters [39]. In addition, the geometric configuration of the legs in the step posture with the non-aligned ankle axes will yield 'structural stiffness', enhancing the overall stiffness. In addition to biasing the estimates of the delay due to differences in intrinsic stiffness, higher muscle activity can be expected to cause a shorter electro-mechanical delay [40], contributing to a shorter effective delay in unipedal standing and step postures.

5.2.2 Position gains

Lumped position gains for all tasks exceeded critical stability (i.e.,$\widehat{K_n} < -1$) except for walking in the AP direction. In the AP direction, the walking position gain was slightly below the critical stiffness, suggesting instability in this direction, likely prevented by changes in the base of support (stepping). The peak walking

gains typically above critical stiffness (i.e., $\widehat{K_n} < -1$) suggests that indeed these changes are used to maintain a stable gait pattern.

Among standing postures, unipedal standing and step posture had significantly larger lumped position gains than normal standing, which can partly be attributed to their higher intrinsic stiffness as mentioned above. However, feedback control might also contribute to these differences, and it is impossible to separate the intrinsic and feedback contributions without applying external perturbations [8]. Thus, it remains unclear to what extent feedback mechanisms contribute to the differences in lumped gains. Interestingly, lumped position gains in unipedal standing were approximately twice the per leg values observed in normal standing, despite the smaller base of support and the reduction in number of muscles that can contribute to the corrective forces. This indicates that the control system compensates for the reduced mechanical stability by increasing the overall stabilizing contribution, reflecting a flexible adjustment of the combined stabilizing mechanisms. Similarly, it is reasonable to speculate that the feedback control in step posture might be decreased due to the additional structural stiffness.

5.2.3 Velocity gains

The lumped velocity gains revealed an under-damped control in both walking and standing, and there was a clear task-dependent modulation, with lumped velocity

gains significantly larger in walking than in standing. The under-damped velocity control observed in standing aligned well with the findings that described human upright posture as an underdamped system [41, 42], likely reflecting that our control system allows some oscillatory behavior during standing.

5.2.4 Ratio of position to velocity gains

According to the XCoM concept, control of pendular movement requires the ratio of position to velocity gains to equal the system's eigenfrequency, yielding a normalized ratio ($\widehat{R_n}$) of 1. The $\widehat{R_n}$ in walking was not significantly different from 1, which is as expected, whereas this value in standing was significantly larger than 1. However, this ratio between walking and standing was not significantly different, and both ratios remained close to the eigenfrequency value.

The fact that the ratio of lumped gains remained consistent and close to the eigenfrequency across all tasks, suggests that the control system modulates the stabilizing mechanisms to keep the whole-body dynamics close to that of an inverted pendulum.

The deviations from the eigenfrequency ratio, particularly in standing, may reflect task-dependent stabilizing mechanisms. The larger ratio observed in standing compared to walking suggests prioritization of position control over velocity, which aligns with the goal of a static task: keeping a fixed reference point.

6. Limitations

Several limitations should be noted. First, we modeled the human body as a single inverted-pendulum in both standing and walking. Although this simplification provided good model fits in all tasks, it does not fully capture the multi-segmented nature of the human body, particularly not during the double-support phase of walking. This may have introduced errors in force decomposition. However, the fact that the ratio of position to velocity gains was close to eigenfrequency across tasks suggests that the task-level stabilization achieves a pendulum-like trajectory, which suggests that this simplification does not substantially affect the estimation of overall stabilizing mechanisms in the current study. Second, we applied different methods to select the effective delay and corresponding lumped gains between standing and walking, which may lead to some bias when comparing the stabilizing parameters. In addition, walking may introduce more soft tissue artifacts in the measurement of kinematics, potentially affecting the parameter estimation. Nonetheless, the estimated parameters aligned well with the task-specific characteristics. Furthermore, while the lumped model captures the overall stabilizing effects, separating intrinsic and feedback contributions would provide more detailed information, but this requires perturbation-based studies. Finally, we

examined only one gait speed in this study, whether and how the observed feedback strategy will change with speed needs further examination.

7. Conclusion

Our results showed that while the lumped stabilizing gains changed significantly across tasks and directions, the lumped position gains were consistently maintained close to critical stiffness, while the velocity was controlled at under-damped level. Notably, the relative ratio between position and velocity gains in both walking and standing remained close to the body's eigenfrequency, which may reflect that, in spite of differences in stabilizing mechanisms, at the behavioral level stabilization of a pendulum-like trajectory is a common goal.

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References

1. Fitzpatrick R, Burke D, Gandevia SC. Loop gain of reflexes controlling human standing measured with the use of postural and vestibular disturbances. J Neurophysiol. 1996;76(6):3994-4008. doi: 10.1152/jn.1996.76.6.3994. PubMed PMID: 8985895.
2. Amiri P, Kearney RE. Ankle intrinsic stiffness changes with postural sway. J Biomech. 2019;85:50-8. Epub 20190111. doi: 10.1016/j.jbiomech.2019.01.009. PubMed PMID: 30655078.

3. Peterka RJ. Sensorimotor integration in human postural control. J Neurophysiol. 2002;88(3):1097-118. PubMed PMID: 12205132.
4. Forbes PA, Chen A, Blouin JS. Sensorimotor control of standing balance. Handb Clin Neurol. 2018;159:61-83. doi: 10.1016/B978-0-444-63916-5.00004-5. PubMed PMID: 30482333.
5. Shanbhag J, Fleischmann S, Wechsler I, Gassner H, Winkler J, Eskofier BM, et al. A sensorimotor enhanced neuromusculoskeletal model for simulating postural control of upright standing. Front Neurosci. 2024;18:1393749. Epub 20240515. doi: 10.3389/fnins.2024.1393749. PubMed PMID: 38812972; PubMed Central PMCID: PMCPMC11133552.
6. Bottaro A, Casadio M, Morasso PG, Sanguineti V. Body sway during quiet standing: is it the residual chattering of an intermittent stabilization process? Hum Mov Sci. 2005;24(4):588-615. Epub 20050906. doi: 10.1016/j.humov.2005.07.006. PubMed PMID: 16143414.
7. Asslander L, Peterka RJ. Sensory reweighting dynamics in human postural control. J Neurophysiol. 2014;111(9):1852-64. Epub 20140205. doi: 10.1152/jn.00669.2013. PubMed PMID: 24501263; PubMed Central PMCID: PMCPMC4044370.
8. van der Kooij H, van Asseldonk E, van der Helm FC. Comparison of different methods to identify and quantify balance control. J Neurosci Methods. 2005;145(1-2):175-203. Epub 20050319. doi: 10.1016/j.jneumeth.2005.01.003. PubMed PMID: 15922036.
9. Reimann H, Fettrow T, Thompson ED, Jeka JJ. Neural Control of Balance During Walking. Front Physiol. 2018;9:1271. Epub 2018/10/03. doi: 10.3389/fphys.2018.01271. PubMed PMID: 30271354; PubMed Central PMCID: PMCPMC6146212.
10. Afschrift M, De Groote F, Jonkers I. Similar sensorimotor transformations control balance during standing and walking. PLoS Comput Biol. 2021;17(6):e1008369. Epub 2021/06/26. doi: 10.1371/journal.pcbi.1008369. PubMed PMID: 34170903; PubMed Central PMCID: PMCPMC8266079.
11. Safavynia SA, Ting LH. Long-latency muscle activity reflects continuous, delayed sensorimotor feedback of task-level and not joint-level error. J Neurophysiol. 2013;110(6):1278-90. Epub 20130626. doi: 10.1152/jn.00609.2012. PubMed PMID: 23803325; PubMed Central PMCID: PMCPMC3763153.
12. Mergner T, Maurer C, Peterka RJ. A multisensory posture control model of human upright stance. Prog Brain Res. 2003;142:189-201. doi: 10.1016/S0079-6123(03)42014-1. PubMed PMID: 12693262.
13. Jakubowski KL, Martino G, Beck ON, Sawicki GS, Ting LH. Center of mass states render multi-joint torques throughout standing balance recovery.

bioRxiv. 2024. Epub 20240819. doi: 10.1101/2024.08.14.607976. PubMed PMID: 39229207; PubMed Central PMCID: PMCPMC11370471.
14. Rafiee S, Kiemel T. Multiple strategies to correct errors in foot placement and control speed in human walking. Exp Brain Res. 2020;238(12):2947-63. Epub 2020/10/19. doi: 10.1007/s00221-020-05949-x. PubMed PMID: 33070229.
15. Reimann H, Bruijn SM. The condition for dynamic stability in humans walking with feedback control. PLoS Comput Biol. 2024;20(3):e1011861. Epub 20240318. doi: 10.1371/journal.pcbi.1011861. PubMed PMID: 38498569; PubMed Central PMCID: PMCPMC10997112.
16. Shiozawa K, Lee J, Russo M, Sternad D, Hogan N. Frequency-dependent force direction elucidates neural control of balance. J Neuroeng Rehabil. 2021;18(1):145. Epub 20210925. doi: 10.1186/s12984-021-00907-2. PubMed PMID: 34563223; PubMed Central PMCID: PMCPMC8466643.
17. Sugimoto-Dimitrova R, Shiozawa K, Gruben KG, Hogan N. Frequency-domain patterns in foot-force line-of-action: an emergent property of standing balance control. J Neurophysiol. 2024;132(5):1445-56. Epub 20241003. doi: 10.1152/jn.00084.2024. PubMed PMID: 39361732.
18. van Dieen JH, Bruijn SM, Afschrift M. Assessment of stabilizing feedback control of walking: A tutorial. J Electromyogr Kinesiol. 2024;78:102915. Epub 20240622. doi: 10.1016/j.jelekin.2024.102915. PubMed PMID: 38936234.
19. Hof AL, Gazendam MG, Sinke WE. The condition for dynamic stability. J Biomech. 2005;38(1):1-8. Epub 2004/11/03. doi: 10.1016/j.jbiomech.2004.03.025. PubMed PMID: 15519333.
20. Hof AL. The 'extrapolated center of mass' concept suggests a simple control of balance in walking. Hum Mov Sci. 2008;27(1):112-25. Epub 20071101. doi: 10.1016/j.humov.2007.08.003. PubMed PMID: 17935808.
21. Geng Y, Bruijn SM, van Dieen JH. Feedback control stabilizing the center of mass can be identified in unperturbed, upright standing. Hum Mov Sci. 2026;106:103470. Epub 20260228. doi: 10.1016/j.humov.2026.103470. PubMed PMID: 41764868.
22. Foulger LH, Liu X, Nasrabadi AM, Qiao CZ, Carpenter MG, Wu LC, et al. Learning to stand with delays alters sensorimotor control but does not cause instability when returning to natural balance. J Physiol. 2025;603(19):5629-53. Epub 20250911. doi: 10.1113/JP288632. PubMed PMID: 40936302; PubMed Central PMCID: PMCPMC12487603.
23. Muehlbauer T, Mettler C, Roth R, Granacher U. One-leg standing performance and muscle activity: are there limb differences? J Appl Biomech. 2014;30(3):407-14. Epub 20140305. doi: 10.1123/jab.2013-0230. PubMed PMID: 24610423.

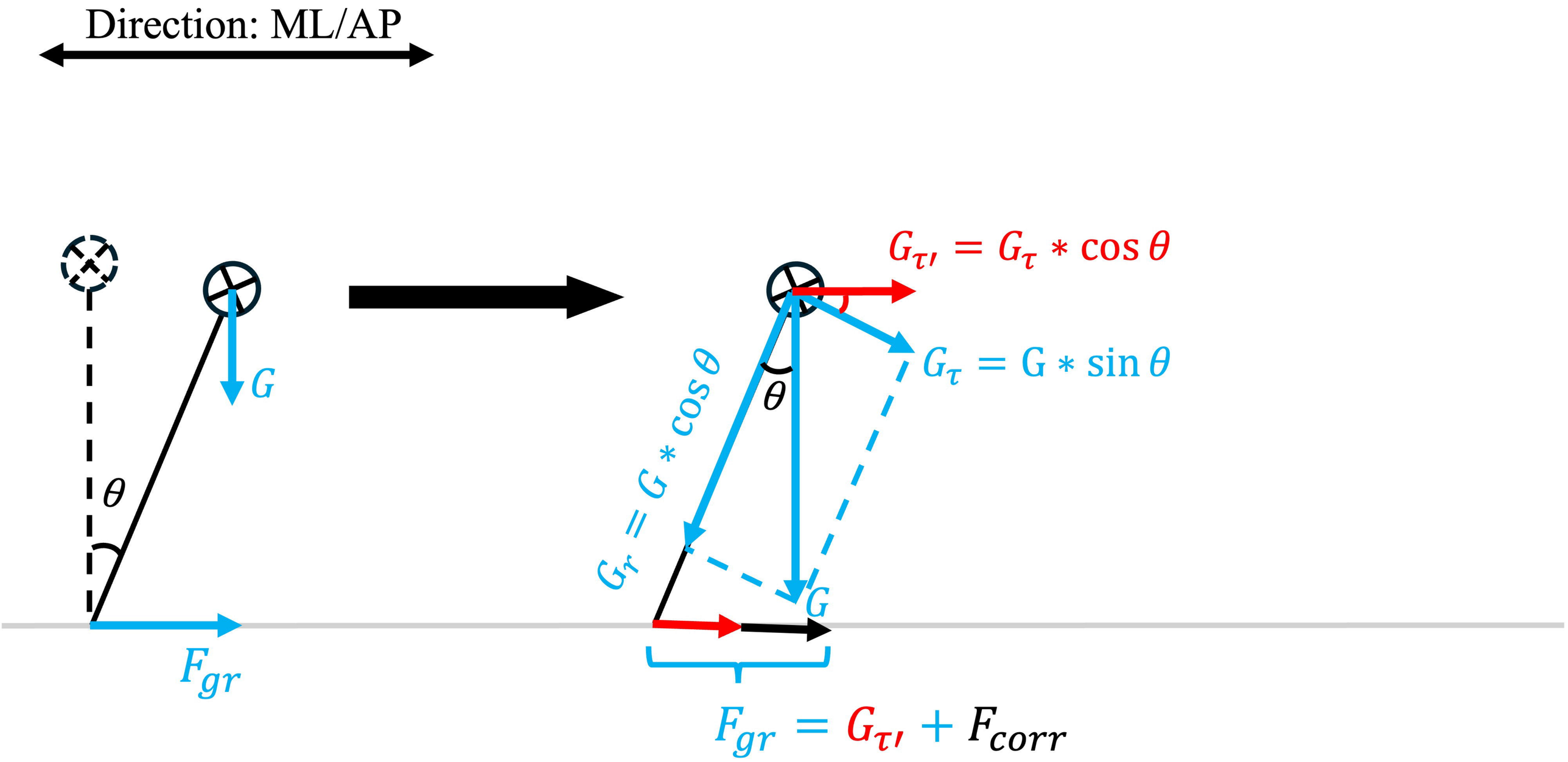
24. Kingma I, deLooze MP, Toussaint HM, Klijnsma HG, Bruijnen TBM. Validation of a full body 3-D dynamic linked segment model. Hum Movement Sci. 1996;15(6):833-60. doi: Doi 10.1016/S0167-9457(96)00034-6. PubMed PMID: WOS:A1996VY04600003.
25. Kuo AD, Donelan JM, Ruina A. Energetic consequences of walking like an inverted pendulum: step-to-step transitions. Exerc Sport Sci Rev. 2005;33(2):88-97. doi: 10.1097/00003677-200504000-00006. PubMed PMID: 15821430.
26. Cohen J. Statistical Power Analysis for the Behavioral Sciences. Hillsdale, NJ: Lawrence Erlbaum Associates; 1988.
27. Kongsuk J, Brown DA, Hurt CP. Dynamic stability during increased walking speeds is related to balance confidence of older adults: a pilot study. Gait Posture. 2019;73:86-92. Epub 20190704. doi: 10.1016/j.gaitpost.2019.06.018. PubMed PMID: 31302337; PubMed Central PMCID: PMCPMC6711748.
28. Harter MJ, Redfern MS, Sparto PJ, Geyer H. Modelling strategies supplemental to foot placement for frontal-plane stability in walking. J R Soc Interface. 2024;21(218):20240191. Epub 20240904. doi: 10.1098/rsif.2024.0191. PubMed PMID: 39226925; PubMed Central PMCID: PMCPMC11371431.
29. Madehkhaksar F, Klenk J, Sczuka K, Gordt K, Melzer I, Schwenk M. The effects of unexpected mechanical perturbations during treadmill walking on spatiotemporal gait parameters, and the dynamic stability measures by which to quantify postural response. PLoS One. 2018;13(4):e0195902. Epub 20180419. doi: 10.1371/journal.pone.0195902. PubMed PMID: 29672558; PubMed Central PMCID: PMCPMC5908091.
30. O'Connor SM, Kuo AD. Direction-dependent control of balance during walking and standing. J Neurophysiol. 2009;102(3):1411-9. doi: 10.1152/jn.00131.2009. PubMed PMID: 19553493; PubMed Central PMCID: PMCPMC2746770.
31. Bruijn SM, van Dieen JH. Control of human gait stability through foot placement. J R Soc Interface. 2018;15(143). doi: 10.1098/rsif.2017.0816. PubMed PMID: 29875279; PubMed Central PMCID: PMCPMC6030625.
32. Gatev P, Thomas S, Kepple T, Hallett M. Feedforward ankle strategy of balance during quiet stance in adults. J Physiol. 1999;514 (Pt 3)(Pt 3):915-28. doi: 10.1111/j.1469-7793.1999.915ad.x. PubMed PMID: 9882761; PubMed Central PMCID: PMCPMC2269093.
33. Wang Y, Srinivasan M. Stepping in the direction of the fall: the next foot placement can be predicted from current upper body state in steady-state walking. Biol Lett. 2014;10(9). Epub 2014/09/26. doi: 10.1098/rsbl.2014.0405. PubMed PMID: 25252834; PubMed Central PMCID: PMCPMC4190959.
34. Wu F, Zhang J, Yang K, Li Y, Li Z, Li T, et al. Surface electromyography analysis of ankle flexor and extensor activity under different standing stability

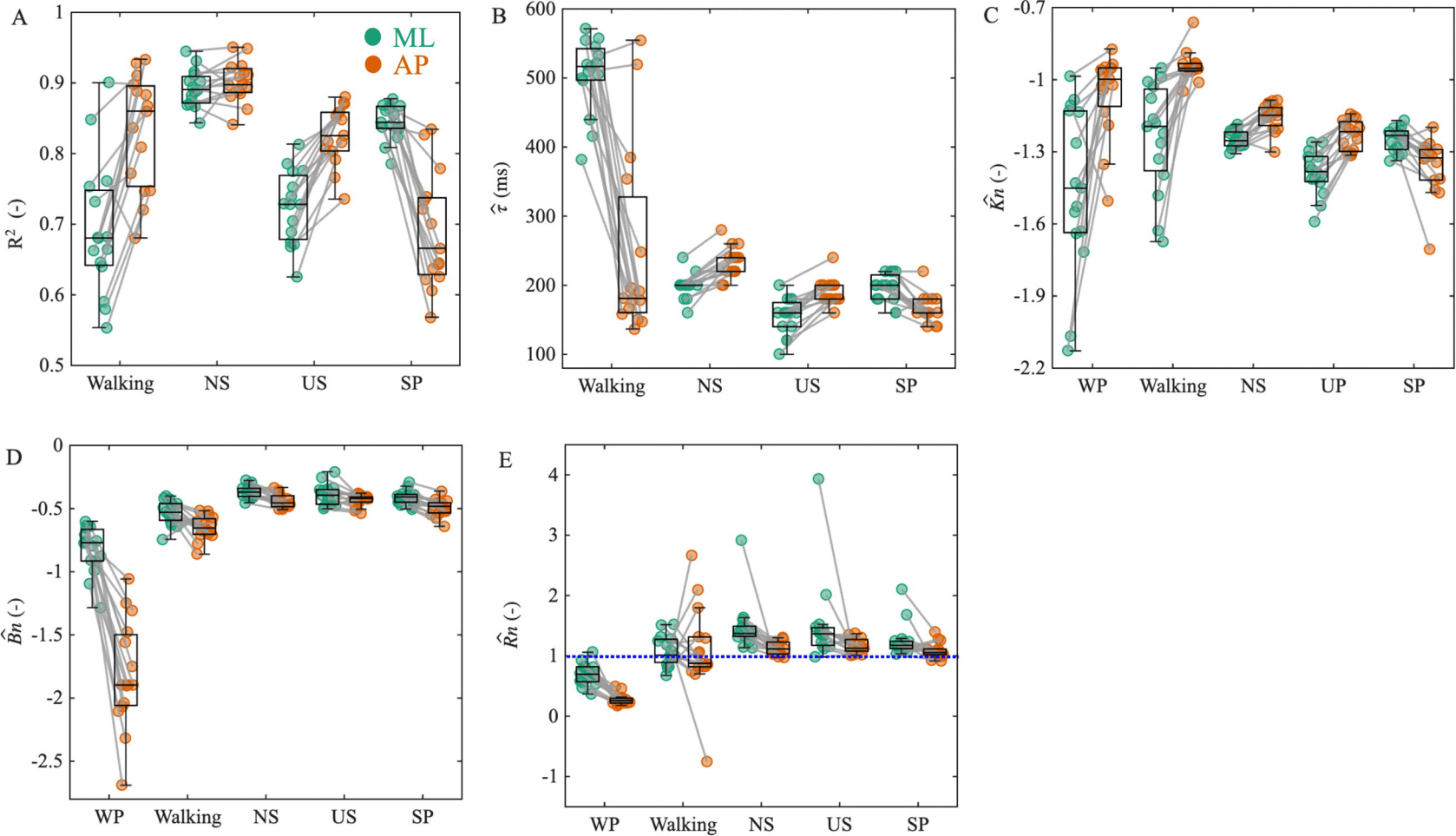
levels. J Orthop Surg (Hong Kong). 2024;32(2):10225536241258336. doi: 10.1177/10225536241258336. PubMed PMID: 38910029.
35. Fok KL, Lee JW, Unger J, Chan K, Musselman KE, Masani K. Co-contraction of ankle muscle activity during quiet standing in individuals with incomplete spinal cord injury is associated with postural instability. Sci Rep. 2021;11(1):19599. Epub 20211001. doi: 10.1038/s41598-021-99151-w. PubMed PMID: 34599267; PubMed Central PMCID: PMCPMC8486862.
36. Baratta R, Solomonow M, Zhou BH, Letson D, Chuinard R, D'Ambrosia R. Muscular coactivation. The role of the antagonist musculature in maintaining knee stability. Am J Sports Med. 1988;16(2):113-22. Epub 1988/03/01. doi: 10.1177/036354658801600205. PubMed PMID: 3377094.
37. Sakanaka TE, Gill J, Lakie MD, Reynolds RF. Intrinsic ankle stiffness during standing increases with ankle torque and passive stretch of the Achilles tendon. PLoS One. 2018;13(3):e0193850. Epub 20180320. doi: 10.1371/journal.pone.0193850. PubMed PMID: 29558469; PubMed Central PMCID: PMCPMC5860743.
38. Sakanaka TE, Lakie M, Reynolds RF. Individual differences in intrinsic ankle stiffness and their relationship to body sway and ankle torque. PLoS One. 2021;16(1):e0244993. Epub 20210122. doi: 10.1371/journal.pone.0244993. PubMed PMID: 33481823; PubMed Central PMCID: PMCPMC7822306.
39. Weiss PL, Kearney RE, Hunter IW. Position dependence of ankle joint dynamics--I. Passive mechanics. J Biomech. 1986;19(9):727-35. doi: 10.1016/0021-9290(86)90196-x. PubMed PMID: 3793747.
40. Vos EJ, Harlaar J, van Ingen Schenau GJ. Electromechanical delay during knee extensor contractions. Med Sci Sports Exerc. 1991;23(10):1187-93. PubMed PMID: 1758296.
41. Winter DA. Human balance and posture control during standing and walking. Gait & Posture. 1995;3(4):193-214. doi: 10.1016/0966-6362(96)82849-9.
42. Winter DA, Patla AE, Prince F, Ishac M, Gielo-Perczak K. Stiffness control of balance in quiet standing. J Neurophysiol. 1998;80(3):1211-21. Epub 1998/09/24. doi: 10.1152/jn.1998.80.3.1211. PubMed PMID: 9744933.

Supporting information

S1 Table. Feedback results in walking and standing (mean±SD).

S1 Figure. Time series of the PCoM (panel A), VCoM (panel B) and corrected ground reaction forces (panel C) during walking in the AP direction from a typical participant.


Direction: ML/AP
G
θ
F_{gr}
$G_{\tau\prime} = G_{\tau} * \cos\theta$
$G_{\tau} = G * \sin\theta$
θ
$G_r = G * \cos\theta$
G
$F_{gr} = G_{\tau\prime} + F_{corr}$


A
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AP
R^2 (-)
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0.8
0.7
0.6
0.5
Walking
NS
US
SP
B
$\hat{\tau}$ (ms)
600
500
400
300
200
100
Walking
NS
US
SP
C
$\hat{K}n$ (-)
-0.7
-1
-1.3
-1.6
-1.9
-2.2
WP
Walking
NS
UP
SP
D
$\hat{B}n$ (-)
0
-0.5
-1
-1.5
-2
-2.5
WP
Walking
NS
US
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E
$\hat{R}n$ (-)
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3
2
1
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WP
Walking
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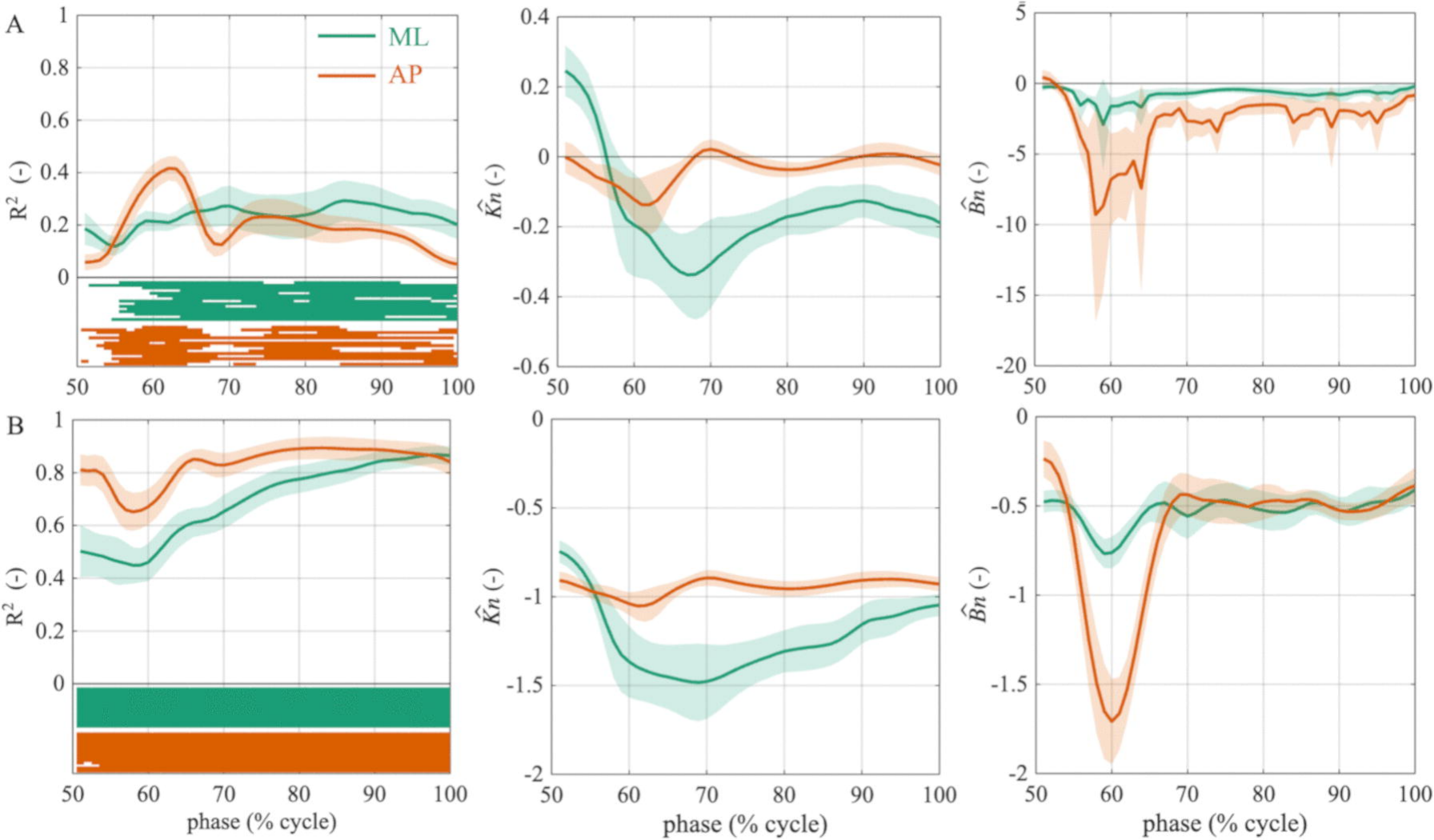
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