Shared feedback control principles across standing and walking

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Abstract

Feedback control is required to maintain stability in both walking and standing, whereas the control parameters may differ due to the inherently different characteristics of these tasks. How feedback is adapted between tasks is unclear. To address this, we applied a unified feedback model, relating preceding center of mass position and velocity information to corrective ground reaction forces, to estimate and compare the control parameters between walking and standing.

15 healthy young participants (21± 4 yrs, 63 ± 9 kg, 1.70 ± 0.10 m, 13 females, 2 males) participated, they walked at 4.5 km/h 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 feedback model and estimate feedback delay and gains. Results showed good model fits for both walking and standing with mean R^2-values higher than 0.69. The feedback delay was significantly longer in walking than in standing. While the feedback position gains and velocity gains varied significantly across tasks and directions, position gains were mostly above critical stiffness and velocity gains all at under-damped level, with as only exception that position gains in the AP direction in walking, which were slightly below critical stiffness. The ratio of position to velocity gains in all tasks remained consistently

close to the eigenfrequency ($\sqrt{g/l}$) as predicted by the extrapolated center of mass concept.

Our findings suggest a robust control strategy in which the sensorimotor system maintains a relative consistent weighting between position and velocity feedback for walking and standing.

1. Introduction

Walking and standing 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 coordination of intrinsic mechanics and feedback control. Intrinsic mechanics provide immediate resistance to perturbations based on segments' inertia and joints' stiffness and damping. The latter can be modulated by muscle co-activation to deal with expected perturbations or uncertainty, but maintaining high levels of co-contraction is energetically costly [1]. In contrast, feedback control is adaptive and generates corrective responses selectively based on sensory information [2, 3].

Given the different temporal and biomechanical characteristics of standing and walking, feedback control parameters can be expected to differ between these motor tasks, reflecting task-specific modulations. Standing is a quasi-static behavior, while walking is a dynamic, cyclic motion. This temporal difference suggests distinct feedback strategies: time-invariant feedback control in standing but a phase-dependent control in walking. Additionally, in standing, the anatomical constraints and smaller base of support (BoS) make stabilization more challenging in the anteroposterior (AP) direction than in the mediolateral (ML) direction [4-6]. However, during walking, the stability requirements shift. Stabilization of AP movement benefits from passive mechanics [7-9], while the ML movement must be actively stabilized [10, 11].

Several feedback models have been developed to identify feedback control in standing [3, 12-14] and walking [15]. These models indicate that sensory estimates of the center of mass (CoM) kinematics are used to modulate corrective responses (e.g., EMG, ankle torque, foot placement) to stabilize standing and walking. However, identification of these models requires perturbations and measurements of physiological signals (e.g., EMG), which poses high experimental demands and limits practical application. As an alternative, van Dieen, Bruijn [16] proposed a feedback model that can identify feedback control in unperturbed walking by fitting a linear relationship between the delayed extrapolated center of mass (XCoM) and horizontal ground reaction forces, without external perturbations or

physiological measurements. More recently, we refined this feedback model by using the CoM position and velocity information as separate predictors instead of the XCoM, and validated that this modified model can be applied to assess feedback control in standing [17]. Until now, these models were derived under the specific context being studied (i.e., either standing or walking), which leaves a gap in our understanding of how stability control is adapted between standing and walking.

In the present study, we addressed this gap by applying the aforementioned feedback model to unperturbed standing and walking. Using this model, we can estimate feedback position and velocity gains and the effective delay, helping us to understand how the CNS modulates feedback control in these tasks, while operating under the same fundamental control principle: generating corrective ground reaction forces based on preceding center of mass position (PCoM) and velocity (VCoM) information.

Hof, Gazendam [18] described the relative importance of position and velocity for maintaining dynamic stability. They showed that stability can be achieved by keeping the XCoM within the base of support (BoS), where the XCoM equals PCoM plus VCoM divided by the eigenfrequency of the body modeled as an inverted pendulum. This stability requirement has been validated in both standing

and walking [18, 19]. The XCoM concept indicates that gains of position and velocity feedback should have a ratio equal to the pendulum's eigenfrequency ($\sqrt{g/l}$). However, whether the CNS modulates feedback gains according to this ratio is unclear. Therefore, we will compare the ratio of position to velocity gains across standing and walking to the eigenfrequency of the body modeled as an inverted pendulum.

While standing is usually studied as bipedal standing with feet parallel, unipedal standing and step postures are commonly observed in daily life, and these postures resemble the behaviors in the single- and double-support phases of walking. These postures have a different BoS (e.g. standing on one versus two feet) and structural stiffness (e.g., feet parallel versus step configuration), which will affect stability requirements. Thus, we also applied the feedback model to unipedal standing and standing in a step posture, to investigate if, and how, feedback gains and effective delay change.

Based on previous studies [16, 17], we hypothesized that: 1) feedback delays are longer in walking because feedback becomes effective mainly after ground contact of the leading leg; 2) feedback gains are larger in walking than in standing postures, to compensate for larger delays (c.f. Foulger, Liu [20];) 3) directional differences exist in feedback control, 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 feedback 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-2018-159). 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 first walked on the instrumented dual-belt treadmill (Motek-Force-link, Amsterdam, Netherlands) with belt speed set at 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 were asked to perform: 1) Normal standing: stand upright with feet together. 2) Unipedal standing: stand on

the preferred leg. We tested the preferred leg only, because previously no differences were observed between standing on the dominant and non-dominant leg [21]. 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. 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 [17]. In short, we collected whole-body 3D kinematic data and ground reaction forces, 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 [22], 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, the PCoM was adjusted by removing its average value (i.e., the reference upright position). We removed the components due to gravitational acceleration from the total ground reaction forces (F_{gr}), based on the assumption that the whole body moved as a single inverted pendulum (IP), in both ML and AP directions, to obtain the corrective ground reaction forces (F_{corr}) [17]. Experimental data from second 6 to 50 of each trial were used to fit the feedback model.

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 [23], particularly during the double-stance phase. Nevertheless, removing the gravity effects may be essential, as the actual corrective effects might be masked if the gravitational component is not removed, potentially leading to an underestimation of the feedback. To address this, we used both F_{gr} and F_{corr} to fit the feedback model. Results supported the use of corrective forces as the model fit was significantly improved when using this over F_{gr} (Fig.1). Thus, for all reported analyses, we used F_{corr}. The whole 300s walking data were used to fit the model.

2.3 Feedback model

We fitted the feedback 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 feedback position and velocity gains, $\boldsymbol{\epsilon_i}$ represents the residual error, i represents the current time point, $\hat{\tau}$ represents the delay ranging from 100 to 1000ms [13].

We evaluated the model's goodness of fit using the coefficient of determination (R^2), and estimated the gains using ordinary least square regression, fitting F_{corr_i} to the linear model specified in equation (1) for each delay ($\hat{\tau}$). The delay at which the model achieved the maximum R^2 was regarded as the feedback delay, and the corresponding $\widehat{K}$ and $\widehat{B}$ were considered as the best estimates of the actual feedback parameters.

For walking, equation (2) was applied to estimate the feedback 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 $\widehat{\boldsymbol{K_J}}$ and $\widehat{\boldsymbol{B_J}}$ represents the phase-dependent 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 feedback delay ranging from 1% to 50% gait cycle.

Model fit was estimated using the same method as in standing. Differently, we selected the time lag that yielded the most negative weighted sum of position and velocity gains averaged over all stance phase as the feedback delay. Under this delay, the 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 control strategy during the whole stance phase, we additionally calculated the mean model fit and mean feedback 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 feedback delay ($\hat{\tau}$), and gains ($\widehat{K}$ and $\widehat{B}$) were estimated for all trials and subsequently averaged for statistical analysis. We further performed normalization of 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 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 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 feedback 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 feedback position and velocity gains ($\hat{K}/\hat{B}$), and further normalized this ratio relative to the IP eigenfrequency by dividing by $\sqrt{g/l}$, represented as $\widehat{R_n}$. If indeed position and velocity gains are modulated according to the extrapolated center of mass concept, we expect that $\widehat{R_n} \approx 1$.

3. Statistical analysis

We examined the effects of Task and Direction on model fit and feedback control 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 feedback 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 α = .05. Results are presented as mean ± standard deviation (mean ± SD).

4. Results

Our feedback model showed good performance with R^2 values ranging from 0.55 to 0.95 across all tasks, directions and participants. All feedback 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 feedback position to velocity gains ($\widehat{R_n}$), which showed only main effects of Task and Direction (Fig 1, Table 1). These results suggested that the feedback control differed across tasks and directions.

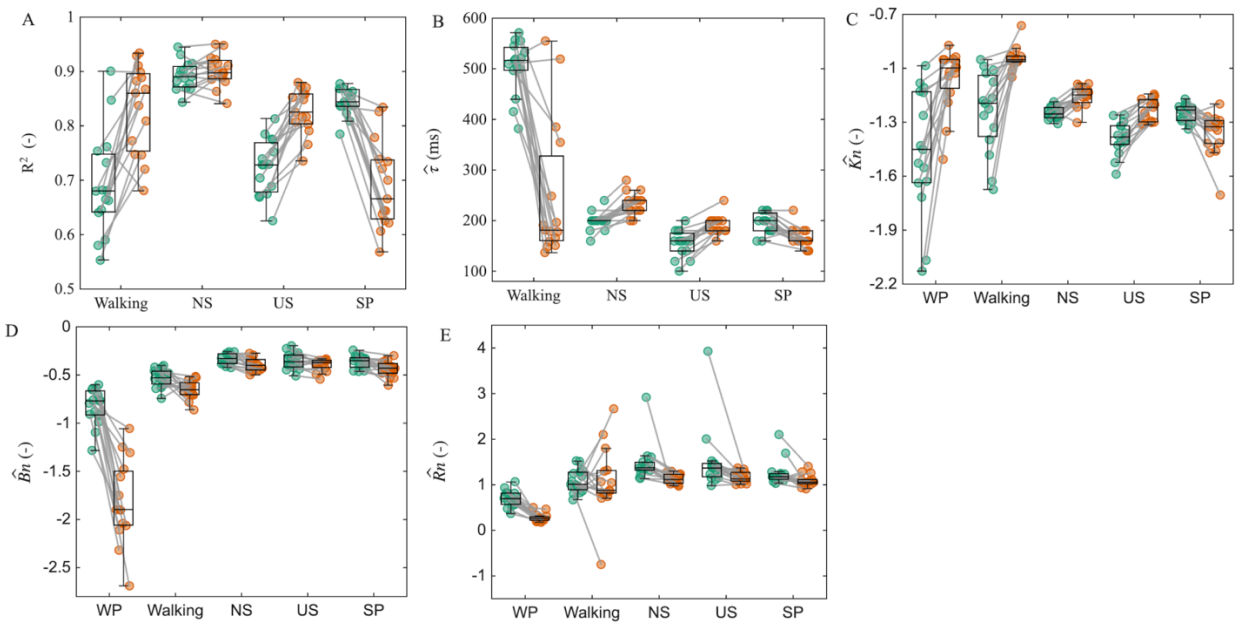

Fig 1. Model fit and estimated feedback parameters of all tasks. A) model fit, B) feedback delay, C) normalized position gain, D) normalized velocity gain, E) normalized position to velocity ratio. Box-plot shows estimated values across all participants, with central line indicating the median, box edges 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	206.04	<0.001**	0.94
	Direction	1,14	64.19	<0.001**	0.82
	Task * Direction	4,56	66.22	<0.001**	0.82
$\widehat{R_n}$	Task	4,56	27.08	<0.001**	0.66
	Direction	1,14	10.93	0.005*	0.44
	Task * Direction	4,56	1.69	0.17	0.11

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

From the data (Fig 1) 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 corrective 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 Feedback results in walking

4.1.1 Fitting model using total forces vs. corrective forces

The model fit (R^2) significantly improved when using corrective forces compared to total ground reaction forces in both ML and AP direction (Fig 2, 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 corrective forces. Notably, using the corrective forces indicated continuous position feedback, which was masked when using total forces (Fig 2).

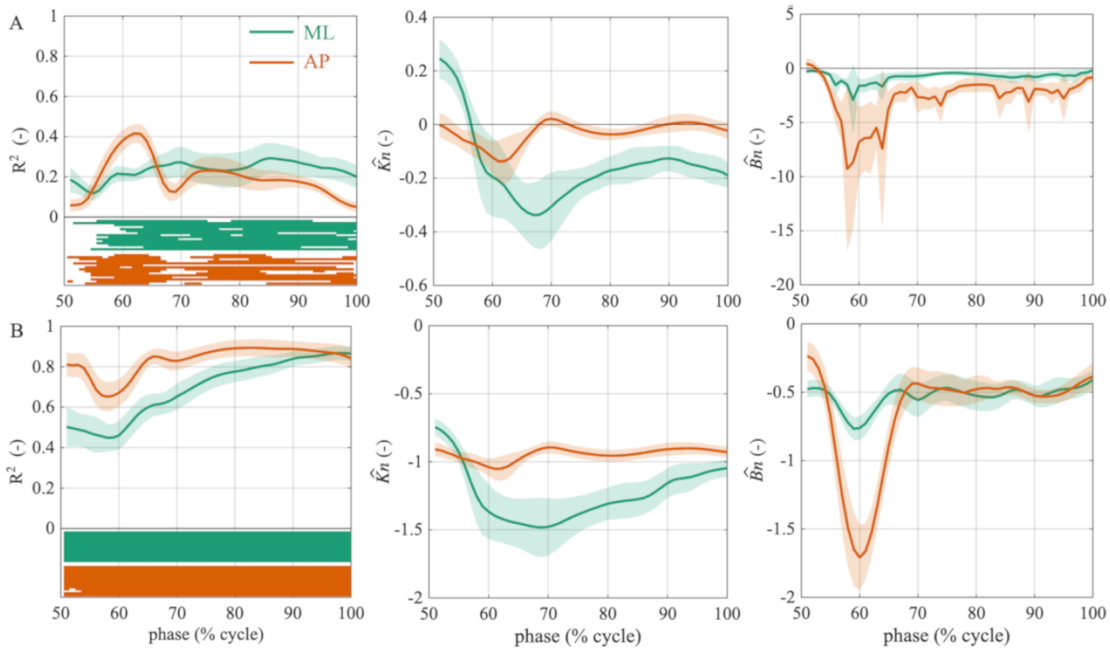

Fig 2. Feedback models identified in walking with the total (panel A) and corrective ground reaction forces (panel B) as predicted variables. From left to right: model fit (R^2), normalized feedback position gains ($\widehat{K_n}$) and velocity gains ($\widehat{B_n}$) across the gait cycle. The green 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<.05).

4.1.2 Peak gains vs. mean gains

Based on the results using corrective forces, the walking feedback delays were 46±5% and 23±13% of the gait cycle in the ML and AP directions, corresponding

to 504±54ms and 250±137ms. The feedback delay in the ML direction was significantly longer than in the AP direction (p<.001) (Table 1, Fig 2).

For the position gains ($\widehat{K_n}$), the peak value was significantly larger than the mean value in the ML direction (p=.001), while no significant difference was observed in the AP direction (p=.14). Moreover, both peak and mean position gains showed larger values in the ML direction than the AP direction (p<.001). The peak velocity gains ($\widehat{B_n}$) were consistently larger than the mean values in both directions (p<.001), and both peak (p=.009) and mean (p<.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<.001) and AP direction (p=.009). $\widehat{R_n}$ of mean gains in the ML direction was significantly larger than in the AP direction (p<.001), whereas no significant directional differences were observed for $\widehat{R_n}$ of the peak gains (p=.98).

4.2 Feedback control across 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 ($p<.001$), followed by the step posture for which model fit was significantly better than for walking and unipedal standing ($p<.001$). 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 ($p<.05$). Moreover, unipedal standing yielded a significantly lower model fit than normal standing ($p<.001$), but comparable to walking ($p=1$). No significant differences were observed between walking and normal standing ($p=.07$).

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 ($p<.001$). In contrast, in the step posture, the model fit was better in the ML direction than in the AP direction ($p<.001$). No directional differences were observed in normal standing ($p=.18$).

4.2.2 Feedback delay

In line with our hypothesis, the post-hoc simple effects showed that the feedback delay was significantly longer in walking than in standing postures in both

directions ($p<.001$). Among standing postures, in the ML direction, unipedal standing had a significantly shorter delay than normal standing($p<.001$) and step posture ($p<.001$), while there were no differences between normal standing and step posture ($p=1$). In the AP direction, normal standing had a significantly longer delay than in unipedal standing ($p<.001$) and step posture ($p<.001$), while no differences were observed between unipedal standing and step posture ($p=.06$).

Comparing directions, significantly longer delays in the ML than in the AP direction were found in walking ($p<.001$) and step posture ($p<.001$), while the opposite was found in normal standing ($p<.001$) and unipedal standing ($p<.001$).

4.2.3 Feedback position gain

In the ML direction, the 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 ($p>.05$). Within standing postures, unipedal standing showed significantly larger position gains than both normal standing ($p<.001$) and step posture ($p<.001$). In the AP direction, the position gain in walking was slightly below its critical value and was significantly smaller than that of all the standing postures ($p<.001$), and the 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 Feedback 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 feedback 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

This study is the first to apply the same model to estimate and compare feedback control during unperturbed walking and standing. Both walking and standing showed good model fits with mean values higher than 0.69, supporting the use of this model to estimate and compare feedback control without external perturbations. Results showed that the phase-dependent characteristics in walking indeed led to significant variations in feedback control over the gait cycle. Accordingly, we used the mean values of walking, representing the overall control strategy during the stance phase, for comparison with standing. For clarity, in the following we refer to these mean values unless explicitly stated otherwise.

Our results showed significantly larger velocity control in walking than in standing in both directions, whereas the position control in walking was significantly smaller than standing in the AP direction. Despite these differences, all tasks exhibited mostly above critical stiffness and under-damped control, with as only exception position gains in the AP direction in walking, which were slightly below critical stiffness. Notably, both walking and standing exhibited a position-to-velocity gain ratio close to the $\sqrt{g/l}$, as predicted by the extrapolated center of mass (XCoM) concept. These findings of feedback parameters which varied significantly across tasks and directions, and consistent relative position and

velocity gains indicate a common strategy of sensorimotor control across both dynamic and static conditions. We will further discuss these results below.

5.1 Feedback control in walking

In line with previous results [24], our results showed phase-dependent feedback control with peak control occurring during the early stance phase. The significantly improved model fit (Fig 2), as well as the observed continuous control in both directions suggest that using corrective forces allows for more accurate estimation of feedback parameters in walking.

Like Afschrift, De Groote [15], we found that gains were modulated across the gait cycle, with velocity control being more phase-dependent than position control in the AP direction. However, our results showed peak control in early stance, while Afschrift, De Groote [15] reported most pronounced control during mid-stance. The similarity likely reflects a common control strategy: the feedback control is performed based on preceding CoM position and velocity information. The difference in timing is likely due to methodological differences: we used corrective forces as the model output and selected the feedback delay based on the variation of gains across the gait cycle, whereas Afschrift, De Groote [15] used the EMG and ankle torque as model output and used a constant feedback delay. Additionally, our study didn't apply perturbations. While we observed more phase-dependent

control for position in the ML direction than in the AP direction, Afschrift, De Groote [15] only investigated AP control.

Both mean and peaks gains showed stronger control of position in the ML direction, while in the AP direction velocity was more tightly controlled. These directional differences are consistent with the foot placement model [25], 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 feedback control across tasks

5.2.1 Feedback delay

As hypothesized, the estimated feedback delay was significantly longer in walking than in standing. This was expected as in walking, feedback corrections are mainly applied after foot contact, while in standing stability control is continuous [26].

Directional differences in walking appear to reflect different stability demands and control strategies in the ML and AP directions. In the ML direction, stability control has been shown to be more challenging [26-29] and rely more on foot placement [28, 30], while in the AP direction, stability control has been suggested to rely more on the ankle strategy [31, 32], which can take effect during the stance phase and thus leads to a shorter delay.

The differences in estimated feedback delays among standing postures can be attributed to different biomechanical and neurophysiological characteristics. As suggested by our previous work [17], increased intrinsic stiffness leads to a negative bias on estimated feedback delays. The observed shorter delays in unipedal standing may thus be explained by the increased intrinsic stiffness due to the higher co-contraction levels [33-38]. 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 [39], contributing to a shorter delay in unipedal standing and step postures. Non-neutral ankle angles in the step posture coincide with higher intrinsic stiffness compared to normal standing, due to the non-linear relationship between ankle angle and elastic parameters [40]. 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.

5.2.2 Feedback position gains

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 position gains than normal standing, consistent with their presumed higher intrinsic stiffness as mentioned above. Interestingly, position gains in unipedal standing were approximately twice the per leg values observed in normal standing, indicating that the control system modulates feedback gains per leg and highlighting its adaptability to changed stability demands.

5.2.3 Feedback velocity gains

The velocity gains revealed an under-damped control in both walking and standing, and there was a clear task-dependent modulation, with 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 [4, 41], 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 inverted pendulum 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 approximation of these ratios to the eigenfrequency is consistent with the view that human body can be modelled as a single inverted pendulum model [4]. The deviations from 1, particularly during standing, likely result from the human body not behaving as a perfect pendulum, but instead stabilizing itself through multi-link segments coordination[42]. The comparable ratios observed in walking and standing suggest that, at least in unperturbed conditions, the sensorimotor system maintains a relative consistent weighting between position and velocity feedback. Such consistency may simply arise from the shared whole-body dynamics of

human body, and may also facilitate a smooth transition between dynamic and static tasks.

6. Limitations

Several limitations should be noted. While we used a unified feedback model to estimate feedback control in walking and standing, the procedure to fit the model differed between tasks. Specifically, the method to select the feedback delay and corresponding gains was different. In addition, as reported in our previous study [17], intrinsic properties lead to errors in estimating feedback parameters in standing. How this will influence results in waking is unclear. Moreover, walking might 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. 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 demonstrated that while the feedback gains changed significantly across tasks and directions, the feedback 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 eigenfrequency, which might reflect a robust control strategy for stabilizing the human body as an inverted-pendulum.

Acknowledgements

The authors thank all the subjects for their participation in this study.

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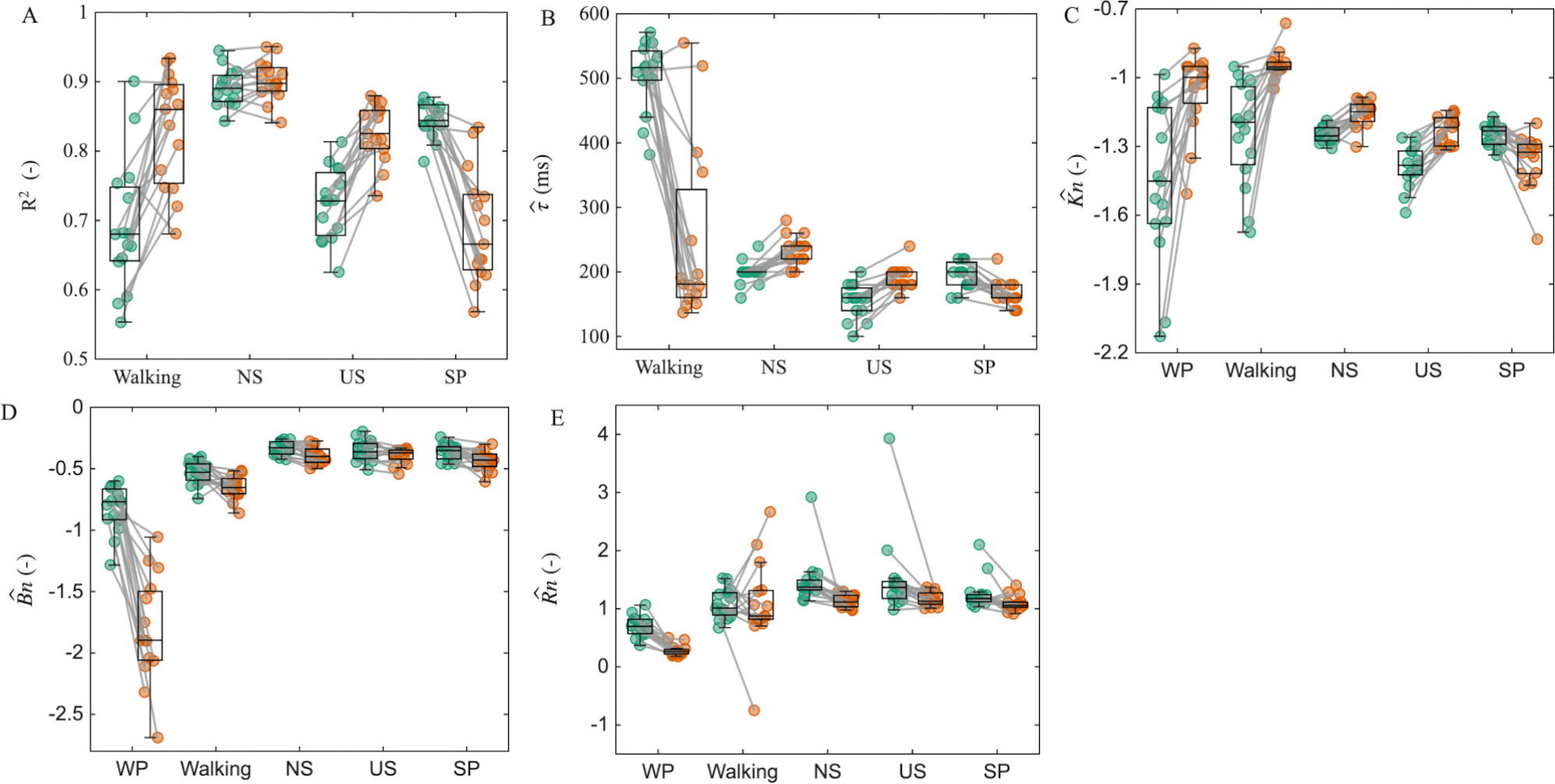
Supporting information

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


A
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R^2 (-)
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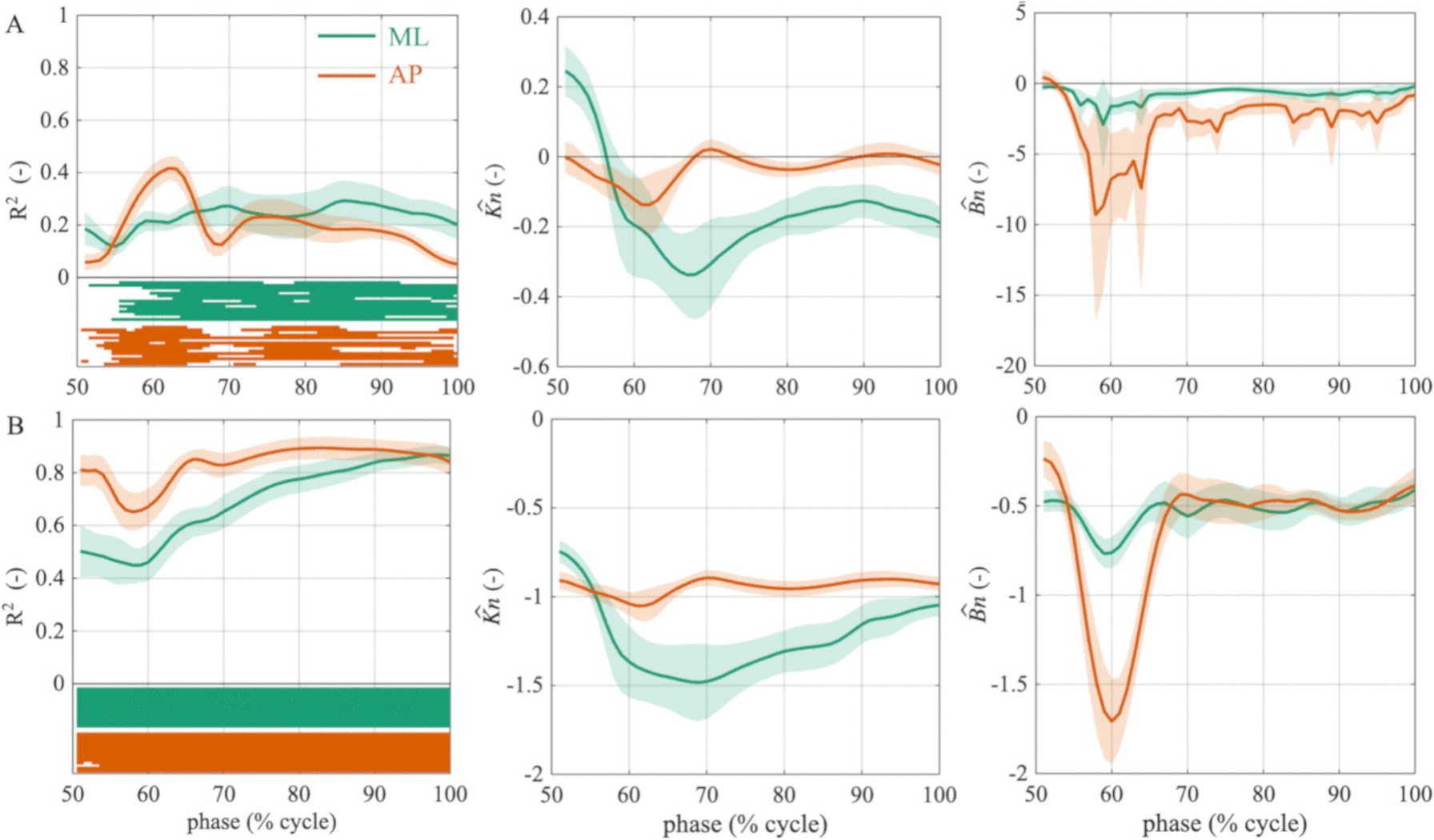
WP
Walking
NS
US
SP


A
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ML
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R^2 (-)
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