

RESEARCH ARTICLE

Control of Movement

Savings in sensorimotor learning during balance-challenged walking but not reaching

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Abstract

Safe and successful motor performance relies on the ability to adapt to physiological and environmental change and retain what is learned. An open question is what factors maximize this retention? One overlooked factor is the degree to which balance is challenged during learning. We propose that the greater need for control and/or perceived threat of falling or injury associated with balance-challenging tasks increases the value assigned to maintaining a learned visuomotor mapping (i.e., the new relationship between visual input and motor output). And we propose that a greater-valued mapping is a more retainable mapping, as it serves to benefit future motor performance. Thus, we tested the hypothesis that challenging balance enhances motor memory, reflected by greater recall and faster relearning (i.e., savings). Four groups of participants adapted to a novel visuomotor mapping induced by prism lenses while performing a reaching or walking task, with and without an additional balance challenge. We found that challenging balance did not disrupt visuomotor adaptation during reaching or walking. We then probed recall and savings by having participants repeat the adaptation protocol 1 wk later. For reaching, we found evidence of initial recall, though neither group demonstrated savings upon reexposure to the prisms. In contrast, both walking groups demonstrated significant initial recall and savings. In addition, we found that challenging balance significantly enhanced savings during walking. Taken together, our results demonstrate the robustness of motor memories formed during walking and highlight the potential influence of balance control on sensorimotor learning.

NEW & NOTEWORTHY Most everyday tasks challenge our balance. Yet, this aspect of daily motor behavior is often overlooked in adaptation paradigms. Here, we show that challenging balance does not impair sensorimotor adaptation during precision reaching and walking tasks. Furthermore, we show that challenging balance enhances savings of a learned visuomotor mapping during walking. These results provide evidence for the potential performance benefits associated with learning during unconstrained, naturalistic behaviors.

adaptation; internal model; locomotion; reaching

INTRODUCTION

Sensorimotor adaptation serves to maintain movement accuracy in response to altered body states, environmental conditions, or task demands. For example, the effects of aging and injury can disrupt the normal relationships (or mappings) between sensory input and motor output, causing errors in movement that are thought to drive adaptation (1–3). An interesting observation following sensorimotor adaptation is the phenomenon known as savings, whereby people demonstrate faster adaptation (or relearning) when they reencounter a familiar perturbation (4, 5). These performance savings are

often considered an indicator of motor memory retention and demonstrate the potential benefit of past experience on subsequent learning. As our bodies and the environment change over time, the ability to adapt to these changes and retain what is learned becomes important for successful motor performance in everyday life. This is also clinically relevant, as it can facilitate rehabilitation by enabling patients to capitalize on previous training.

Research in both reaching and walking demonstrates that motor memories formed during sensorimotor adaptation are retained for extended periods of time (4–17). However, the extent to which motor memories are retained is often dictated



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by the initial training conditions, such as the size of the perturbation (11, 15, 18) and exposure duration (6, 17, 19–22). Interestingly, previous studies demonstrate that motor memories formed during overground walking are stored for at least 1 wk and even up to 1 yr without additional training and despite exposure to a competing mapping in the first testing session (13, 14). This suggests that motor memories formed during walking are, at least to some extent, resistant to interference.

From making your morning coffee to running to catch a bus, most everyday movements require the individual to control balance to achieve some predetermined goal. However, this aspect of daily motor behavior is often overlooked in experimental paradigms, particularly in studies that assess sensorimotor adaptation during seated, reaching tasks where maintaining balance is not a major concern. Consequently, most adaptation research does not account for the possible role that balance plays in sensorimotor learning. In a recent study from our laboratory, we explored the notion that balance-challenges associated with unconstrained, real-life movements may increase the value to the nervous system for using a more accurate and comprehensive internal model for motor control (23). We reasoned that when balance is challenged, the effects of dynamic coupling between body segments, where motion of one segment results in acceleration of another, become more pronounced because of the interconnected nature of our musculoskeletal system (24–26). Consequently, the nervous system requires a more comprehensive internal model for better control over the body to ensure safe and successful task performance. As it is less tailored to a specific task, a more comprehensive model may be a more generalizable model. Indeed, we found that challenging balance during sensorimotor adaptation significantly increased generalization in both reaching and walking tasks (23), suggesting that the effects of challenging balance may apply broadly to sensorimotor learning.

How might a high-value internal model affect motor memories? By definition, for something to have value it must be useful or important, which implies there is potential for some prospective gain or benefit. It seems reasonable that our memory systems are tuned to remember certain kinds of information better than others, particularly if we are able to capitalize on that information for a future advantage. For instance, it is more important to remember information about potential threats or rewards as opposed to arbitrary occurrences. From a motor control perspective, this may pertain to drawing from past experiences to help safely navigate new environments or recalling information that may increase the likelihood of future task success. This concept is referred to as adaptive memory and it is based on the premise that our memory systems evolved to process and retain survival-related information (27–29). Following this reasoning, one might expect that people would exhibit enhanced recall and/or savings for motor memories formed under threatening conditions. Although research on this topic is limited, there is evidence to suggest that perceived threat can modulate motor memory retention. For instance, studies show that older adults are able to rapidly learn to resist falls from repeated-slip exposure and that these motor memories are retained for months after a single training session (30–32). We argue, be it from the greater need for control over moving body segments

or from a greater perceived threat, challenging balance increases the subjective value assigned to maintaining a learned visuomotor mapping. Thus, a greater-valued mapping is a more retainable mapping.

Here, we tested the hypothesis that challenging balance during adaptation enhances motor memory, reflected by greater recall and faster relearning (i.e., savings). To test this hypothesis, we encouraged four groups of participants to adapt to a new visuomotor mapping induced by prism lenses while performing a standing-based reaching or walking task, with or without an additional balance manipulation. To regain movement accuracy and perform the task successfully, two complementary learning processes likely occur: a deliberate (explicit) aiming component (33) and an implicit internal model recalibration based on sensory prediction error (34). Thus, both components can compensate for the new, prism-induced mapping. We assessed the effects of challenging balance during adaptation on both standing-based reaching and walking to determine whether these effects, if any, were specific to the task or applied to sensorimotor learning more generally. We then probed recall and savings of the prism-induced visuomotor mapping by having participants repeat the adaptation protocol 1 wk later.

MATERIALS AND METHODS

Participants

This study included a total of 48 young adults (means age \pm SD, 22.9 ± 3.7 yr; 25 males, 23 females; right-limb dominant, as defined by the limb used to either kick or throw a ball), with no known visual (4 participants wore corrective lenses or glasses), neurological, or musculoskeletal disease. These participants were part of a previous study which focused on the effects of challenging balance on generalization (23). Following the initial training session, the participants returned to the laboratory 1 wk later. This study focusses on the effects of challenging balance on motor memories formed during reaching and walking tasks. The Office of Research Ethics at Simon Fraser University approved the study protocol, and all participants provided informed written consent before their participation.

Experimental Tasks and Data Collection

All participants adapted to a novel visuomotor mapping induced by prism lenses (Fig. 1A), while performing either a precision reaching or walking task. Participants performed these tasks without an additional balance manipulation (balance-unchallenged; Fig. 1C) or while balance was challenged (balance-challenged; Fig. 1D). We randomly assigned participants to one of four adaptation groups ($n = 12$ each), namely, balance-unchallenged reaching, balance-challenged reaching, balance-unchallenged walking, and balance-challenged walking. We assessed how the balance manipulation affected adaptation to a novel visuomotor mapping and relearning (or savings) of the learned mapping 1 wk later.

For the precision reaching tasks, participants stood in front of a screen positioned at a distance of $\sim 90\%$ of their arm's length. Each participant placed the index finger of their reaching hand on their chin before the start of each trial. Once cued by an audible tone, participants reached

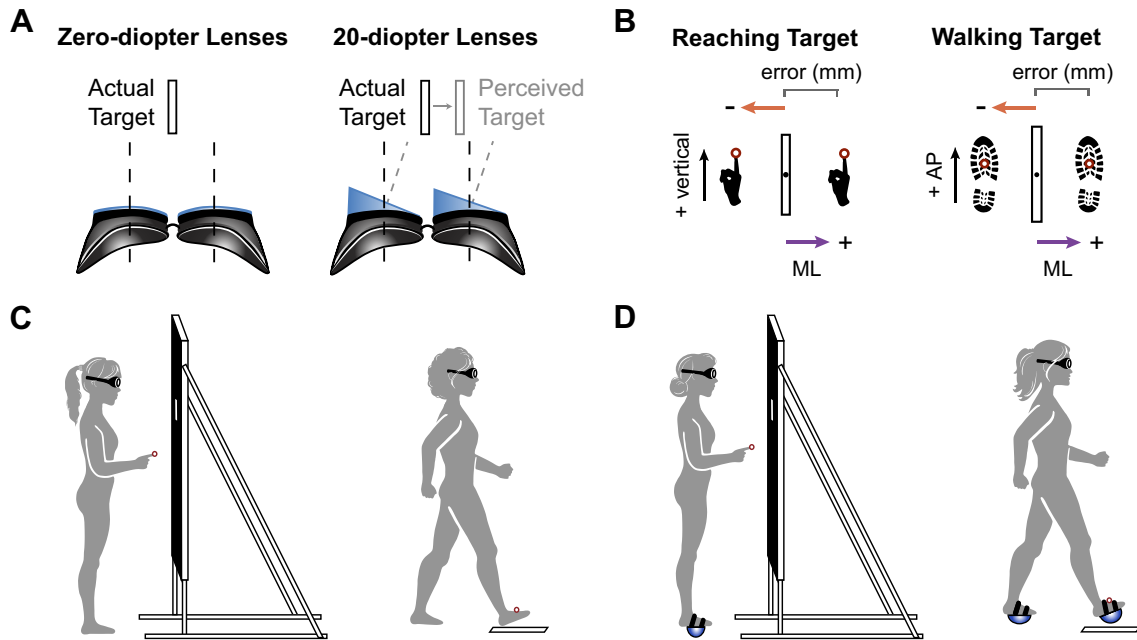


Figure 1. Experimental tasks. **A:** a simulated view of the target through the goggles coupled with zero-diopter (nonvisual-field-shifting) lenses and 20-diopter prism lenses that shift the perceived location of the target 11.4° to the right. **B:** an illustration showing positive (+) and negative (–) medial-lateral (ML) end-point error, defined as the distance between a position marker on the limb and the center of the target line. AP, anterior-posterior direction in laboratory space. **C:** an illustration of the balance-unchallenged reaching and walking tasks. **D:** an illustration of the balance-challenged reaching and walking tasks.

using their index finger to the medial-lateral (ML) center of a target (width: 1 cm; vertical length: 12 cm; Fig. 1B). Because the prism goggles shift visual perception in the ML direction, we only evaluated ML end-point error, and we used a longer target to reduce the demand for accuracy in the vertical dimension. We used a projector (Epson EX7200) to back-project the target onto a screen (279×218 cm) and aligned the top of the target to the height of the participant's chin for each balance condition. We configured the reaching target's size and position in MATLAB (The MathWorks, Natick, MA) with the Psychophysics Toolbox, v. 3 (35, 36). Participants wore comfortable walking shoes and performed the task without an additional balance manipulation or while balance was challenged. For the balance-unchallenged condition, participants performed the task while standing with their feet approximately shoulder-width apart (Fig. 1C). For the balance-challenged condition, participants performed the task with inflatable rubber hemispheres (radii: 8.5 cm) attached to the soles of their shoes (Fig. 1D). These rubber hemispheres reduce the control afforded by shifting the center of pressure under the base of support and significantly increase the root mean square (RMS) of trunk acceleration, end-point-error variability, and lower-limb muscle activity (23). We instructed the participants to stand with their feet as close together as possible without the rubber hemispheres touching each other. During the balance-challenged tasks, an experimenter helped stabilize the participants between each trial. Thereafter, the participant performed the reach without any assistance.

For the precision-walking tasks, participants stood at the beginning of a walkway (~ 6 -m long) and waited for an audible tone to signal the start of each trial. At the sound of the

tone, participants walked and stepped with their right foot onto the ML center of a projected target (3×36 cm) without stopping (Fig. 1B). We used an LCD projector (Epson PowerLite 5535 U; brightness of 5500 Lumens) to display the stepping target on a black uniform mat covering the walking path. Participants performed this task without an additional balance manipulation or while balance was challenged. For the balance-unchallenged condition, participants performed the task while wearing comfortable walking shoes (Fig. 1C). For the balance-challenged condition, participants performed the task with the same inflatable rubber hemispheres attached to the soles of their shoes as in the reaching task (Fig. 1D). An experimenter helped stabilize the participants between each balance-challenged trial. However, the participant performed the walking task without assistance. Participants took a minimum of two steps before and after the step to the target. The two preceding steps allowed participants to determine their walking trajectory and align themselves in preparation for the step to the target, which we positioned in the center of the walkway for all trials. We randomized the participant's anterior-posterior (AP) starting location (between 1.5 and 2.5 m) for each trial to increase the demand for visual feedback during the task and to prevent participants from learning a specific walking sequence.

To track body motion during the reaching and walking tasks, we used an Optotrak Certus motion capture camera (Northern Digital, Waterloo, ON, Canada) that recorded (at 120 Hz) infrared emitting position markers placed on the participant's midback (in line with the sternum), index finger of the right hand, and bilaterally on the heel, midfoot (second-third metatarsal head), and the toe (third metatarsal). For all

tasks, we instructed participants to be as accurate as possible when reaching or stepping to the target. We also instructed participants to perform the tasks at a quick and constant pace to minimize online corrections of the finger or leg/foot trajectory to more closely match previous experiments in which the movements are ballistic. These guidelines also encourage the use of sensory feedback before the reach or step to the target. To minimize adaptation between trials, participants had their eyes open only when they were performing the task and received visual feedback of their performance through the lenses. To increase target visibility and reduce the influence of environmental references, participants performed both tasks under reduced light conditions (~ 0.9 lux). An experimenter demonstrated each task before testing. In addition, participants were attached to a safety harness system suspended from the ceiling at all times which prevented falling to the ground in the event of a loss of balance. The harness did not provide any body weight support, and no participant engaged the system during the course of the experiment.

Experimental Protocol

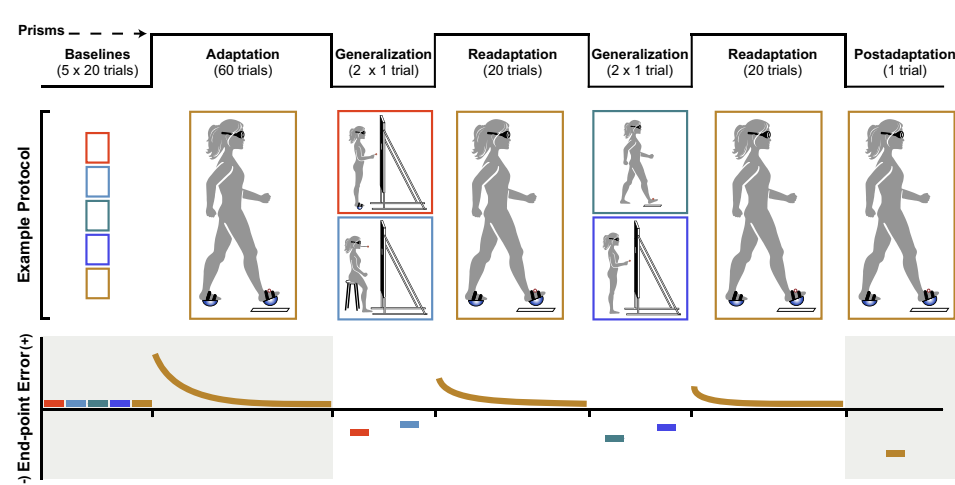
We measured adaptation over two testing sessions, separated by 1 wk. Figure 2 illustrates an example of the experimental protocol for both testing sessions and the predicted end-point error responses for each phase of testing. During the first testing session, participants performed five baseline phases (20 trials each); one for each reaching and walking task, as well as a seated, nonlimb-based reaching task. This latter task is described in Bakkum et al. (23) and is not relevant to this study. Participants performed the baseline phases while wearing zero-diopter (i.e., nonvisual-field-shifting) lenses. The baseline trials for the adaptation task were performed last, just before the adaptation phase. We randomized the remaining baseline conditions for each participant. During the adaptation phase, participants learned a

novel visuomotor mapping induced by 20-diopter prism lenses while performing 60 trials of their assigned adaptation task (e.g., balance-challenged walking). The 20-diopter prism lenses altered the relationship between visual inputs and motor commands by shifting the perceived location of the target to the right ($\sim 11.4^\circ$; Fig. 1A). The goggles blocked a portion of the peripheral visual field, such that the participants had no choice but to look through the lenses during the tasks. Each participant performed a total of four generalization trials, which we split into two phases with two generalization tasks each. Participants performed a single generalization trial of each of the other group's adaptation tasks, as well as a seated, nonlimb-based reaching task. This study focuses on the adaptation phases across the two testing sessions. Details regarding generalization are found elsewhere (23). To mitigate any deadadaptation that occurred during the generalization trials, participants performed 20 readaptation trials after each generalization phase while wearing the 20-diopter prism lenses (i.e., readaptation phases). Finally, participants performed a single trial of their respective adaptation tasks after the second readaptation phase with the zero-diopter lenses to confirm whether the novel mapping is stored (i.e., postadaptation trial). One week later (Fig. 2), participants returned to the laboratory and performed 20 baseline trials of their respective adaptation tasks with the zero-diopter lenses. Participants then performed 60 trials of their adaptation task while wearing the 20-diopter lenses, followed by one postadaptation trial with the zero-diopter lenses.

Data and Statistical Analyses

We analyzed data using custom-written MATLAB programs. We filtered kinematic data using a fourth-order, low-pass Butterworth algorithm with a cut-off frequency of 6 Hz. We calculated reaching time and gait speed over 2 m using the position markers placed on the index finger and the

Session 1: Visuomotor Adaptation and Generalization



Session 2: Recall and Savings

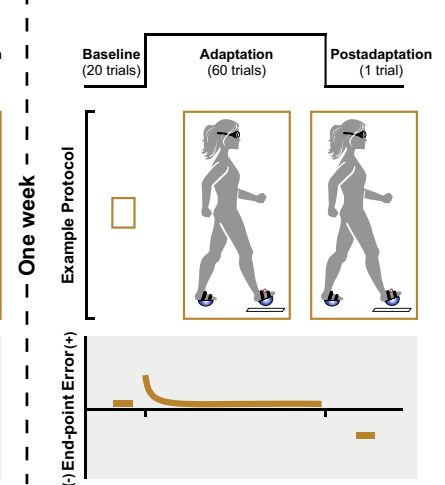


Figure 2. Experimental protocol. An example using the balance-challenged walking group of the experimental tasks performed throughout the testing session, as well as the predicted end-point error profiles for each phase of testing. During the first testing session, all participants performed baseline, adaptation, generalization, readaptation, and postadaptation phases. Depending on the phase, participants wore goggles paired with either zero-diopter or 20-diopter lenses. To assess motor memory, participants repeated the adaptation protocol 1 wk later. This study focuses on the baseline, adaptation, and postadaptation phases across the two testing sessions, as denoted by the shaded boxes. See text for details.

midback infrared marker, respectively. To confirm the lack of online corrections, we verified the absence of sudden trajectory changes by analyzing the displacement and velocity profiles of the finger and midfoot markers.

All participants performed their respective tasks at a quick and constant pace throughout the experiment, as instructed. We did not detect significant differences in the average reaching times during the adaptation phase ($t_{22} = 0.2$, $P = 0.847$) between the balance-unchallenged (0.49 ± 0.1 s) and the balance-challenged (0.48 ± 0.1 s) reaching groups. For the walking groups, we found no significant difference in the average gait speeds across groups during the adaptation phase trials (balance-unchallenged: 1.33 ± 0.13 m/s; balance-challenged: 1.22 ± 0.19 m/s; $t_{22} = 1.6$, $P = 0.133$). We also found no significant difference in the reaching times ($F_{3,44} = 0.02$, $P = 0.996$) and gait speeds ($F_{3,44} = 0.8$, $P = 0.155$) between the baseline and adaptation phases or balance condition. Finally, we found no significant differences in reaching times ($F_{1,22} = 0.1$, $P = 0.705$) or gait speeds ($F_{1,22} = 0.7$, $P = 0.429$) between balance conditions during the adaptation phases across testing sessions.

We determined finger placement on the reaching target as the time at which point the position marker's AP velocity and acceleration profiles stabilized to near zero. We determined foot placement on the target as the moment of heel strike of the foot, derived using the vertical velocity of the midfoot marker on the right foot (13). The ML distance between the respective position markers and the center of the target at these time points defined the ML end-point error. A positive value represents errors in the direction of the prism shift (right), and a negative value represents errors in the left direction, opposite to the prism shift (Fig. 1B).

We used JMP software v. 15 (SAS Institute Inc., Cary, NC) with an α level of 0.05 for all statistical analyses. To determine the effects of challenging balance on adaptation, we compared end-point error during the baseline phase (average of the last ten trials), first adaptation trial, late adaptation (average of the last 10 trials), and postadaptation trials during the first testing session using separate two-way (group \times phase) mixed-model ANOVAs for the reaching and walking tasks, where we included participant as a random effect. We used Tukey post hoc tests for significant main effects and interactions. When checking for the assumptions of an ANOVA, we found a potential outlier for the balance-challenged walking group (studentized residual > 4.0). Excluding this data point did not change the results, suggesting it was noninfluential. Thus, we included this data point in the final statistical model.

To assess relearning 1 wk later, we quantified three measures: the first adaptation trial error (representing the initial recall of the mapping), early adaptation error (i.e., mean of adaptation trials 2 to 8), and rate of adaptation. The early adaptation measure captures the large, rapid reduction in error early in the adaptation phase and is model-free, as it does not assume that participants follow a specific pattern (13, 15, 17). Model-based rate measures are also used to quantify adaptation and savings (37, 38). Thus, we also calculated the rate of adaptation by fitting an exponential model to the end-point-error data during the 60 adaptation trials. We define the rate of adaptation as the time constant, which represents the

number of trials taken to reach $\sim 63.2\%$ of adaptation (39). We used the following equation:

$$y = a - b \times e^{-x/c},$$

where a is residual error after steady state (i.e., the asymptote), b is the magnitude of the adaptation required from the first trial to reach a , c (the decay constant) represents the rate of adaptation, and x is the trial number. The goodness of fit (means \pm SD, range) for the exponential models for each participant were as follows: reaching, balance-unchallenged (session 1: $R^2 = 0.51 \pm 0.16$, range = 0.31–0.82; session 2: $R^2 = 0.53 \pm 0.15$, range = 0.25–0.70), reaching, balance-challenged (session 1: $R^2 = 0.49 \pm 0.11$, range = 0.32–0.69; session 2: $R^2 = 0.46 \pm 0.11$, range = 0.29–0.66), walking, balance-unchallenged (session 1: $R^2 = 0.74 \pm 0.15$, range = 0.46–0.93; session 2: $R^2 = 0.70 \pm 0.10$, range = 0.58–0.88), walking, balance-challenged (session 1: $R^2 = 0.73 \pm 0.12$, range = 0.54–0.90; session 2: $R^2 = 0.63 \pm 0.11$, range = 0.48–0.89).

We used separate two-way (group \times session) mixed-model ANOVAs (with participant as a random effect) to determine differences in first adaptation trial error, early adaptation error, adaptation rates, and postadaptation trial error between groups and across testing sessions. When checking for the assumptions of an ANOVA, we found two potential outliers (studentized residuals > 3.5) for the balance-unchallenged reaching groups and the balance-challenged walking group, respectively. Excluding these data points did not change the results, suggesting that they were noninfluential. Thus, we included all data in the final statistical models. This analysis provides an indication as to whether end-point error differs between testing sessions and whether groups differ in each of the two testing sessions. Therefore, to determine if challenging balance resulted in better relearning, we calculated the difference in first adaptation trial error, early adaptation error, and rate of adaptation between the first and second testing session. Subsequently, we used separate two-sample t tests or Wilcoxon rank sum tests, depending on data normality, to compare between the balance-unchallenged and balance-challenged reaching and walking groups for each of these measures.

Research suggests that movement variability may affect aspects of motor learning (40). Therefore, we quantified performance variability across the sixty adaptation trials of the first testing session based on either finger-placement or foot-placement error, depending on the task. Specifically, for each participant, we calculated the difference between the actual end-point error in a given trial and the predicted value based on the exponential fits. Subsequently, we calculated the standard deviation of these residuals for each participant. To determine whether performance variability predicted savings, we performed separate regression analyses with the early adaptation and adaptation rate measures.

RESULTS

Four groups of participants adapted to a novel visuomotor mapping induced by prism lenses while performing either a precision-reaching or walking task, with or without an additional balance manipulation. We determined how challenging balance affected the ability to adapt and retain the novel visuomotor mapping. Our previous work based on the same

data reports the effects of our balance manipulation on measures of balance (23). In brief, we quantified trunk motion, performance variability, and muscle activity (from four muscles on each leg) during the baseline phase. For the reaching tasks, the rubber hemispheres significantly increased trunk acceleration RMS in the AP (balance-unchallenged: $287 \pm 78 \text{ mm/s}^2$; balance-challenged: $403 \pm 125 \text{ mm/s}^2$) and ML (balance-unchallenged: $364 \pm 120 \text{ mm/s}^2$; balance-challenged: $464 \pm 180 \text{ mm/s}^2$) dimensions, end-point error variability (balance-unchallenged: $6.5 \pm 2.5 \text{ mm}$; balance-challenged: $9.0 \pm 3.7 \text{ mm}$), and lower-limb muscle activity (balance-unchallenged: 0.8 ± 0.5 ; balance-challenged: 2.3 ± 1.2 ; values normalized). Similarly, the rubber hemispheres significantly increased trunk acceleration RMS (AP: balance-unchallenged: $1,018 \pm 229 \text{ mm/s}^2$; balance-challenged: $1,461 \pm 342 \text{ mm/s}^2$; ML: balance-unchallenged: $1,444 \pm 291 \text{ mm/s}^2$; balance-challenged: $1,969 \pm 409 \text{ mm/s}^2$), end-point error variability (balance-unchallenged: $13.4 \pm 3.8 \text{ mm}$, balance-challenged: $20.2 \pm 5.3 \text{ mm}$), and lower-limb muscle activity (balance-unchallenged: 5.7 ± 2.3 ; balance-challenged: 8.6 ± 3.8 ; values normalized) during the walking tasks. Thus, these results confirm that the rubber hemispheres worn under the feet successfully challenged balance during both reaching and walking.

Challenging Balance Does Not Affect the Ability to Adapt to a New Visuomotor Mapping

All participants adapted to the novel visuomotor mapping. Upon initial exposure to the 20-diopter (rightward-shifting) prism lenses, participants showed a large, rightward deviation in limb end-point placement relative to the target for the reaching and walking tasks. The end-point error gradually returned to near-baseline levels as the participants adapted to the prisms. These results are illustrated in Figs. 3 and 4 for reaching and walking, respectively.

To determine the effects of challenging balance on adaptation, we compared end-point error over several phases during the first testing session. For the reaching groups, end-

point error differed depending on the phase (Fig. 3B; phase main effect: $F_{3,66} = 186.31$, $P = 3.76\text{e-}32$). Post hoc tests for this main effect revealed significantly greater end-point error during the first adaptation trial compared with the other phases. Furthermore, the end-point error during the postadaptation trials differed significantly from each other phase. We found no significant differences between the balance-unchallenged and balance-challenged reaching groups across the different phases (nonsignificant group \times phase interaction: $F_{3,66} = 0.18$, $P = 0.912$; nonsignificant group main effect: $F_{1,22} = 0.10$, $P = 0.752$). Similarly, end-point error differed depending on the phase for the walking groups (Fig. 4B; phase main effect: $F_{3,66} = 676.90$, $P = 1.75\text{e-}49$). Post hoc tests for this main effect showed a significant difference between the first adaptation trials and each other phase. Similarly, postadaptation end-point error differed significantly from the other phases. We did not detect any significance differences between the balance conditions for the walking tasks across the testing phases (non-significant group \times phase interaction: $F_{3,66} = 0.58$, $P = 0.630$; nonsignificant group main effect: $F_{1,22} = 2.19$, $P = 0.153$). Taken together, these results suggest that our balance manipulation did not affect the ability to adapt to the novel, prism-induced visuomotor mapping.

Challenging Balance Enhanced Savings in Walking But Not Reaching

To determine the effects of challenging balance on recall and savings, all participants repeated the adaptation protocol 1 wk later. Figures 5A illustrates group mean end-point error across trials for both testing sessions for the reaching groups. We found a reduction in first adaptation trial error during the second testing session compared to first testing session (Session main effect: $F_{1,22} = 8.22$, $P = 0.0089$), demonstrating recall of the learned mapping after 1 wk (Fig. 5B).

To quantify savings, we compared early adaptation error (i.e., mean of adaptation trials 2 to 8) and rate of adaptation across testing sessions. A faster reduction in error (i.e., faster

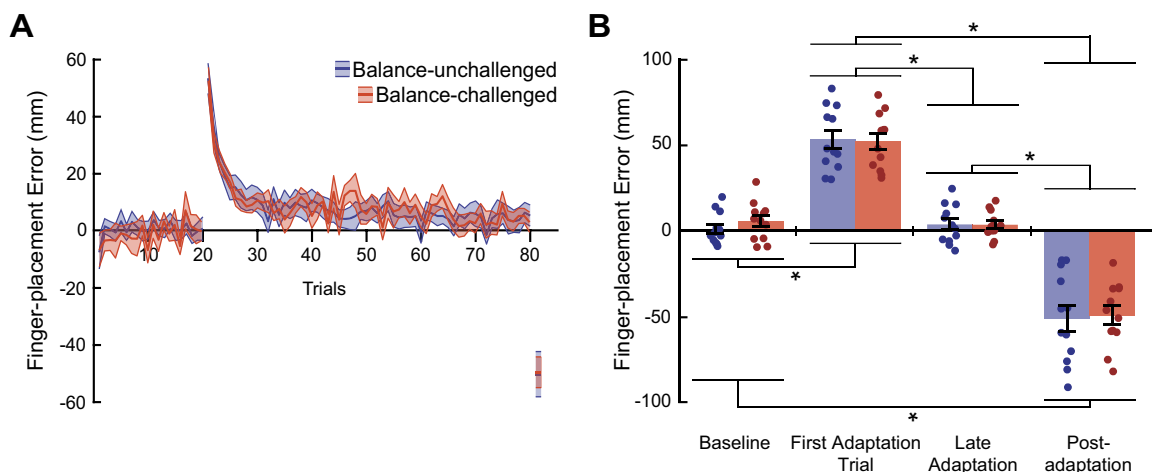


Figure 3. Visuomotor adaptation in reaching during session 1. **A:** group means \pm SE finger-placement error across all trials for baseline, adaptation, and postadaptation phases during the first testing session for the balance-unchallenged (blue) and balance-challenged (red) reaching groups. **B:** group means \pm SE finger-placement error for the baseline phase (average of the last 10 trials), first adaptation trial, late adaptation (average of the last 10 trials), and postadaptation trials for the first testing session for the balance-unchallenged (blue) and balance-challenged (red) reaching groups. Individual participant values are superimposed. *Values are significantly different from each other based on post hoc tests ($P < 0.05$).

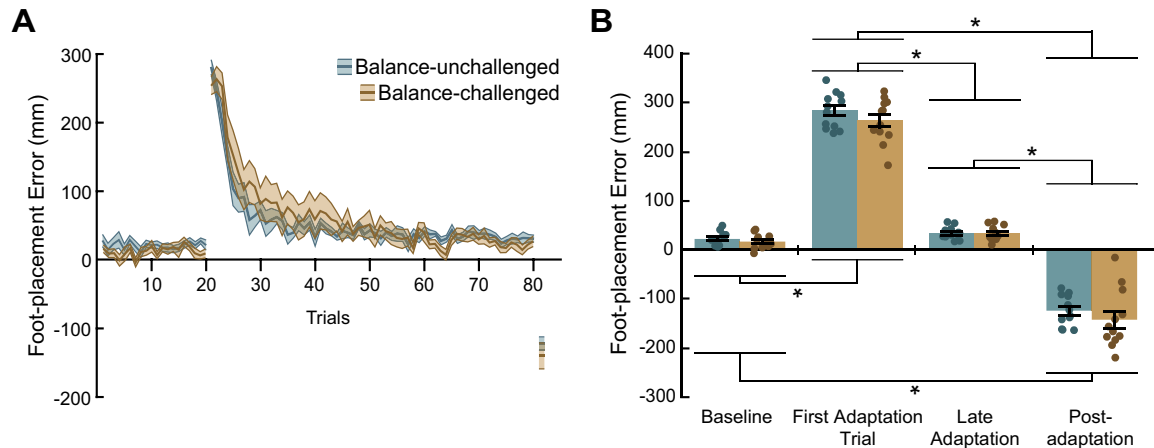


Figure 4. Visuomotor adaptation in walking during session 1. *A*: group means \pm SE foot-placement error across all trials for baseline, adaptation, and postadaptation phases during the first testing session for the balance-unchallenged (teal) and balance-challenged (gold) walking groups. *B*: group means \pm SE foot-placement error for the baseline phase (average of the last 10 trials), first adaptation trial, late adaptation (average of the last 10 trials), and postadaptation trials for the first testing session for the balance-unchallenged (teal) and balance-challenged (gold) walking groups. Individual participant values are superimposed. *Values are significantly different from each other based on post hoc tests ($P < 0.05$).

relearning of the mapping, or savings) indicates that the learned mapping was retained. We found no evidence of savings for either reaching group (Fig. 5B). Specifically, we did not detect significant main effects or interactions for early adaptation error or adaptation rates ($P > 0.05$). Interestingly, we found that the balance-challenged reaching group had significantly less end-point error in the postadaptation trial for session 2 compared with session 1 and both sessions for the balance-unchallenged reaching group (group \times session interaction: $F_{1,22} = 2.41$, $P = 0.025$).

To determine if challenging balance improved motor memory during reaching, we compared the difference in first adaptation trial error, early adaptation error, and rate of adaptation between the first and second testing session. In this case, a greater positive change in these measures reflects greater recall and/or savings. We did not detect significant differences for the change in first adaptation trial error ($t_{22} = 1.33$, $P = 0.197$), early adaptation error ($t_{22} = 0.35$, $P = 0.731$), or rate of adaptation (Wilcoxon: $Z = 0.116$, $P = 0.908$) between the balance-unchallenged and balance-challenged groups (Fig. 5C). We also did not detect a significant difference in the change in postadaptation error between groups (Wilcoxon: $Z = 1.76$, $P = 0.078$). Overall, challenging balance did not appear to affect visuomotor savings during reaching.

Figures 6A illustrates group mean end-point error across trials in both testing sessions for the walking groups. Unlike the results for reaching, we found evidence of initial recall and savings for both walking groups. Specifically, we found a significant reduction in first adaptation trial error during the second testing session compared to first testing session (Session main effect: $F_{1,22} = 11.6$, $P = 0.003$), demonstrating recall of the learned mapping (Fig. 6B). We also found evidence for faster relearning for both walking groups, reflected by our early adaptation error (group \times session interaction: $F_{1,22} = 6.69$, $P = 0.017$) and adaptation rate (group \times session interaction: $F_{1,22} = 6.1$, $P = 0.022$) measures. Based on post hoc tests, however, we did not detect differences between groups for each session. Similar to the reaching groups, we found that the balance-challenged walking group had

significantly less end-point error in the postadaptation trial for session 2 compared with session 1 and both sessions for the balance-unchallenged walking group (group \times session interaction: $F_{1,22} = 9.6$, $P = 0.005$).

To determine if challenging balance led to greater recall and savings during walking, we compared groups using the difference in first adaptation trial error, early adaptation error, and rate of adaptation between the first and second testing session. We found no significant difference for the change in first adaptation trial error ($t_{22} = 0.13$, $P = 0.895$), indicating similar recall of the mapping between the walking groups. However, we found that the balance-challenged walking group showed a significantly greater positive change in early adaptation error ($t_{22} = 2.32$, $P = 0.030$) and rate of adaptation ($t_{22} = 2.46$, $P = 0.022$) compared to the balance-unchallenged walking group, indicating greater savings. When the results of the mixed-model ANOVAs above are considered, it appears as though small, nonsignificant changes in both adaptation sessions contribute to the significant differences in change scores between groups. In addition, the balance-challenged walking group showed a reduction in postadaptation trial error (or less aftereffect) across testing sessions compared to the balance-unchallenged group ($t_{22} = 3.11$, $P = 0.005$). Taken together, both walking groups showed evidence of faster relearning assessed 1 wk later. Furthermore, challenging balance enhanced savings in our walking task.

Performance variability did not affect savings. The results of our regression analyses are illustrated in Fig. 7. We did not detect a significant relationship between finger-placement error variability and early adaptation error in the second testing session ($R^2 = 0.06$, $P = 0.237$) or with the change score across testing sessions ($R^2 = 0.01$, $P = 0.630$). Similarly, we did not detect a significant relationship between finger-placement error variability and adaptation rate in the second testing session ($R^2 = 0.12$, $P = 0.096$) or with the change score across sessions ($R^2 = 0.001$, $P = 0.858$). For the walking task, we did not detect a significant relationship with the early adaptation error in the second testing session ($R^2 = 3.90 \times 10^{-4}$, $P =$

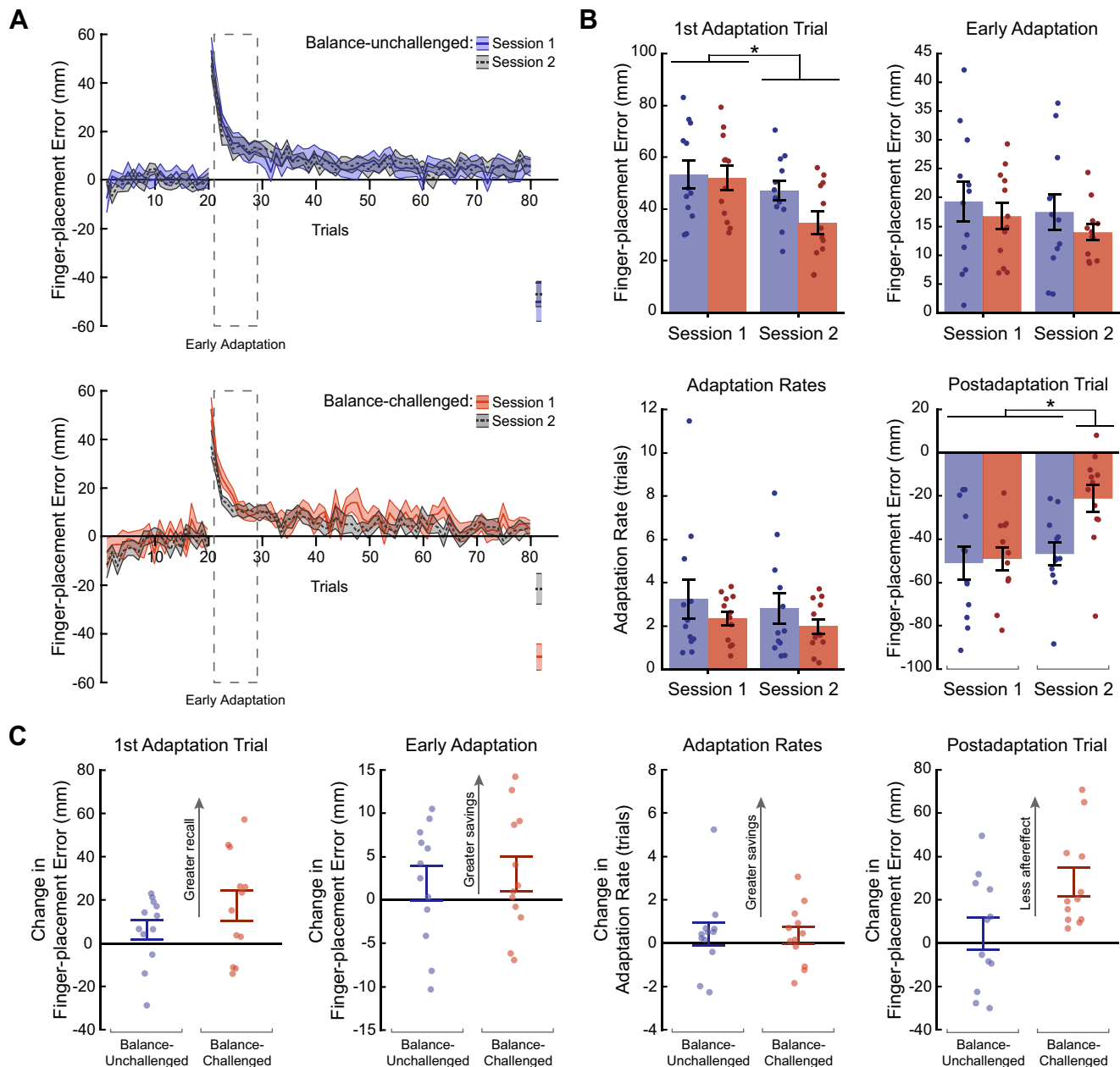


Figure 5. Challenging balance and visuomotor memory in reaching. **A:** group means \pm SE finger-placement error for all trials in the baseline, adaptation, and postadaptation phases across testing sessions for the balance-unchallenged (*top*) and balance-challenged (*bottom*) reaching groups. **B:** group means \pm SE for the first adaptation trial error, early adaptation error, rate of adaptation, and postadaptation trial error across testing sessions for the balance-unchallenged (blue) and balance-challenged (red) reaching groups. **C:** the change in first adaptation trial error, early adaptation trial error, rate of adaptation, and postadaptation trial error across testing sessions for the balance-unchallenged (blue) and balance-challenged (red) reaching groups. Group means \pm SE and individual values are shown for each measure. Testing sessions occurred 1 wk apart. *Values are significantly different from each other based on post hoc tests ($P < 0.05$).

0.927). Similarly, after removing highly influential outliers (initial outlier, Cook's $D = 1.76$; another outlier, also removed, appears upon removal of the first, with a Cook's $D = 1.08$), we did not detect a significant relationship between foot-placement error variability and the early adaptation error change score across sessions ($R^2 = 0.03$, $P = 0.438$). Furthermore, we did not detect a significant relationship between foot-placement error variability and adaptation rate in the second testing session ($R^2 = 6.79 \times 10^{-4}$, $P = 0.904$) or with the change score across sessions ($R^2 = 0.04$, $P = 0.352$).

DISCUSSION

The ability to adapt to physiological and environmental change and retain what is learned is important for safe and successful motor performance in everyday life. Here, we tested the hypothesis that challenging balance during adaptation would enhance motor memory, reflected by greater recall and savings assessed 1 wk later. We found that challenging balance did not affect the ability to adapt to the new, prism-induced visuomotor mapping and that

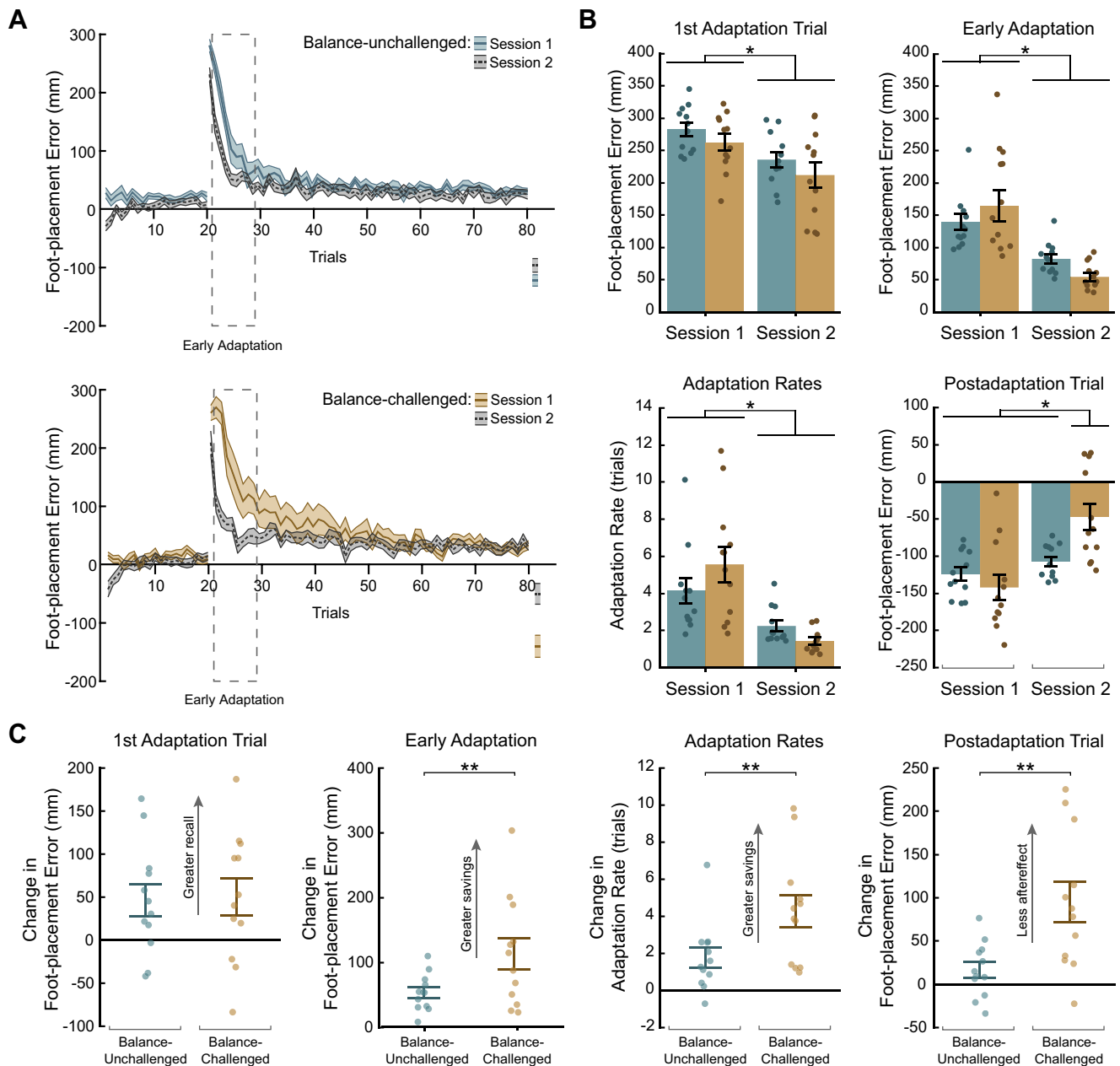


Figure 6. Challenging balance and visuomotor memory in walking. **A:** group means \pm SE foot-placement error for all trials in the baseline, adaptation, and postadaptation phases across testing sessions for the balance-unchallenged (*top*) and balance-challenged (*bottom*) walking groups. **B:** group means \pm SE for the first adaptation trial error, early adaptation error, rate of adaptation, and postadaptation trial error across testing sessions for the balance-unchallenged (teal) and balance-challenged (gold) walking groups. **C:** the change in first adaptation trial error, early adaptation trial error, rate of adaptation, and postadaptation trial error across testing sessions for the balance-unchallenged (teal) and balance-challenged (gold) walking groups. Group means \pm SE and individual values are shown for each measure. Testing sessions occurred 1 wk apart. *Values are significantly different from each other based on post hoc tests ($P < 0.05$). **Magnitude of change across testing sessions is significantly different between the balance-unchallenged and balance-challenged groups ($P < 0.05$).

only the walking groups demonstrated savings. Crucially, we found that challenging balance enhanced savings during walking. Thus, although challenging balance did not dictate whether or not recall and/or savings occurred, this condition increased savings in tasks where participants retained the new visuomotor mapping. These results highlight the robustness of motor memories associated with walking, as well as the potential influence of balance control on sensorimotor learning.

One hypothesis for our findings is that challenging balance increases the value assigned to maintaining the learned visuomotor mapping. This potential value may arise from two related factors: the necessity for better control over the whole body to ensure safe and successful task performance or from a greater perceived threat of falling typically associated with balance challenges. We discuss the rationale and support for these factors.

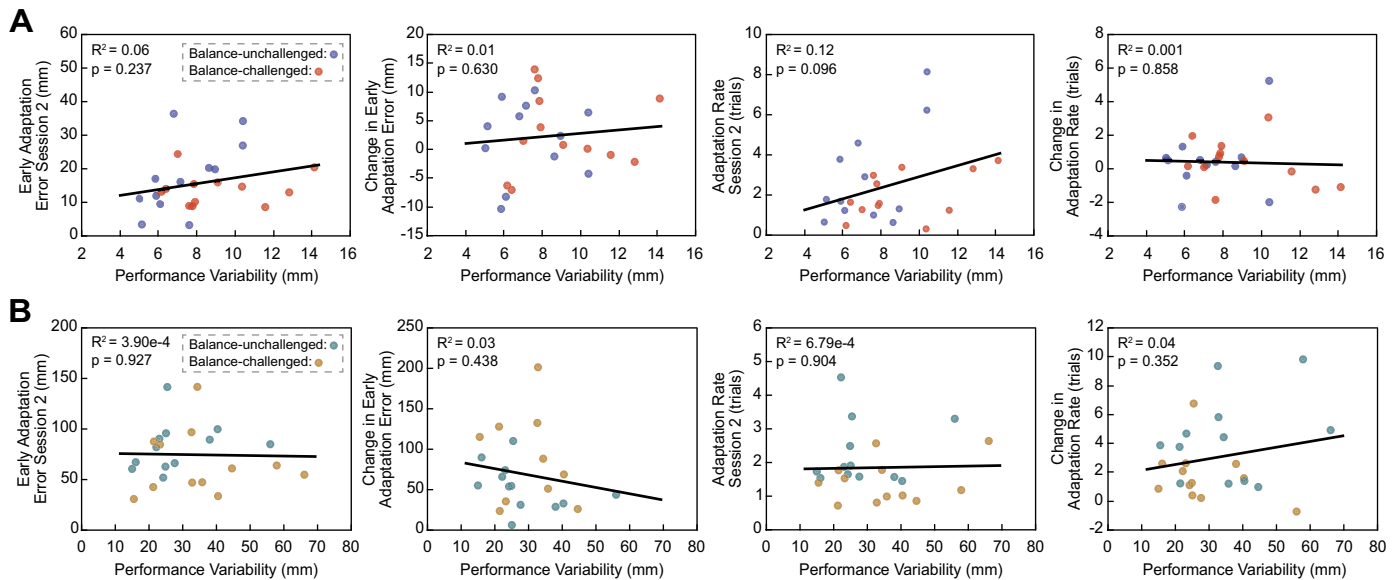


Figure 7. Relationship between performance variability and savings. Scatter plots illustrating the relationship between end-point error variability and early adaptation error in the second testing session, early adaptation error change scores across testing sessions, adaptation rate in the second testing session, and adaptation rate change scores across testing sessions for the balance-unchallenged (blue) and balance-challenged (red) reaching groups (A) and the balance-unchallenged (teal) and balance-challenged (gold) walking groups (B). The solid lines show the linear fits obtained from the regression analyses.

For the balance-challenged group, the brain must contend with two experimental manipulations as it tries to ensure foot-placement accuracy in our task: a new, prism-induced visuomotor mapping and the instability created by the rubber hemispheres. This mapping shifts the perceived location of the target and causes foot-placement error, which can be viewed as a disturbance to the body's motion. The rubber hemispheres challenge balance by making the body more sensitive to disturbances, such as those arising from unmodeled shifts in the visuomotor mapping. This is because the foot has a smaller base of support, thus reducing the ability to control the body through changes to the center of pressure. Although participants are not able to resolve the balance disturbance—they cannot give themselves bigger feet—they are able to adapt to the prism-induced visuomotor mapping. As a result, they are able to increase their foot-placement accuracy and reduce the disturbance created by the mapping. The control of balance is fundamental to movement. Because the brain is learning the new mapping while it is also attempting to control balance, the memory it creates must integrate the strategies for dealing with each. There is value in retaining this memory, since it increases the probability of ensuring safe and successful motor performance. Most memories are transient in nature, and we tend to forget information or actions that are unlikely to be useful in the future. In contrast, information or actions that increase the likelihood of future gains may be perceived as more valuable and therefore more readily retained. For instance, we might expect amateur and professional athletes to focus on recalling actions that lead to task success rather than those that worsen performance. This idea is aligned with studies demonstrating that monetary rewards enhance motor memory retention (41, 42). As value increases with the magnitude and probability of reward (43), we might infer that subject-

ive value, monetary or otherwise, can modulate savings. In our study, while both walking groups demonstrated recall and savings, challenging balance significantly increased savings assessed 1 wk later. These results highlight the significance of balance control for sensorimotor learning.

As with most balance challenges, there is an element of risk associated with falling and getting injured. While we did not directly assess fear or anxiety associated with our balance-challenged tasks, it is possible that the greater perceived risk of falling contributed to the enhanced savings observed during walking. Imagine having just slipped on ice. When remembering that unpleasant experience, you might choose to modify your gait (44) or simply avoid a similar area to mitigate the threat of falling in the future. Thus, from a safety perspective, it is important to prioritize information that reduces the risk associated with threatening environments. Correspondingly, studies using Pavlovian fear-conditioning paradigms demonstrate that perceived threat can significantly influence memory (see e.g., Ref. 45). This is aligned with the notion that our memory systems are optimized to retain survival-related information (27, 29). While the effects of perceived threat on motor memory are less clear, research shows that balance recovery responses from gait trip- or slip- perturbations can be retained for extended periods of time (30–32, 46). This suggests that fear of falling can modulate motor memory. Thus, the greater perceived threat associated with balance challenges may further increase the value assigned to the mapping during adaptation and enhance the motor memory.

Research shows that movement variability can influence one of the hallmarks of motor learning, generalization (40). Does this variability explain savings in our paradigm? As illustrated in Fig. 7, we did not detect a significant relationship

between end-point error variability and measures of savings in either reaching or walking tasks. However, it is still possible that other sources or measures of variability can help to explain our data.

Another reasonable question to ask is whether there is something unique about balance challenges or whether one can expect similar results with other forms of manipulation that influence task difficulty, such as dual-tasking, the addition of a time constraint, or having participants wear a leg brace. Although we cannot distinguish between task difficulty in general and our balance challenge specifically, there is no a priori reason to expect, and no empirical evidence to suggest, that all forms of increasing task difficulty would improve savings. In fact, in some cases, increasing task difficulty may serve to prevent savings. Given the importance of maintaining balance during most movements, we believe that our results are strongly related to challenging balance.

It is possible that the presence of the rubber hemispheres, or the balance challenge itself, may have increased the reliance on an explicit, cognitive-based strategy and contributed to our findings. Research suggests that savings may result from a memory of errors experienced during adaptation (47) or through the recall of a deliberate aiming strategy (7, 18). One idea is that the rubber hemispheres served as an additional contextual cue driving faster recall of the mapping. Contextual cues that contain sensory information about movement dynamics (e.g., limb orientation or proprioceptive states) can play an important role in the formation and recall of motor memories (48–50), though these effects are not always apparent (51, 52). Here, the exacerbated movements associated with the balance-challenged tasks may have strengthened the association between the rubber hemispheres and learned visuomotor mapping, enabling rapid recall of an explicit aiming strategy upon reexposure to the prisms. In this scenario, we might expect the balance-challenged walking group to demonstrate greater recall of the mapping, reflected by a greater positive change in first adaptation trial error compared to the balance-unchallenged walking group. However, this was not the case, and our findings suggest that both walking groups demonstrate comparable recall. This also appears to be the case for our reaching tasks where neither group showed savings. Furthermore, given that participants performed baseline trials before relearning to return their performance to preadaptive levels, any immediate contextual cues associated with the rubber hemispheres would have been washed out before the second testing session's adaptation phase. Thus, it seems unlikely that the additional context provided by the rubber hemispheres is responsible for the enhanced savings observed during balance-challenged walking. This does not, however, rule out the possibility that an explicit aiming strategy contributed to the enhanced savings in the balance-challenged walking group. Rather, participants may have assigned a higher value to maintaining a memory of a deliberate aiming strategy used to compensate for the prism lenses regardless of any effect of contextual cue. Although we previously showed that people update an internal model in our paradigm (34), we are unable to determine to what extent this implicit learning process contributes to our findings versus an explicit-based learning process. Thus, it is unclear as to whether the enhanced savings is a result of an explicit

aiming strategy based on the motor memory of the visuomotor mapping, selecting the appropriate implicitly learned internal model that represents the mapping, or some combination of both. Regardless, our argument that the greater need for control or the increased threat of falling associated with the balance challenge supports each of these notions.

In contrast to the walking groups, we found that neither reaching group exhibited savings 1 wk after adaptation. The reasons for this are unclear, however the nature of the reaching task may provide an explanation. For instance, the structure of initial learning, such as perturbation size (11, 15, 18) and exposure duration (6, 17, 19, 21) can influence motor memory. Here, all participants adapted to a 20-diopter visual shift to the right ($\sim 11.4^\circ$) (Fig. 1A). However, the distance between the eye and the floor (and foot) is larger than the distance between the eye and the target screen (and hand). This means that there is a larger perceived target shift to the right for the walking groups. This may explain the differences in initial end-point error between tasks (~ 60 mm for reaching compared with ~ 300 mm for walking; see Figs. 3A and 4A). Thus, the magnitude of the error experienced during adaptation may be less effective at eliciting week-long savings during reaching. Differences between the reaching and walking groups may also relate to the fact that participants in the latter exhibited greater end-point error variability (as evident in Fig. 7). However, since variability does not appear to predict savings, this explanation is doubtful. In addition, participants in the walking task groups had increased prism exposure during the steps before and after the target, which may further facilitate savings and explain our results. However, we feel that this is unlikely, as participants only interact with the target once per trial regardless of the task and they performed the tasks under reduced light conditions (~ 0.9 lux) and on a black mat to minimize the influence of environmental references. Alternatively, these findings may provide further evidence for the robustness of motor memories associated with walking and observed in previous studies (6, 14, 15).

An interesting observation in this study was that both the reaching and walking balance-challenged groups significantly decreased their postadaptation trial error after relearning. Although the reasons for this are unclear, we speculate that it relates to the increased value associated with maintaining the new visuomotor mapping formed during the balance-challenged tasks. Following adaptation, participants performed a single trial of their respective adaptation tasks without the prism lenses. An error in the opposite direction to the visual shift (i.e., a negative aftereffect) indicates internal model recalibration and storage of the new, prism-induced mapping (53), with larger aftereffects typically interpreted as greater learning. However, it is unclear what the postadaptation trial error represents after reexposure to a previously learned mapping. If we assume that it is still a means to quantify learning, does a reduction in error across exposures signify a reduction in learning? We do not believe this to be the case. Rather, we argue that a reduction in postadaptation error reflects a greater capacity to switch between learned mappings (i.e., prisms on vs. off). Anecdotally, this is aligned with the observation that, over time, people can adapt to wearing new prescription lenses and are soon able to switch between visuomotor mappings (i.e., glasses on and off) with little to no disruption to

performance. This notion is supported by research demonstrating people can learn, retain, and switch between different visuomotor mappings (54–57). Furthermore, a recent study demonstrated increased savings with smaller aftereffects after each repeated exposure to a learned split-belt treadmill-walking pattern (6). Given that only the balance-challenged groups demonstrate smaller aftereffects after relearning, we speculate that a greater value assigned to maintaining the new visuomotor mapping enhanced the ability to switch between mappings (indicative of greater savings) to ensure safe and successful task performance.

How do the effects of challenging balance on generalization compare to those observed for relearning? In our previous study (23), we found that challenging balance during adaptation increased generalization during reaching and walking, suggesting that the benefits are observed immediately and apply broadly to sensorimotor learning. However, here we show that challenging balance had little effect on motor memory during the reaching tasks, likely a result of the fact that savings did not occur to begin with. In contrast, we found that both walking groups demonstrated recall and savings of the prism-induced visuomotor mapping 1 wk later, with the balance-challenged group demonstrating increased savings. One possible explanation for the robust motor memories formed during our walking tasks may relate to the greater threat of falling associated with walking while wearing the prism lenses. Although both reaching and walking tasks require the participant to be accurate, the consequences of stepping inaccurately and possibly falling during walking are greater than simply missing the reaching target. The threat of falling is further increased with the addition of our balance manipulation, which reduces the control afforded by shifting the foot's center of pressure due to the much smaller base of support. Thus, the greater consequence of failure associated with the walking tasks may serve to reinforce the value placed on maintaining the learned visuomotor mapping and further contribute to the robust motor memory observed for this task.

In summary, we found that challenging balance enhanced savings during walking without penalizing performance during initial adaptation. We propose that challenging balance increases the value of a learned visuomotor mapping because of a greater need for control and/or greater perceived risk of falling. Because a greater-valued mapping may serve some future benefit, it is a more retainable mapping. Overall, our study demonstrates the significance of balance control during sensorimotor learning and the potential performance benefits associated with learning during unconstrained, naturalistic tasks.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

A.B., J.M.D., and D.S.M. conceived and designed research; A.B. performed experiments; A.B. analyzed data; A.B. and D.S.M. interpreted results of experiments; A.B. prepared figures; A.B. and D.S.M. drafted manuscript; A.B., J.M.D., and D.S.M. edited and revised manuscript; A.B., J.M.D., and D.S.M. approved final version of manuscript.

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