SCIENCE ROBOTICS | RESEARCH ARTICLE

HUMAN ROBOT INTERACTION

Robotic manipulation of human bipedalism reveals overlapping internal representations of space and time

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Effective control of bipedal postures relies on sensory inputs from the past, which encode dynamic changes in the spatial properties of our movement over time. To uncover how the spatial and temporal properties of an upright posture interact in the perception and control of standing balance, we implemented a robotic virtualization of human body dynamics to systematically alter inertia and viscosity as well as sensorimotor delays in 20 healthy participants. Inertia gains below one or negative viscosity gains led to larger postural oscillations and caused participants to exceed virtual balance limits, mimicking the disruptive effects of an additional 200-millisecond sensorimotor delay. When balancing without delays, participants adjusted their inertia gains to below one and viscosity gains to negative values to match the perception of balancing with an imposed delay. When delays were present, participants increased inertia gains above one and used positive viscosity gains to align their perception with baseline balance. Building on these findings, 10 naïve participants exhibited improved balance stability and reduced the number of instances they exceeded the limits when balancing with a 200-millisecond delay compensated by inertia gains above one and positive viscosity gains. These results underscore the importance of innovative robotic virtualizations of standing balance to reveal the interconnected representations of space and time that underlie the stable perception and control of bipedal balance. Robotic manipulation of body physics offers a transformative approach to understanding how the nervous system processes spatial information over time and could address clinical sensorimotor deficits associated with delays.

INTRODUCTION

As we interact with the world, our sensors encode both self- and external motions as they occur in space and time. The nervous system receives information from the past and must account for delays in movement generation, including the transduction, conduction, and processing of sensory information, to accurately sense and control the spatiotemporal properties of self-motion (*1*). Pointing to potentially common neural mechanisms for the perception of space and time, both dimensions are compressed over a similar temporal period near the onset of saccadic eye movements (*2*, *3*). Time also interacts with internal constructs of space for the neural control of movement: Sensorimotor delays are represented as a spatial gain change during visually controlled arm reaching (*4*). Similarly, the physics of self-motion in the environment can alter the timing between our actions and their consequences. For example, computer simulations predict that the increased inertia of larger animals requires motor responses to occur over a longer duration to correct for unexpected disturbances (*5*). Hence, delays in the consequences of our actions also stem from the mechanical properties of the body and environment, and these should also be taken into account by the nervous system. This interconnected relationship between space-time in the nervous system and space-time in the physical world leads to the critical question of how humans sense and control the spatial and temporal properties of body-environment interactions. Here, we leveraged the unique real-time capabilities afforded by the robotic virtualization of human body dynamics to examine these relationships in a standing balance model given the simple dynamics governing its motion and the importance of bipedal behaviors in daily life.

Given the mechanical instability of the upright body, standing balance requires the integration of multisensory signals to generate balance responses compensating for the toppling torque induced by gravity. The transduction of self-motion cues originating from somatosensory, visual, vestibular, and auditory sensors all encode motion with different dynamics and reach neural circuits sensing and controlling balance with varying delays (*6*). The nervous system decodes and processes action potentials relayed through these sensory channels to build and update internal representations of balance-related self-motion, accounting for changing spatial properties of the body (*7*) and neural delays (*8*) as we grow and age. Computational feedback models of balance predict that decreased ankle viscosity or imposed delays inserted in the balance control task increase postural oscillations (*9*–*12*), whereas empirical data reveal that increasing inertia can diminish the destabilizing effects of added mass during standing balance (*13*). We have experimentally validated some of these predictions using our standing balance simulator, showing smaller postural oscillations when balancing with increased viscosity (*6*) and increased postural instability when balancing with imposed delays (*14*, *15*). Despite these implied links between the spatial and temporal properties of self and the environment, it is essential to examine how sensory signals encoding these properties give rise to the perception of balance and are integrated to control upright stance to reveal how the nervous system resolves the interconnections between space and time.

Here, we performed three experiments with participants standing on a robotic balance simulator (see Fig. 1A and movie S1) that we developed and validated (*16*) to virtualize and manipulate the sensorimotor control of standing balance in the anteroposterior (AP) and mediolateral (ML) directions. By imposing time delays and altering the body dynamics, this system uniquely enabled us to

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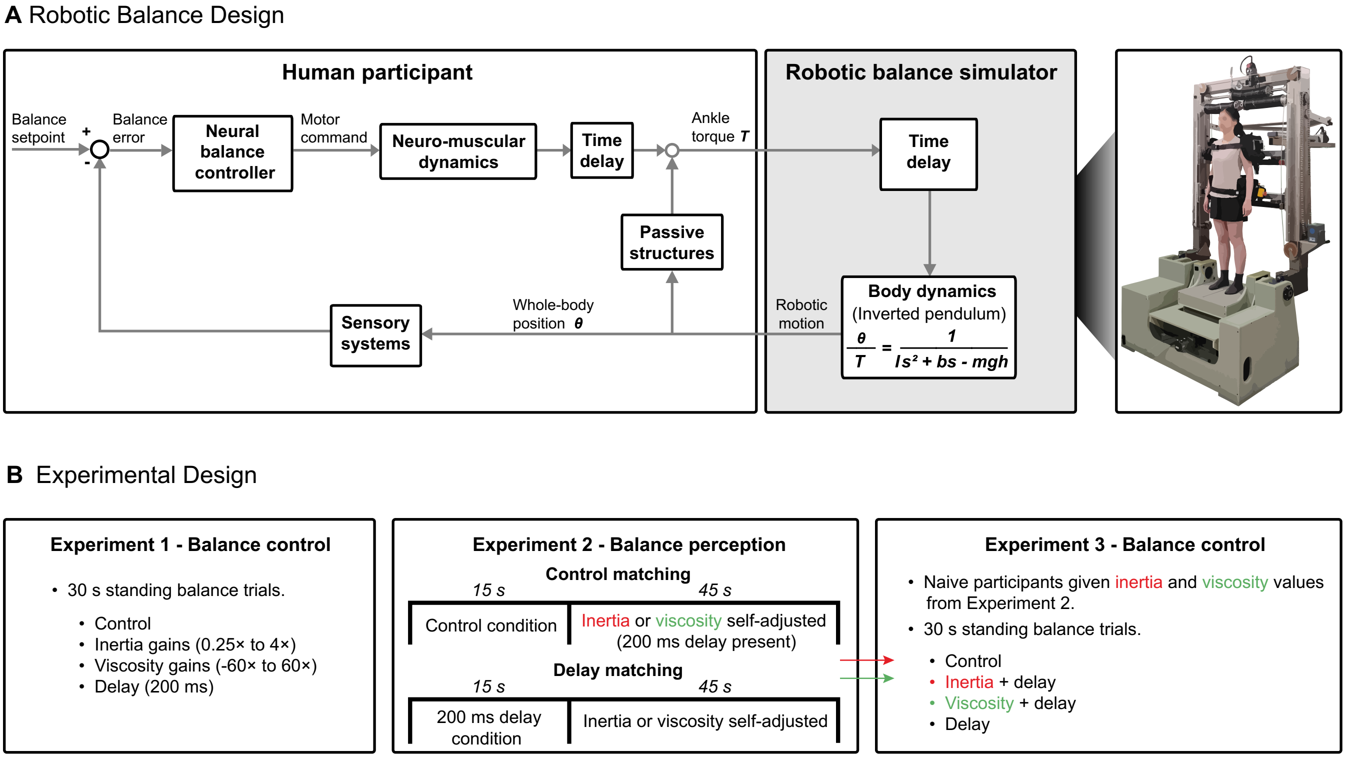

Fig. 1. Robotic balance system control block diagram and experimental setup. (**A**) Participants stood on two force plates while being secured at the hip and shoulder to a rigid backboard. Three independent motors controlled the rotation of the backboard and linear motion of the hip and shoulder brackets, which allowed for movement in the AP and ML directions. Motion of the robot was controlled by torques applied to the force plates by the participant, which were then converted into whole-body motion through a simulated inverted pendulum in the robotic balance controller. For the conditions of each experiment, the dynamics of the simulated inverted pendulum were modified by adding a time delay between applied torque and whole-body sway or adjusting the viscosity and inertia. (**B**) A visual representation of the experimental design. This study included three separate experiments, with experiments 1 and 3 investigating balance control and experiment 2 investigating the perception of balance.

investigate how the nervous system senses and regulates spatial and temporal properties of balance—questions that would be otherwise unattainable with conventional methods. First, we characterized postural behavior in response to an imposed 200-ms sensorimotor delay (in addition to the natural loop delay of ~100 to 160 ms) and changes in body inertia and viscosity. We hypothesized that participants would remain upright for shorter durations and balance with larger oscillations when a delay was present or when their body inertia and viscosity decreased. Next, we assessed potential overlaps in the perception of balance motion induced by a sensorimotor delay and changes in inertia and viscosity. We hypothesized that participants would identify balancing with decreased inertia and negative viscosity as perceptually equivalent to balancing with an added 200-ms delay. Last, we asked naïve participants to control their balance with increased inertia and positive viscosity in the presence of an added 200-ms delay to determine whether spatial properties of the body could compensate for the balance-destabilizing effects of the imposed 200-ms delay. We hypothesized that participants balancing with an added 200-ms delay compensated with proper inertia or viscosity would effectively control upright balance, decreasing their whole-body oscillations and minimizing virtual falls (in other words, exceeding the balance limits) associated with the presence of a sensorimotor delay. Overall, the findings established using our unique robotic balance simulator supported our hypotheses, demonstrating commonalities in the neural representation of space and time, similar to the rules of the physical world, in the perception and control of standing balance.

RESULTS

Experiment 1: Changes in balance control caused by delays, inertia, and viscosity

Using simulation-driven predictions (see the Supplementary Materials and fig. S1), we designed our first experiment to examine whether decreases in body inertia and viscosity can evoke balance instabilities akin to those induced by an added delay of 200 ms. Participants ($n = 20$) stood quietly on a robotic balance simulator for brief periods (30 s) while spatial and temporal properties of their body dynamics were modified (movie S1). The robot was programmed to simulate the dynamics of whole-body balance in both the AP and ML directions. We programmed angular position limits of 4° anterior and 2° posterior for AP and 4° left/right for ML balance to represent the virtual limits of whole-body position during standing (see Materials and Methods). First, we confirmed that when a delay of 200 ms was added to the control loop, all participants exhibited periods of instability where they exceeded the virtual balance limits of the robotic system (representing when they would have fallen) and increased whole-body oscillations (Fig. 2). Compared with the baseline condition, the duration participants spent within the virtual balance limits was 30.9% ($P < 0.001$) shorter when balancing with the imposed delay [control: 100%, IQR (interquartile range) 0%; delay: 69.1%, IQR 36.3%]. Correspondingly, the overall balance oscillations, characterized by the average center of mass (CoM) speed, increased 11-fold ($P < 0.001$) when balancing with the delay during periods that participants balanced within the virtual limits (control: 0.29°/s, IQR 0.10°/s; delay: 3.22°/s, IQR 1.02°/s; Figs. 2 and 3).

We next asked whether participants exhibited instabilities when balancing with inertia gains (see Materials and Methods) smaller than one (0.25× and 0.5×). In all participants, we observed increased whole-body postural oscillations with inertia gains below one (Fig. 2), and 69% (11 of 16) of participants exceeded the virtual balance limits (specifically with 0.25× inertia) during these 30-s balance trials. Conversely, inertia gains above one (2× and 4×) had limited effects on postural oscillations, which decreased in only a few participants (Fig. 2). Confirming our hypothesis, the duration participants remained within the virtual balance limits was 3.8% ($P = 0.004$) shorter when balancing with an inertia gain of 0.25× (96.2%, IQR 6.3%) relative to the control condition (100%, IQR 0%), but the duration within the balance limits did not differ for all other inertia conditions relative to control (all $P > 0.05$, Table 1 and fig. S2). Compared with the control condition, participants also increased their average CoM speed by 272 and 20.6% during the 0.25× (1.08°/s, IQR 1.88°/s) and 0.5× (0.35°/s, IQR 0.18°/s) inertia conditions (both $P < 0.001$, Table 1), respectively, but no changes were observed during the 2× and 4× inertia conditions (both $P > 0.05$, Table 1 and Fig. 3).

We further tested whether negative normalized viscosities (hereafter referred to as viscosity; see Materials and Methods), which imposed destabilizing torques proportional to whole-body velocity, would induce postural control instability. In all participants, we observed increased whole-body postural oscillations with negative viscosity gains (specifically during the condition applying a viscosity gain of −60×; Fig. 2), and 56% (9 of 16) of participants exceeded the virtual balance limits during these 30-s balance trials. In support of our prediction, participants decreased the duration they spent within the virtual balance limits by 1.7% ($P = 0.009$) at a −60× viscosity gain (98.3%, IQR 24.3%) but remained upright within the limits for 100% of trial duration (median) for all other viscosity conditions (multiple $P > 0.05$, Table 1 and fig. S2). Furthermore, compared with the control condition, participants increased their average CoM speed by 89.6 and 276% for the −30× (0.55°/s, IQR 0.34°/s) and −60× (1.09°/s, IQR 1.81°/s) viscosity gain conditions (both $P < 0.001$, Table 1), respectively, and decreased their average CoM speed by 34.5 and 55.2% for the 30× (0.19°/s, IQR 0.09°/s) and 60× (0.13°/s, IQR 0.04°/s) viscosity gain conditions (both $P < 0.001$, Table 1 and Fig. 3). Overall, these results support our hypothesis and indicate that, compared with natural balance, below one inertia and negative viscosity gains lead to difficulties remaining upright and variable whole-body oscillations as observed with an added 200-ms delay.

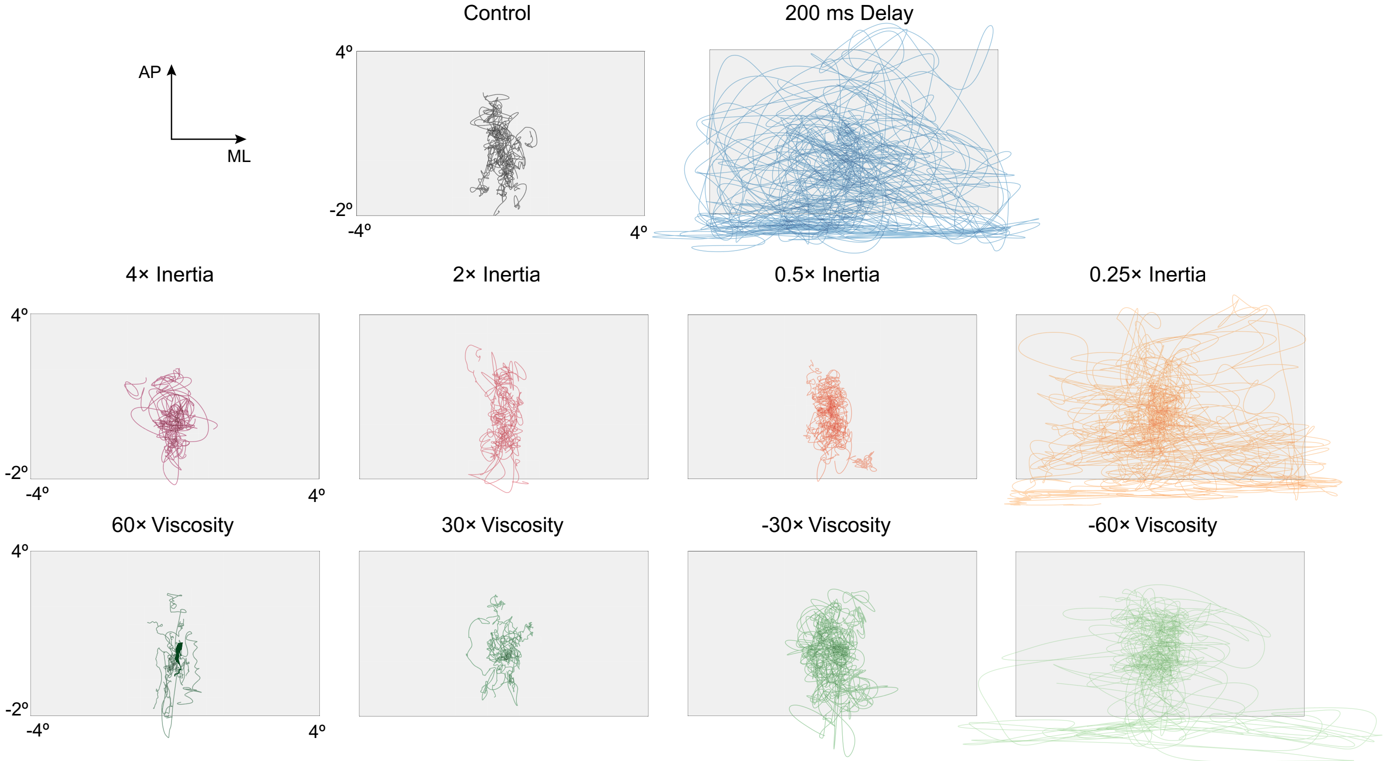

Fig. 2. CoM motion from all participants during balance trials (experiment 1). CoM motion from all participants ($n = 16$) is depicted in the AP and ML directions for all control, delay, inertia, and viscosity trials. The gray shaded regions indicate the virtual limits (4° anterior and mediolateral; 2° posterior) within which the software of the robotic balance device simulated the inverted pendulum dynamics. CoM motion traces that are outside of the shaded regions indicate when participants exceeded the balance limits (considered virtual falls).

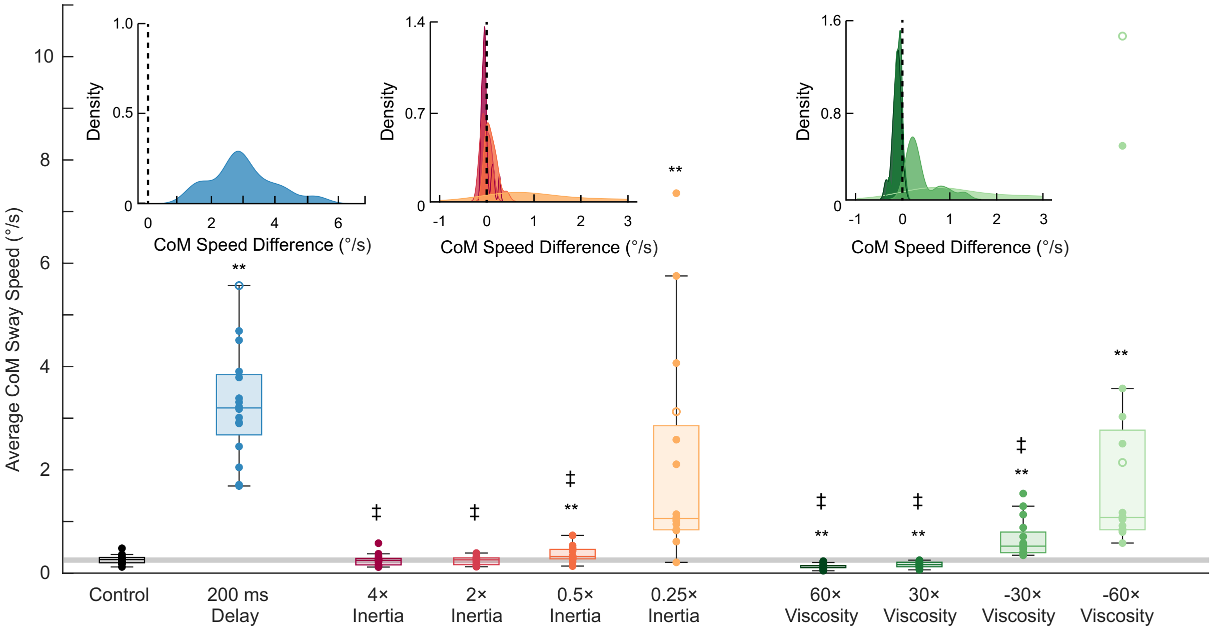

Fig. 3. Average CoM speed from all participants during balance trials (experiment 1). The average CoM speed, calculated from the Euclidean distances of the total sway path divided by duration within the virtual limits for each trial, is presented for each participant ($n = 16$). In general, the average CoM speed increased as inertia gain decreased below one and as viscosity gain became more negative. Group data are plotted using bar-and-whisker plots, where the central line in each box represents the median, the boundaries of the box indicate the IQR (25th to 75th percentiles), and the whiskers (vertical lines extending from the box) show the most extreme data points within 1.5× IQR. Data points beyond the whiskers are illustrated as outliers. When participants balanced for less than 2 s consecutively within the limits (see trial duration within the limits results, fig. S2), the associated CoM speed data points were plotted as open circles. Delay conditions are depicted in blue, inertia conditions are shown in red/orange (darkness of shade increases with inertia), and viscosity conditions are shown in green (darkness of shade increases with viscosity). Conditions marked with ** indicate a significant difference (Wilcoxon signed-rank test, $P < 0.05$) when compared with the control condition, whereas conditions marked with ‡ indicate a significant difference (post hoc Conover's test, $P < 0.05$) when compared with the delay condition. Insets show the estimated kernel density function of the difference in CoM speed for each condition relative to control (black dotted line). These estimates were performed with Gaussian kernels and bandwidths based on Scott's rule (*71*) using the kdeplot function from the Seaborn library in Python.

Experiment 2: Perceptual equivalence between the spatial and temporal properties of balance

Given the variable balance behaviors induced by both body dynamics and temporal delays, we then assessed whether the perception of whole-body movements associated with spatial and temporal manipulations of balance overlap. Here, using the real-time capabilities afforded by our robotic virtualization of human body dynamics, participants ($n = 20$) manually adjusted either the inertia or viscosity of the robotic system using a computer mouse until they matched their sensations to balancing with an added 200-ms delay while exposed to baseline (natural/no delay) balance and to baseline balance while exposed to an added 200-ms delay. They performed these two tasks in 45-s trials to determine whether lower inertia and negative viscosity gains felt equivalent to balancing with an added 200-ms delay and whether adding inertia or positive viscosity while balancing with an added 200-ms delay felt equivalent to balancing naturally. Participants were divided into two groups, adjusting either their inertia ($n = 10$) or viscosity ($n = 10$) gains in the two different perception matching tasks. The perceptual responses were used to calculate the point of subjective equality (PSE). Participants identified perceptual equivalence between body dynamics and time delays with ease: All participants successfully performed the perception matching tasks, and only three trials ($n = 2$ participants) required an extension of the trial period (to a total of 90 s).

First, we tested the hypothesis that balancing with lower inertia or negative viscosity would feel equivalent to balancing with an added 200-ms delay. In the inertia group, participants perceived matching values ranging from 0.15× to 7.5× inertia gains, with 97% of their responses being below one and 77% (116 of 150) at or below 0.75×. The median PSE for all participants was 0.44× inertia (IQR 0.25; Fig. 4 and fig. S3), and the median coefficient of variation was 0.34 (IQR 0.19). In the viscosity group, all participants chose negative viscosity gains. The perceived viscosity gains ranged from −75× to −12.5×, with 75% (113 of 150) of responses at or below gains of −40×. The median PSE viscosity matching the perception of balancing with an added 200-ms delay was −47× viscosity (IQR 30; Fig. 4 and fig. S4), with a median coefficient of variation of 0.19 (IQR 0.17). These results support our hypothesis and show that participants can modify their body dynamics to match their sense of balance to standing upright with an imposed delay. Furthermore, the lower coefficient of variation for the viscosity group than the inertia group (Mann-Whitney U test = 10.000, $P < 0.001$) indicated that these participants more consistently matched their perception of balancing with viscosity to balancing with an added 200-ms delay.

Next, we tested whether participants could match their sense of balance to natural standing by adding inertia or positive viscosity to their body while balancing with an added 200-ms delay. Participants in the inertia group perceived that inertia gains ranging from 1 to 7.5× best matched their sensation of natural balance, with 70% (105 of 150) of responses falling between 2 and 7×. The median PSE for the inertia gain was 3.30× (IQR 2.75; Fig. 4 and fig. S3), with a median coefficient of variation of 0.29 (IQR 0.15). In the viscosity group,

Table 1. Balance outcomes and statistical comparisons across conditions of altered delay and body dynamics from balance control trials (experiment 1). The balance outcomes for each condition are reported using the median with 25 and 75% quartile ranges ($n = 16$). Statistical outcomes are presented for each condition as compared with either the control condition (Wilcoxon signed-rank test, reporting the Z statistic) or the 200-ms delay condition (post hoc Conover's test, reporting the T statistic). Empty cells indicate condition comparisons with themselves or are presented in another cell. N/A, not available.

Balance condition	Duration in the limits			Average speed		
	%	Comparison with control	Comparison with delay	°/s	Comparison with control	Comparison with delay
Control	100 (100–100)			0.29 (0.23–0.33)		
200-ms delay	69.1 (45.5–81.8)	$Z = 3.516$ $P < 0.001$*		3.22 (2.81–3.83)	$Z = -3.516$ $P < 0.001$*	
4× inertia	100 (100–100)	$Z = 0.447$ $P = 1.000$	$T = 5.628$ $P < 0.001$*	0.27 (0.19–0.31)	$Z = 1.189$ $P = 0.252$	$T = 5.627$ $P < 0.001$*
2× inertia	100 (100–100)	$Z = 1.461$ $P = 0.201$	$T = 5.370$ $P < 0.001$*	0.28 (0.20–0.32)	$Z = 0.827$ $P = 0.433$	$T = 5.296$ $P < 0.001$*
0.5× inertia	100 (100–100)	$Z = 0.447$ $P = 1.000$	$T = 6.017$ $P < 0.001$*	0.35 (0.31–0.49)	$Z = -2.585$ $P = 0.008$*	$T = 3.531$ $P = 0.008$*
0.25× inertia	96.2 (93.7–100)	$Z = 2.934$ $P = 0.004$*	$T = 3.041$ $P = 0.035$*	1.08 (0.86–2.74)	$Z = -3.516$ $P < 0.001$*	$T = 0.993$ $P = 1.000$
60× viscosity	100 (100–100)	$Z = 1.342$ $P = 0.371$	$T = 5.024$ $P < 0.001$*	0.13 (0.12–0.16)	$Z = 3.464$ $P < 0.001$*	$T = 6.510$ $P < 0.001$*
30× viscosity	100 (100–100)	N/A†	$T = 5.668$ $P < 0.001$*	0.19 (0.14–0.23)	$Z = 3.413$ $P < 0.001$*	$T = 5.186$ $P < 0.001$*
−30× viscosity	100 (98.6–100)	$Z = 1.782$ $P = 0.093$	$T = 4.573$ $P < 0.001$*	0.55 (0.43–0.77)	$Z = -3.516$ $P < 0.001$*	$T = 3.200$ $P = 0.022$*
−60× viscosity	98.3 (75.7–100)	$Z = 2.666$ $P = 0.009$*	$T = 2.769$ $P = 0.075$	1.09 (0.86–2.67)	$Z = -3.516$ $P < 0.001$*	$T = 1.103$ $P = 1.000$

*Significant differences in the comparisons. †Trial duration within the limits was 100% for all participants.

participants added viscosity gains from 0 to 75× into their control of balance with an added 200-ms delay to match their natural perception of balance, with 79% (119 of 150) of responses above 40× viscosity. The median PSE was 53× viscosity (IQR 30; Fig. 4 and fig. S4), with a median coefficient of variation of 0.17 (IQR 0.10), which did not differ (Mann-Whitney U test = 28.000, $P = 0.053$) from the inertia group. Together, our results show that participants can increase their body inertia and viscosity to match their natural sense of balance despite standing with an imposed 200-ms delay.

Experiment 3: Body dynamics can compensate for the instability induced by sensorimotor delays

Thus far, we have shown that increases in inertia and viscosity induce opposite effects to delays on the control of balance. We also established the perceptual mapping for the sense of balance induced by spatial and temporal manipulations of balance. Next, we asked whether increases in body inertia or viscosity imposed by the robotic simulator can partially compensate for the detrimental effects typically induced by sensorimotor delays on the control of balance. To address this question, we asked 10 additional (and naïve) participants who were uninformed about the robotic manipulations to balance naturally on the robot for periods of 30 s. All participants were exposed to an added 200-ms delay in combination with the 3.3× inertia or 53× viscosity gains identified (median PSE values) from matching the perception to natural standing balance in experiment 2. Participants also balanced with only an added 200-ms delay and under baseline control conditions to assess whether changes in body dynamics ameliorate the destabilizing effects of the delay.

Compared with the 200-ms delay condition, participants exceeded the virtual balance limits less frequently and reduced postural oscillations when they experienced a 3.3× inertia gain or 53× viscosity gain in addition to the delay (Fig. 5). Across participants, the median percentage trial duration spent within the limits was 100% for both the 3.3× inertia (IQR 5.5%) or 53× viscosity gains (IQR 0%), both increasing by 30.3% (multiple $P < 0.010$, Table 2 and fig. S5) compared with the delay condition (69.7%, IQR 29.5%). Furthermore, participants also decreased their average CoM speed by 75.5 and 80.1% when the 3.3× inertia (0.76°/s, IQR 0.59°/s; $P = 0.028$, Table 2) or 53× viscosity gains (0.62°/s, IQR 0.90°/s; $P = 0.004$, Table 2 and Fig. 6) were added to the delay (3.11°/s, IQR 1.03°/s), respectively. These results show that the postural instability induced by sensorimotor delays can be partially compensated by increases in body inertia or viscosity.

Next, we tested whether increases in body dynamics render the control of balance with an added 200-ms delay equivalent to balancing without a delay (control condition). Results from our bootstrap analysis (see Materials and Methods) generated a 90% confidence interval (CI) for the difference between conditions for both duration within the limits and average CoM speed. Comparison of these CIs with predefined equivalence bounds (using Cohen's $d = 0.5$) revealed that the differences observed when balancing with combined delays and 3.3× inertia or 53× viscosity gains did not fall within the equivalence bounds relative to the control condition (see Table 2), suggesting statistical nonequivalence for both duration within the limits and average CoM speed (Fig. 6 and fig. S5). Participants exhibited increased average CoM speed for both inertia (153%) and

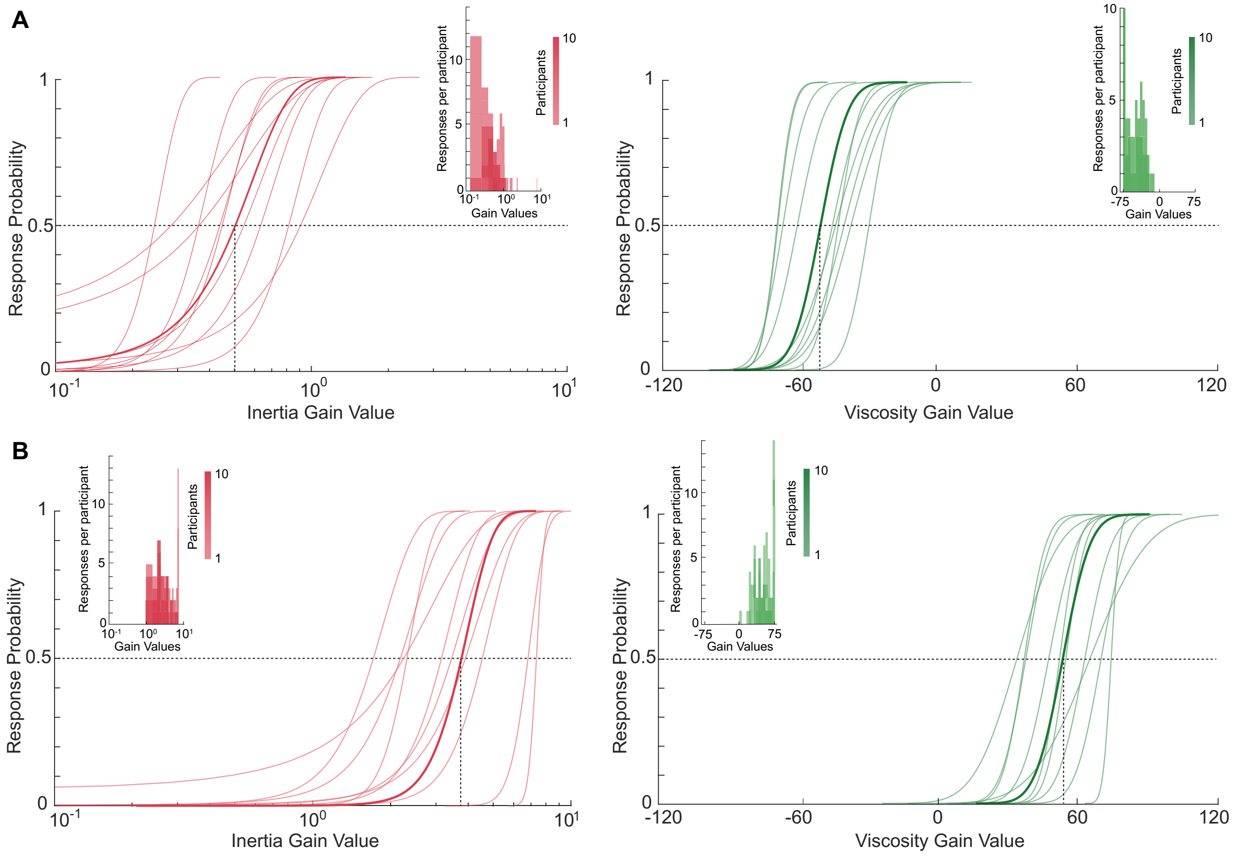

Fig. 4. Psychometric functions of perceptual matching tasks for inertia and viscosity parameters to changes in balance control during perception matching trials (experiment 2). (**A**) Psychometric functions fit to the perceptual responses of each participant for the inertia (*n* = 10; red) and viscosity (*n* = 10; green) groups. Participants balanced in these baseline conditions (no delay) and were instructed to modify their dynamics (inertia or viscosity) to match their perception of balance behavior to the 200-ms delay condition. The thin red (inertia) or green (viscosity) lines indicate individual participant responses, and the bold red (inertia) or green (viscosity) lines are the median psychometric curves. Intersection with the black dotted line indicates the PSE for each participant. Insets show the response distribution across all participants, with darker shading representing a greater number of responses. (**B**) Psychometric functions fit to the perceptual responses of each participant for the inertia (*n* = 10; red) and viscosity (*n* = 10; green) groups. Participants balanced with the imposed 200-ms delay and were instructed to modify their dynamics (inertia or viscosity) to match their perception of balance behavior to the baseline conditions. The thin red (inertia) or green (viscosity) lines indicate individual participant responses, and the bold red (inertia) or green (viscosity) lines are the median psychometric curves. Intersection with the black dotted line indicates the PSE for each participant. Insets show the response distribution across all participants, with darker shading representing a greater number of responses.

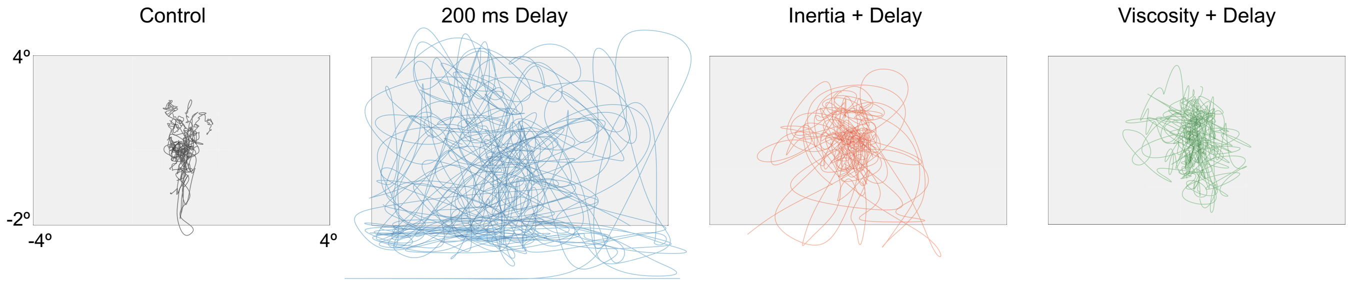

Fig. 5. CoM motion of all participants during instability compensation trials (experiment 3). CoM motion from all participants (*n* = 10) in the AP and ML directions for control, inertia with 200-ms delay, viscosity with 200-ms delay, and 200-ms delay trials in experiment 3. The gray shaded regions indicate the virtual limits (4° anterior and mediolateral; 2° posterior) within which the software of the robotic balance device simulated the inverted pendulum dynamics. CoM motion traces that are outside of the shaded regions indicate movements during balance where the participant exceeded a virtual limit.

viscosity (107%) conditions with the 200-ms delay compared with the control condition (0.30°/s, IQR 0.13°/s). These results indicate that neither inertia nor viscosity in isolation fully compensated for the destabilization effects resulting from the presence of an added 200-ms delay in the control of balance. Overall, concurrent robotic alterations of body dynamics and temporal delays in naïve participants demonstrate (at least partial) overlap in the neural representations of space and time for the control of balance.

Table 2. Balance and statistical comparison test outcomes from instability compensation trials (experiment 3). The balance outcomes are presented for each condition as median with quartile ranges ($n = 10$). Statistical results are presented for each condition with the outcomes from the comparison with control [bootstrap 90% confidence interval (CI_{boot}) for the difference between conditions compared with equivalence bounds defined using Cohen's $d = 0.5$] and comparison with 200-ms delay (post hoc Conover's test, reporting the T statistic). Empty cells indicate condition comparisons with themselves or were not performed for this analysis.

Balance condition	Duration in limits (%)	Comparison with control	Comparison with delay	Average speed (°/s)	Comparison with control	Comparison with delay
Control	100 (100–100)			0.30 (0.25–0.38)		
200-ms delay	69.7 (51.1–80.6)			3.11 (2.65–3.68)		
Inertia + delay	100 (94.3–100)	Eq. bounds = [−1.921, 1.921] 90% CI_{boot} = [0.320, 5.610]	$T = 3.363$ $P = 0.010^*$	0.76 (0.61–1.20)	Eq. bounds = [−0.193, 0.193] 90% CI_{boot} = [−0.902, −0.361]	$T = 2.907$ $P = 0.028^*$
Viscosity + delay	100 (100–100)	Eq. bounds = [−0.648, 0.648] 90% CI_{boot} = [0.000, 1.230]	$T = 4.111$ $P = 0.002^*$	0.62 (0.35–1.24)	Eq. bounds = [−0.226, 0.226] 90% CI_{boot} = [−0.861, −0.228]	$T = 3.801$ $P = 0.004^*$

*Significant differences in the comparisons.

DISCUSSION

Here, we found that the neural encoding and processing of space-time for bipedal balance share commonalities for the perception and control of upright standing. We performed three experiments that virtualized human body dynamics using a unique robotic balance system to examine how the nervous system encodes the spatial and temporal properties of self in the environment. In the first experiment, we showed that balancing a body with inertia gains below one or negative viscosity gains led to postural effects similar to the addition of sensorimotor delays including a decrease in the duration participants remained within the virtual balance limits and increased postural oscillations. On the other hand, balancing with positive viscosity gains led to decreased postural oscillations. In the second experiment, participants perceived that standing with 0.44× inertia or −47× viscosity gains felt equivalent to balancing with an added 200-ms delay. Participants also reported that balancing with an added 200-ms delay felt equivalent to balancing naturally (without a delay) when their body inertia and viscosity were increased to 3.3× and 53× their typical values, respectively. Last, in the third experiment, the body dynamics (3.3× body inertia or 53× viscosity gains) required to perceive natural balance in the presence of a delay partially compensated for the detrimental effects induced by sensorimotor delays on the control of balance. These spatial body properties enabled naïve participants to increase the duration they balanced within the limits and decrease the postural oscillations induced by an added 200-ms delay. Overall, our results indicate an overlap in the internal representations of spatial (inertia and viscosity) and temporal (delay) self-motion attributes for the perception and control of standing balance. These results imply that spatiotemporal features of bipedalism can be harnessed using robotic devices to compensate for the potentially destabilizing consequences of either dimension.

Balance control instabilities induced by decreases in inertia and viscosity

Before assessing how body dynamics and time delays are sensed and internally represented for the perception and control of balance, we first determined how changes in body inertia and viscosity influenced balance behavior. Replicating our previous findings (*14*, *15*, *17*), we observed that the duration participants spent within the virtual limits decreased and whole-body oscillations increased when balancing with an added 200-ms delay compared with a control condition. Results from the initial experiment also confirmed our first hypothesis: The duration that participants remained within the virtual balance limits decreased for the 0.25× inertia and −60× viscosity gains compared with the control condition, and participants exhibited larger CoM oscillations for below unity inertia and negative viscosity gains. On the other hand, only larger viscosity gains decreased the participants' whole-body oscillations. Our results empirically confirm predictions from computational models suggesting that decreases in viscosity induce larger pendulum sway amplitudes (*9*). In addition, the observed decrease in CoM oscillations associated with larger viscosity aligns with our previous findings (*6*). The lack of postural effects induced by inertia gains above one partially supports the results of Costello and colleagues (*13*), who increased inertia in isolation for balancing participants by mechanical means, although we extended their observations by showing that inertia gains below one increased CoM oscillations. This latter condition could only be implemented using our robotic system, which virtualizes the inertia such that we can adjust it arbitrarily. Overall, we showed that below unity inertia and negative viscosity gains induced balance changes in the same direction as the 200-ms delay condition. These empirical results confirm predictions from modeled sensitivity analyses demonstrating that reduced inertia/viscosity and delays increased the gain of the balance control system near the natural frequency of a pendulum, whereas increased inertia has minimal influence on the peak gain of the system (*18*). Hence, we demonstrated that specific changes in body dynamics (spatial domain) can have similar destabilizing effects as sensorimotor delays (temporal domain).

Correspondence of body dynamics and delays to the perception of balance

Despite representing distinct dimensions in space and time, participants matched their body dynamics to time delays for their perception of balance with ease. Only two participants (total 3 of 600 trials) requested an extension to match their perception. Confirming this match between spatiotemporal variables, participants demonstrated a well-defined directionality in their responses: They selected inertia gains below one (96.6% of trials) or negative viscosity gains (100% of trials) to match their perception of balancing with an added 200-ms delay. These results establish our ability to perceive the consequences of inertia or viscosity on balance motion and to relate these to effects resulting from a change in the temporal relationship between motor

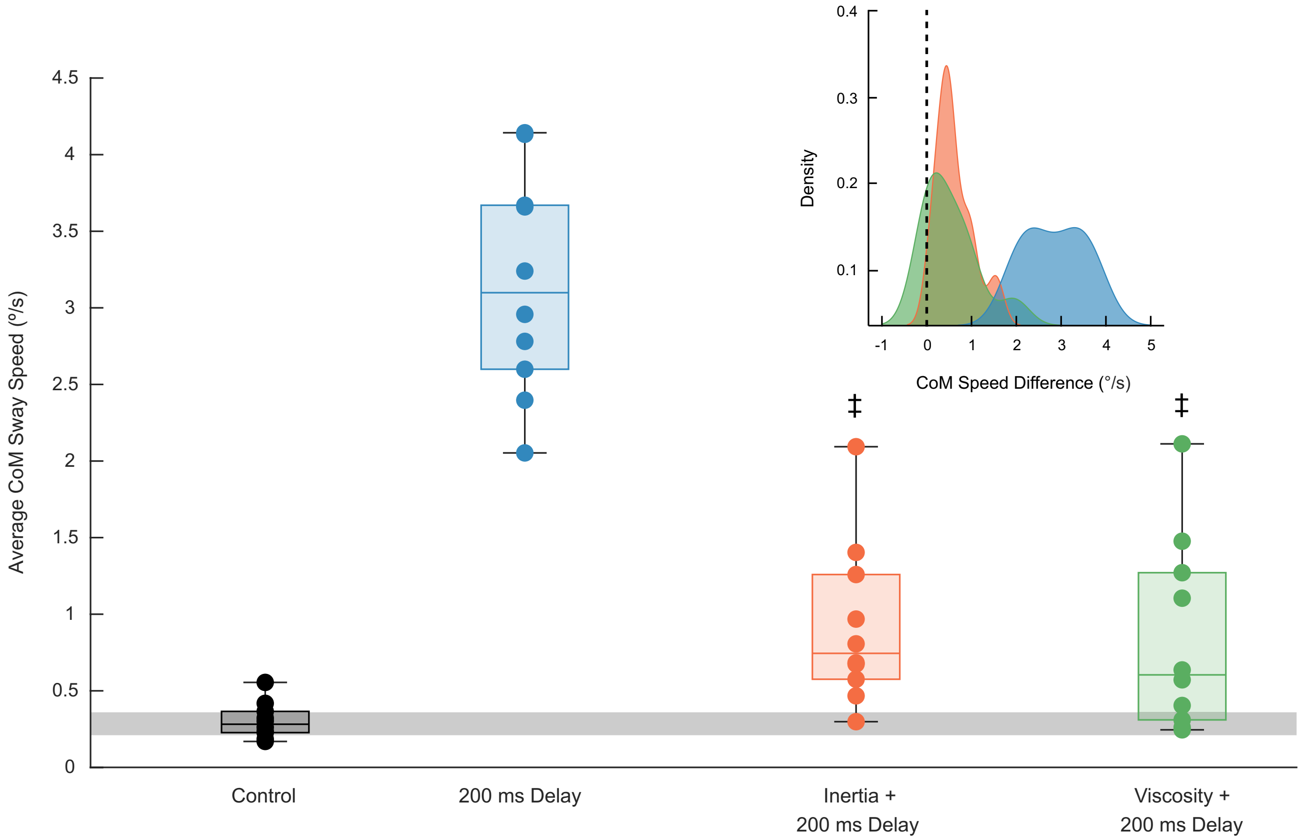

Fig. 6. Average CoM sway speed of all participants during instability compensation trials (experiment 3). The average CoM sway speed, calculated from the Euclidean distances of the total sway path divided by duration within the virtual limits for each trial, is presented for each participant ($n = 10$). Group data are plotted using bar-and-whisker plots, where the central line in each box represents the median, the boundaries of the box indicate the interquartile range (25th to 75th percentiles), and the whiskers (vertical lines extending from the box) show the most extreme data points within 1.5× IQR. Data points beyond the whiskers are illustrated as outliers. Conditions marked with ‡ indicate a significant difference (post hoc Conover's test, $P < 0.05$) when compared with the delay condition. Insets show the estimated kernel density function of the difference in CoM speed for each condition relative to control (black dotted line). These estimates were performed with Gaussian kernels and bandwidths based on Scott's rule (*71*) using the kdeplot function from the Seaborn library in Python.

commands and their sensory consequences. This notable ability aligns with our earlier results: Most participants reported their experience of balancing with delays as resulting from a change in gain of the robotic simulation (amplified effects of their motor actions) instead of a delay between their motor commands and resulting sensation (*15*).

Why do we perceive delays in the control of balance similar to changes in our body dynamics? Our observations that inertia gain values of the body below one (and negative viscosity) were needed to perceive balance similar to a delay may appear to contradict predictions from Mohamed Thangal and Donelan (*5*). These authors proposed that increases in inertia (instead of decreases in inertia as we observed) induce delays in the consequences of our actions because of increases in phase lag between muscle actions and subsequent body acceleration (*18*). We do not challenge their predictions; however, our results demonstrate that participants did not try to match the mechanical delay induced by larger inertia to the 200-ms delay imposed between their motor commands and resulting body motion. Instead, we propose that for the sense of balance, the nervous system interprets sensory signals related to variations in balance control rather than distinguishing between mechanical or temporal changes. We asked participants to match their perception of balance between conditions, which likely led them to evaluate the sensory consequences of their balance-correcting actions. From a controls perspective, alterations in the gain of the balance control system induced by changes in inertia/viscosity and sensorimotor delay are similar near the natural frequency of an inverted pendulum (*18*). Consequently, the sensory signals resulting from balance-correcting actions may not be strictly differentiated into spatial or temporal information by the nervous system as proposed by Eagleman (*19*). Instead, participants likely reported on their overall sense of balance and determined that decreasing their body inertia or viscosity as well as imposed delays increased postural oscillations. Supporting this interpretation, the balance behaviors in experiment 1 were consistent across alterations in both body dynamics and sensorimotor delay. Furthermore, this idea aligns with brain regions associated with perception, such as the posterior parietal cortex (*20*), which is known to contain neurons encoding both space and time. Some authors have proposed that this region may serve as a common area for the interpretation of space and time (*21*, *22*), reinforcing the notion that the nervous system may not distinguish between these dimensions for balance perception.

Although participants exhibited stereotyped responses when identifying body dynamics that matched their perception of balancing with an added 200-ms delay, they showed a lower coefficient of variation when modifying their viscosity instead of inertia. In line with previous arguments (see above), we propose that the sensory consequences of balance-correcting actions associated with negative viscosity resulted from whole-body oscillations exhibiting characteristics closer to a delay than when the body had lower inertia. This interpretation follows our preliminary computer simulations, where stability plots exhibited more overlap between the viscosity and delay simulations than the inertia simulations (see fig. S1). In addition, simulation results from Pasma *et al.* (*18*) showed a shift in the pendulum's natural frequency with alterations in inertia that were absent for manipulations in viscosity or delay. Together, these findings suggest that the nervous system may interpret viscosity as more equivalent to delays than inertia because of the closer correspondence in their effects on balance control dynamics.

Participants balancing with an added 200-ms delay also self-adjusted their body inertia and viscosity to larger gains to match their sense of balance to baseline. For viscosity, the averaged gains they chose (53× viscosity) nearly corresponded to the oppositely signed gains (−47× viscosity) needed to match their perception of balancing to conditions with an added 200-ms delay. This suggests a near symmetry in the body viscosity required to mimic or cancel the sense of balance resulting from an added 200-ms delay. For inertia gains, the average results were nearly but not exactly symmetric around one (0.44× versus 3.30×). These outcomes may imply that the effects of increasing and decreasing inertia do not induce symmetrical changes in balance oscillations and resulting sense of balance. This interpretation, however, should be taken carefully given the variability in responses observed (and larger coefficient of variation) for inertia. Overall, the results from the perceptual experiments suggest that spatial and temporal properties of the body induce consequences to the control of balance that can exhibit overlap in their internal representation of the balance sense.

Counteracting the destabilizing effects of delays through body dynamics

We used the perceptual data to inform the inertia and viscosity gains that may compensate the destabilizing effects of an added 200-ms delay. Naïve participants balanced 96.8 to 100% of the trial duration within the limits when compensating inertia or viscosity gains were added to the control of balance with an added 200-ms delay. This percentage trial duration within the limits was comparable to the control condition (100%) and a notable improvement compared with the delay condition (69.7%). Postural oscillations also decreased by 76 to 80% with the compensating inertia and viscosity compared with the delay condition but remained 2.1 to 2.5× larger (that is, 107 to 153% increase) than the control condition (see Discussion below regarding these differences). The balance improvements in the presence of a delay induced by modifications to body dynamics support an intriguing hypothesis regarding the covariation of sensorimotor delays with mass across animals of different sizes (*23*). On the basis of our results, and in line with arguments suggesting that greater inertia benefits motor control by enabling animals to resist larger perturbations (*5*), we hypothesize that larger animals may derive a key benefit from their mechanical properties. Specifically, delays associated with greater inertia (scales according to mass$^{0.35}$) and viscosity may help them control their posture more effectively by compensating for the increased uncertainty introduced by longer sensorimotor delays (scales according to mass$^{0.21}$) (*5*, *23*, *24*).

The observed improvements in balancing with a delay, when combined with altered body dynamics, mirrored the perceptual alignment to natural balance. This alignment suggests that, under certain conditions, the nervous system integrates spatial and temporal features of the body into a common internal representation of self-motion for sense and control of balance (*25*, *26*). However, previous studies indicate that perceptual and control processes for balance do not always share a unified body representation (*27*–*29*), suggesting that specific sensory inputs may be weighted differently for each process depending on task demands or whole-body and environment characteristics. We propose that the sensory afferents encoding whole-body oscillations from spatial and temporal properties of the body and environment provided input to the nervous system with similar statistical properties. Given that balance depends on detecting and correcting errors in standing posture (*30*–*33*)—whether because of imposed spatial or temporal perturbations—the central processing of the accompanying sensory consequences may lead to similar internal estimates of self-motion governing the sense and control of balance. This underscores how the nervous system integrates sensory feedback and biomechanical properties to maintain stability across a range of body dynamics and sensorimotor delays.

The control of balance involves subcortical networks including brainstem and cerebellar structures that generate motor actions that can remain outside of perception (*34*–*36*). For example, participants who experience large delays (up to 400 ms) or changes in body dynamics initially exhibit decreases in their vestibular control of balance (*6*, *14*). Consequently, the observed overlap between variables related to space and time for the control of balance provide insights regarding how balance-correcting actions (outside of perception) emerge from the sensory encoding of self in the environment. The changes in whole-body oscillations (experiment 1) that accompany spatial and temporal manipulations are encoded as action potentials in sensory neurons using rate coding or spike timing (*36*–*39*), leading to updated internal estimates of the body orientation and movement in the environment. For example, delays increase the uncertainty of self-motion encoded within the nervous system (*40*), whereas negative viscosities amplify self-generated motion (*41*). Consequently, the probabilistic maps between balance motor actions and associated multisensory feedback will change in the face of alterations to body dynamics and the addition of sensorimotor delays. Here, we propose that any updates to these maps will exhibit some overlap, enabling the neural networks responsible for standing balance to integrate and potentially benefit from specific combinations of spatiotemporal parameters. We used the same closed-loop model of human balance that guided our experimental design to examine how increasing inertia or viscosity might restore stability in the presence of an added 200-ms delay by evaluating their effects on the region of stable feedback gains. The results indicate that the region of stability for the delayed condition (with an additional 200-ms delay) partially overlaps with that of the control condition (including only natural sensorimotor delays) when compensated with increased inertia or viscosity (see fig. S6). Further indirectly supporting this proposal, Avraham *et al.* (*4*) used empirical and simulated data to argue that the nervous system represents and learns to control movement with delays through updates in spatial variables (gain) for visuomotor tasks. Neurophysiological data provide further insights into the space-time interplay in the nervous system: Spatial representation of sensory events is needed to extract temporal features and facilitate learning (*42*), and certain hippocampal cells encode both space and time (*43*, *44*).

Although inertia gains above one and positive viscosity gains partially compensated for the destabilizing effects of delays, the compensation was not perfect, and participants exhibited whole-body oscillations 2.1 to 2.6× larger than when balancing naturally. These results suggest that the altered inertia and viscosity gains used for balance control (experiment 3) were not perfectly matched to the delays for individual participants. Several factors could explain this mismatch. First, the applied inertia and viscosity gains were derived from a separate group of participants; better matching of the perception and control of balance might have been achieved by using within-participant parameters. However, this approach would have risked introducing adaptation effects from repeated exposure to delay conditions. Second, a related consideration is that experiment 2 allowed participants to learn and adapt to the imposed delay before making their perception-based adjustments, whereas experiment 3 purposefully did not incorporate a similar learning phase. This difference in adaptation may have influenced the observed mismatch in compensation, given that perceptual and motor responses may have been shaped partly by prior learning (*14*). Third, although the spatiotemporal parameters for sensing and controlling balance were similarly matched, the control of balance can be (dis)engaged and transformed independent of perceptual awareness (*27*, *28*, *45*, *46*). Thus, inertia and viscosity gains extracted from a comparable balance experiment may lead to minor improvements. Last, it is also possible that the changes in probabilistic bipedal sensorimotor maps induced by added delays do not fully overlap with those associated with changes in either inertia or viscosity alone. Instead, a combination of body dynamics parameters may be required to fully compensate for balancing with an additional delay. Future experiments are needed to address these possibilities.

Potential implications

The potential to compensate for the balance destabilizing effects of delays may also have important implications for robotic and clinical applications. Classical controllers for bipedal robots typically represent space and time variables independently for the maintenance of upright posture, which can be susceptible to imprecise modeling or calibration of the spatial and temporal parameters. Our work suggests that a higher-order abstraction of space and time could achieve both stable and robust balance that reduces the dimensionality of the representation, perhaps achieved through more modern control architectures like deep reinforcement learning (*47*, *48*). Clinically, aging, diabetic polyneuropathy, multiple sclerosis, and Freidreich's ataxia can exacerbate natural sensorimotor control loop delays by up to 25 to 165 ms in the transmission and processing of information in the nervous system (*49*–*54*). These reported delays in the onset of stabilizing balance responses are based on electromyographic (EMG) responses. Hence, they do not include potential changes in the development of force by the musculoskeletal system that in older adults can lead to additional delays of 20 to 30 ms (*55*, *56*). Together, these factors may contribute to the balance deficits and potentially falls in older adults or patients presenting with these neurological conditions (*57*–*61*).

We propose that training protocols and wearable/assistive devices leveraging the overlap between spatial and temporal properties of balance control could be carefully developed to compensate for balance deficits associated with sensorimotor delays. For these approaches to be effective, the nervous system must adapt to the spatial and temporal properties of modified balance. Although muscle cocontraction and related changes in passive muscle stiffness are predicted to occur on the basis of computational modeling of balance with increased delays (*62*), our previous work emphasizes the importance of modulating the vestibular control of balance as participants learned to stand with imposed delays (*14*). In addition, real-time alterations in body inertia and viscosity that (partially) restore an individual's control of balance could be coupled with gyroscopic actuators that induce angular momentum for balance assistance (*63*–*66*). Together, our results suggest that mechatronic devices leveraging the interplay between body dynamics and time delays for the control of balance could prove transformative for the prevention and mitigation of falls.

Conclusions

Overall, we demonstrated using a robotic balance device that the representation of space and time variables overlaps for the perception and control of balance. This unique system allowed us to address questions about how the nervous system integrates spatial and temporal information in balance that would be otherwise unapproachable with conventional methods. We propose that the equivalence between spatial and temporal features of the body in the environment emerges for both the sense and control of balance because of partial overlap in the internal probabilistic maps between balance-correcting actions and their resulting consequences. Leveraging this overlap may have important implications for the development of future innovative methods for bipedal robots and fall prevention. Together, our results represent a critical step toward understanding how the nervous system processes sensorimotor information related to self and the environment that is experienced in space as time unfolds.

MATERIALS AND METHODS

Robotic virtualization of human body dynamics

For our experiments, participants stood in a robotic balance system (*16*) that virtualizes the real-time body dynamics of standing balance in the AP and ML directions (Fig. 1A). This system uses a robot-in-the-loop approach, actively integrated into human balance control by simulating the whole body as an inverted pendulum in both directions, which was essential to manipulate the spatial and temporal properties of balance. For the present experiments, we leveraged this robotic system to scale the estimated inertia and viscosity of the upright body by applying gains to each parameter reported as multipliers (for example, a 2× inertia gain refers to doubling the expected inertia of a participant; see "Experimental design" section) and to increase sensorimotor delays in the balance control loop. A real-time controller computed CoM motion in response to the net ankle torque applied by participants to the ground (resolved at the midpoint between the ankles) and the current state of the system (for details, see the Supplementary Materials).

Participants

For our experiments, we recruited 30 healthy participants (15 female; mean age: 24.9 ± 3.5 years; range: 20 to 34 years) with no self-reported history of sensorimotor deficits. All research and recruitment procedures were reviewed and approved by the University of British Columbia Clinical Research Ethics Board, and we obtained written informed consent from each participant before beginning data collection. We measured participants' anthropometrics to simulate their control of balance and adequately manipulate inertia and viscosity; we present normalized viscosity gains as the torque imposed when varying the viscosity gain is dependent on anthropometry (see the Supplementary Materials).

Experimental design

Participants were split evenly into three groups: inertia perception ($n = 10$), viscosity perception ($n = 10$), and balance compensation ($n = 10$). The inertia and viscosity perception groups participated in experiments 1 and 2, whereas the balance compensation group only participated in experiment 3.

Experiment 1: Changes in balance control caused by delays, inertia, and viscosity

To characterize the whole-body oscillations in response to imposed delays and altered body dynamics, we recorded how participants maintained their upright balance on the robot when sensorimotor delay, inertia, and viscosity were manipulated. The added delay values included 0 ms (control condition) and 200 ms. For the inertia manipulations, we adjusted the participant's moment of inertia ($I = 0.35mH^2$; where m and H represent body mass and height, respectively; see Supplementary Materials) by multiplying it by 0.25, 0.5, 2, and 4 during the 0-ms delay condition (viscosity gain equals zero). For the viscosity manipulations, we introduced damping (positive or negative) into the standard state-space model of the inverted pendulum simulation (characterized by a 0-ms delay and baseline inertia). To do so, we applied viscosity gains of −60, −30, 30, and 60 (normalized to each participant's characteristics—see Supplementary Materials) to the baseline viscosity factor of 0.1 Nm/(°/s) (*67*). We validated the capability of the robot to manipulate body dynamics within these ranges of values for both inertia and viscosity (see the Supplementary Materials and fig. S7). Participants performed a single trial of 30 s for each balance condition, resulting in 10 total trials. The conditions were randomized in their presentation for each participant to mitigate potential order effects.

Experiment 2: Perceptual equivalence between the spatial and temporal properties of balance

To investigate whether participants perceived sensorimotor delays as changes in body dynamics, we asked them to manipulate their own body dynamics when balancing upright. Participants were separated into two groups to test the effects of inertia and viscosity in isolation. In each group ($n = 10$), participants performed two conditions. In the first condition, they manipulated their simulated body dynamics (inertia or viscosity) when balancing with no added delay to match their perception of balancing with an added 200-ms delay, and in the second condition, they manipulated their simulated body dynamics (inertia or viscosity) when balancing with an added 200-ms delay to match their perception of natural (baseline) balance. The first condition (self-manipulating inertia or viscosity to perceive balance motion as delayed) addressed whether changes in body dynamics could induce perceptions similar to balancing with delays. The second condition (self-manipulating inertia or viscosity to perceive delayed balance motion as natural) tested whether changes in body dynamics could compensate for the perception of balancing with temporal delays. The presentation order of these two conditions was randomized between participants. To self-adjust their inertia or viscosity, participants from both groups held a computer mouse to make real-time changes to the gain of their body dynamics simulated by the robotic balance system using a custom LabVIEW virtual instrument. We instructed participants that scrolling up on the mouse (increasing the gain value) would make their balance "easier to control," whereas scrolling down on the mouse (decreasing the gain value) would make their balance "harder to control," without any explicit reference to inertia or viscosity.

Participants first balanced in the target condition (either baseline or 200-ms delay) for 15 s, after which they were passively returned to the neutral posture. They then controlled the robotic simulation (with or without delay) for 45 s, using the computer mouse to match their ongoing sensation of balance to the previous 15-s period. For each condition, participants were exposed to 15 trials. We adapted the method of adjustment (*68*, *69*) as an effective and practical approach to quantify perceptual equivalence in the participant's sense of balance.

Experiment 3: Body dynamics compensation of the instability induced by sensorimotor delays

To assess how spatial and temporal information are integrated for the control of balance, we investigated whether the balance instability induced by an added 200-ms delay could be compensated by manipulating body dynamics (inertia or viscosity). For this experiment, 10 naïve participants with no experience with the robot balanced under three conditions: control (no delay), 200-ms delay with modified inertia, and 200-ms delay with modified viscosity. For these latter two conditions, we used the median PSE (*70*) values identified from all participants in experiment 2 (see the "Data analysis" section), wherein participants self-manipulated their body dynamics (inertia or viscosity) during delayed balance to match their perception of control (baseline) balance (second condition in experiment 2). Participants were only exposed to a single 30-s trial per condition (baseline and delayed balance; similar to experiment 1) to reduce the possibility of adaptation to a specific condition. Participants were instructed to maintain themselves upright naturally but had no knowledge of the different conditions being presented to them. The order of the three trial conditions was randomized between participants. After these three trials, participants experienced a fourth 30-s trial where they balanced with only an imposed 200-ms delay.

Data analysis

All data analyses were performed using custom-written MATLAB scripts (version 2023a, MathWorks, Massachusetts, USA).

Characterizing balance behavior (experiments 1 and 3)

Experiments 1 and 3 targeted the neural control of balance in the presence of sensorimotor delays and body dynamics and their interactions. We addressed the hypotheses that inertia gain values less than one and negative viscosity gains would increase postural oscillations (experiment 1) and that properly matched inertia or viscosity gains would compensate for the postural oscillations induced by a sensorimotor delay (experiment 3). For both experiments, we quantified the percentage of trial duration participants spent in the virtual balance limits and their postural oscillations by calculating the average speed of the CoM (see the Supplementary Materials). We calculated the sway path vector based on the Euclidean distance of the AP and ML CoM angular displacement for each time step. For this estimate, we only included data for which participants remained within the virtual limits. We then divided the total path length by the total duration within the virtual limits to estimate the average CoM speed. Average CoM speed was preferred over total path length given the varying durations participants spent within the limits across conditions.

Perception of balance (experiment 2)

To address how sensorimotor delays and body dynamics interact for the perception of balance (experiment 2), we recorded the inertia or viscosity gain values that participants self-selected to create a perception of balance motion matching their sense of balance with and without an added 200-ms delay. For each participant, we fitted a normal cumulative distribution to the self-identified inertia or viscosity gain values to generate participant-specific psychometric functions.

We used the mean value of the fitted psychometric function to obtain each participant's PSE. This perceptual equivalent metric was used to address our hypotheses that participants would experience percepts when balancing with below unity inertia or negative viscosity gains similar to those when balancing with an added 200-ms sensorimotor delay and percepts when balancing with an added 200-ms delay with above unity inertia or positive viscosity gains similar to those for baseline balancing. To assess the consistency in the perceptual equivalence associated with the inertia and viscosity conditions, we calculated the coefficient of variation by dividing the SD of the psychometric curve by its mean value (PSE) for each participant. The median coefficient of variation across all participants was also calculated for inertia and viscosity gains obtained when matching perception to the 200-ms delay and baseline balancing conditions.

Statistical analyses

Given the lack of normality (Shapiro-Wilk test) and unequal variance (Levene's test) in the data between conditions in experiment 1, we performed Wilcoxon signed-rank tests for each dependent variable (percentage of trial duration within limits and average CoM speed) using the baseline balance condition as the comparison reference point. This allowed us to address the hypothesis that balance performance would improve with increased inertia and positive viscosity gains, whereas it would worsen for inertia gains below one and negative viscosity gains when compared with baseline conditions. To further assess whether there were differences in the balance behavior between the spatial (inertia and viscosity) and temporal (delay) dynamic conditions, we ran a secondary analysis using nonparametric (Friedman) repeated measures analyses of variance (ANOVAs) for each dependent variable (percentage of trial duration within the limits and average CoM speed) to compare balancing with an added 200-ms delay with balancing with the inertia and viscosity conditions. We used Conover's post hoc tests to determine whether the individual conditions showed a difference relative to the delay condition.

Using the data from the perception matching task in experiment 2, we performed a Mann-Whitney U test (based on the unequal variance and lack of normality found in the Shapiro-Wilk test and Levene's test, respectively) to compare the coefficient of variation of the PSE values between inertia and viscosity for both the delay and baseline matching conditions. To determine whether participants improved their control of balance with an added 200-ms delay when inertia gains above one or positive viscosity gains were added to the body dynamics in experiment 3, we performed separate Friedman ANOVAs on the percentage of trial duration within limits and average CoM speed variables with conditions (200-ms delay, inertia plus delay, and viscosity plus delay) as a repeated measures factor. We used Conover's post hoc tests to compare each body dynamics condition with the 200-ms delay condition. For additional exploratory analyses, we performed a bootstrapping procedure to assess potential equivalence in balance behavior between the control condition and the inertia plus delay and viscosity plus delay conditions. Specifically, we tested whether the differences in balance metrics (trial duration within limits and average CoM speed) fell entirely within a predefined equivalence margin, defined as a medium effect size (Cohen's $d = 0.5$), and scaled using the SD of the paired differences. To do this, we resampled the paired differences between conditions 10,000 times to generate a bootstrap distribution of the mean difference, from which we extracted the 90% CI. Equivalence was concluded if the entire 90% CI fell within the predefined bounds. This allowed us to examine whether the control of balance with an added 200-ms delay properly compensated by inertia and viscosity gains was statistically equivalent to the baseline control of balance.

All statistical analyses were performed using JASP (the JASP Team, the Netherlands) or MATLAB (version 2023a, MathWorks, Massachusetts, USA). Statistical significance was set at $\alpha < 0.05$.

Supplementary Materials

The PDF file includes:
Supplementary Methods
Figs. S1 to S7
Legend for movie S1
References (*72–91*)

Other Supplementary Material for this manuscript includes the following:
Movie S1
MDAR Reproducibility Checklist

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