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RESEARCH ARTICLE | *Control of Movement*

Challenging balance during sensorimotor adaptation increases generalization

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Bakkum A, Donelan JM, Marigold DS. Challenging balance during sensorimotor adaptation increases generalization. *J Neurophysiol* 123: 1342–1354, 2020. First published March 4, 2020; doi: 10.1152/jn.00687.2019.—From reaching to walking, real-life experience suggests that people can generalize between motor behaviors. One possible explanation for this generalization is that real-life behaviors often challenge our balance. We propose that the exacerbated body motions associated with balance-challenged whole body movements increase the value to the nervous system of using a comprehensive internal model to control the task. Because it is less customized to a specific task, a more comprehensive model is also a more generalizable model. Here we tested the hypothesis that challenging balance during adaptation would increase generalization of a newly learned internal model. We encouraged participants to learn a new internal model using prism lenses that created a new visuomotor mapping. Four groups of participants adapted to prisms while performing either a standing-based reaching or precision walking task, with or without a manipulation that challenged balance. To assess generalization after the adaptation phase, participants performed a single trial of each of the other groups' tasks without prisms. We found that both the reaching and walking balance-challenged groups showed significantly greater generalization to the equivalent, non-adapted task than the balance-unchallenged groups. Additionally, we found some evidence that all groups generalized across tasks, for example, from walking to reaching and vice versa, regardless of balance manipulation. Overall, our results demonstrate that challenging balance increases the degree to which a newly learned internal model generalizes to untrained movements.

NEW & NOTEWORTHY Real-life experience indicates that people can generalize between motor behaviors. Here we show that challenging balance during the learning of a new internal model increases the degree of generalization to untrained movements for both reaching and walking tasks. These results suggest that the effects of challenging balance are not specific to the task but instead apply to motor learning more broadly.

adaptation; generalization; internal model; locomotion; reaching

INTRODUCTION

Humans are able to make an assortment of coordinated movements. This versatility is achieved to a large extent by adapting acquired motor skills to specific sensorimotor conditions or task demands. It is thought that our nervous system uses internal models of the body's dynamics to help estimate the body's state and to determine appropriate motor commands for a given task (Shadmehr et al. 2010; Wolpert et al. 2011), though model-free mechanisms may also be relevant (see, for example, Huang et al. 2011). The ability to transfer, or generalize, learned behaviors to novel contexts is critical for successful performance of everyday movements. This is also of practical importance after physical rehabilitation, as it enables patients to generalize what is learned in a clinical setting to the real world.

Research exploring generalization has focused predominantly on adaptation during isolated upper limb movements. The extent of generalization in these tasks varies widely, but it is often quite limited (Balitsky Thompson and Henriques 2010; Carroll et al. 2014; Ghahramani et al. 1996; Krakauer et al. 2000; Morton et al. 2001; Wang 2008; Wang and Sainburg 2004). There is evidence to suggest that practicing a broader range of movements during force field adaptation (Berniker et al. 2014) or sampling more of the visuomotor workspace during training (Krakauer et al. 2000) is advantageous for performance during generalization. However, the benefits of broad experience are not always apparent (Mattar and Ostry 2007, 2010). Interlimb generalization is also often asymmetric, with some studies reporting that adaptation with the nondominant arm generalizes to the dominant arm but not vice versa (Wang and Sainburg 2003, 2004) whereas others have found the opposite (Balitsky Thompson and Henriques 2010). These patterns can depend on the location of the workspace and handedness (Wang and Sainburg 2006a, 2006b).

Unlike many experimental paradigms, most everyday motor tasks make use of multiple body segments and limbs. For instance, both hands are typically used to open a jar, walking requires the coordination of both legs, and reaching to grasp a doorknob requires coordination of multiple upper limb joints as well as the trunk and legs. It seems reasonable that the nervous system requires a more comprehensive internal model to coordinate the entire body compared with the movements of a single finger or limb. We use the term "more comprehensive" to describe an internal model that represents more of the body's degrees of freedom, whether they arise from additional body segments, joints, muscles, neurons, or other aspects of the body's biomechanics and physiology. Without a more comprehensive model, the nervous system would not account for the dynamic coupling between body segments, where motion of one segment results in acceleration of another (Nott et al. 2010; Yu et al. 2011; Zajac 1993).

How might whole body movements, where a more comprehensive model is important, affect generalization? Although

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research addressing this question is limited, symmetric generalization between the two legs does occur when learning a leg tracking task while walking (Krishnan et al. 2017). In addition, we have shown that prism adaptation while walking and stepping on targets or over obstacles generalizes between the two tasks, albeit not completely (Alexander et al. 2013). Furthermore, the adaptation to split-belt treadmill walking generalizes to overground walking to some degree (Choi and Bastian 2007; Torres-Oviedo and Bastian 2012), though there is limited generalization of this adaptation between walking and running (Ogawa et al. 2012). Interestingly, Morton and Bastian (2004) showed that prism adaptation of walking generalized to standing-based reaching but not vice versa. Other research using different reaching and walking tasks, however, found the opposite (Michel et al. 2008): prism adaptation during reaching generalized to walking, but that during walking did not generalize to reaching. Taken together, these findings indicate that simply using more of the body during adaptation does not appear to maximize generalization, suggesting that other factors are involved.

Balance is fundamental to virtually all meaningful motor tasks. For instance, both reaching to grab a box of cereal from a shelf and walking across different terrain rely on appropriate foot placement and extensive muscle coordination to control the body. The seated, isolated upper limb tasks typically studied in the laboratory fail to account for the balance required in real-life movements and the possible role that balance plays in sensorimotor learning. Even in many laboratory-based walking paradigms (e.g., Roemmich and Bastian 2015), balance is not challenged to the same extent as in real-world environments. Challenges to balance increase the body's sensitivity to movement disturbances, including disturbances that arise from discrepancies between the nervous system's internal model of the body's dynamics and the body's actual dynamics. For instance, under stable conditions some unintended motion may be ignored and not represented in the nervous system's internal model of the body, since the effects of this motion are trivial. When balance is challenged, however, the same motion might destabilize the body to a greater extent and therefore needs to be modeled to prevent a fall. We argue that the necessity to control exacerbated body motions associated with balance-challenged, whole body movements increases the value to the nervous system of using an accurate and comprehensive internal model. A more comprehensive model is also a more generalizable model—it is less customized to a specific task. Therefore, we tested the hypothesis that challenging balance during adaptation enhances generalization.

To test our hypothesis, we had different groups of participants adapt to a novel visuomotor mapping induced by prism lenses while performing a standing-based reaching or walking task, with and without a manipulation that challenged balance. The prisms caused a mismatch between what the participants saw and how they moved, making their current internal model obsolete. The nervous system had to adapt its model to perform the task successfully. Previous work from our laboratory demonstrated model-based learning in prism adaptation during a precision walking task similar to that used in this study (Maeda et al. 2017a). We then probed generalization of this new model by having participants perform a different, nonadapted task/condition. As a primary test of our hypothesis, we probed generalization between balance-unchallenged and balance-challenged reaching and between balance-unchallenged and balance-challenged walking. Given the conflicting results of past research (Michel et al. 2008; Morton and Bastian 2004; Savin and Morton 2008), and as a secondary test of our hypothesis, we also probed generalization across the standing-based reaching and walking tasks.

MATERIALS AND METHODS

Participants. Forty-eight participants (mean ± SD age = 22.9 ± 3.7 yr; 25 men, 23 women; right limb dominant, as defined by the limb used to either kick or throw a ball) with no known musculoskeletal, neurological, or visual disease participated in this study. Four participants wore corrective lenses (glasses or contact lenses) during the experiments. The Office of Research Ethics at Simon Fraser University approved the study, and each participant provided written informed consent before participating.

Experimental tasks and data collection. We randomly assigned participants to one of four adaptation groups (n = 12 each). Each group learned a novel visuomotor mapping induced by prism lenses (Fig. 1*A*) while performing either a precision reaching or walking task. These tasks were performed while balance was challenged (balance challenged) or without an additional balance manipulation (balance unchallenged). This created the following groups: balance-unchallenged reaching, balance-challenged reaching, balance-unchallenged walking, and balance-challenged walking. We assessed how the balance manipulation affected *1*) the generalization of the learned visuomotor mapping across the different balance conditions for the same task (e.g., generalization from the balance-unchallenged to the balance-challenged walking task) and *2*) the generalizability of learning across different tasks (e.g., from balance-unchallenged reaching to balance-unchallenged walking). To assess generalization, participants performed a single trial of each of the other groups' tasks without prisms, as well as a non-limb-based, seated reaching task using head movements. Figure 1*C* illustrates the experimental tasks performed during the testing session.

For the standing-based reaching tasks, participants stood at ~90% of their arm's length away from a screen (279 × 218 cm) and reached to the medial-lateral (ML) center of a back-projected target (width: 1 cm; vertical length: 12 cm) with the index finger of their right hand (Fig. 1*B*). As we were primarily concerned with end-point error in the ML dimension, we used a longer target to reduce the accuracy demand in the vertical dimension. Participants wore comfortable walking shoes and performed this task while having their balance challenged or without any additional balance manipulation. For the balance-unchallenged condition, participants performed the task with their feet approximately shoulder width apart (Fig. 1*C1*). For the balance-challenged condition, participants performed the task with inflatable rubber hemispheres (radii: 8.5 cm) attached to the soles of their shoes to reduce the control afforded by shifting the center of pressure under the base of support (Fig. 1*C2*). We instructed participants to stand with their feet as close together as possible without the rubber hemispheres touching each other. Participants placed the index finger of their reaching hand on their chin before the start of each trial. An experimenter helped stabilize the participants before the start of each trial; thereafter, the participant performed the reach without any assistance. A safety harness system attached to the participants at all times prevented falling to the ground in the event of a loss of balance; however, no participant engaged the system during the course of the experiment.

For the precision walking tasks, participants walked and stepped with their right foot onto the ML center of a projected target (3 × 36 cm) without stopping (Fig. 1*B*). As we were primarily concerned with end-point error in the ML dimension, we used a longer target to reduce the accuracy demand in the anterior-posterior (AP) dimension and to prevent participants from using shuffle steps near the target area. Participants took a minimum of two steps before and after the

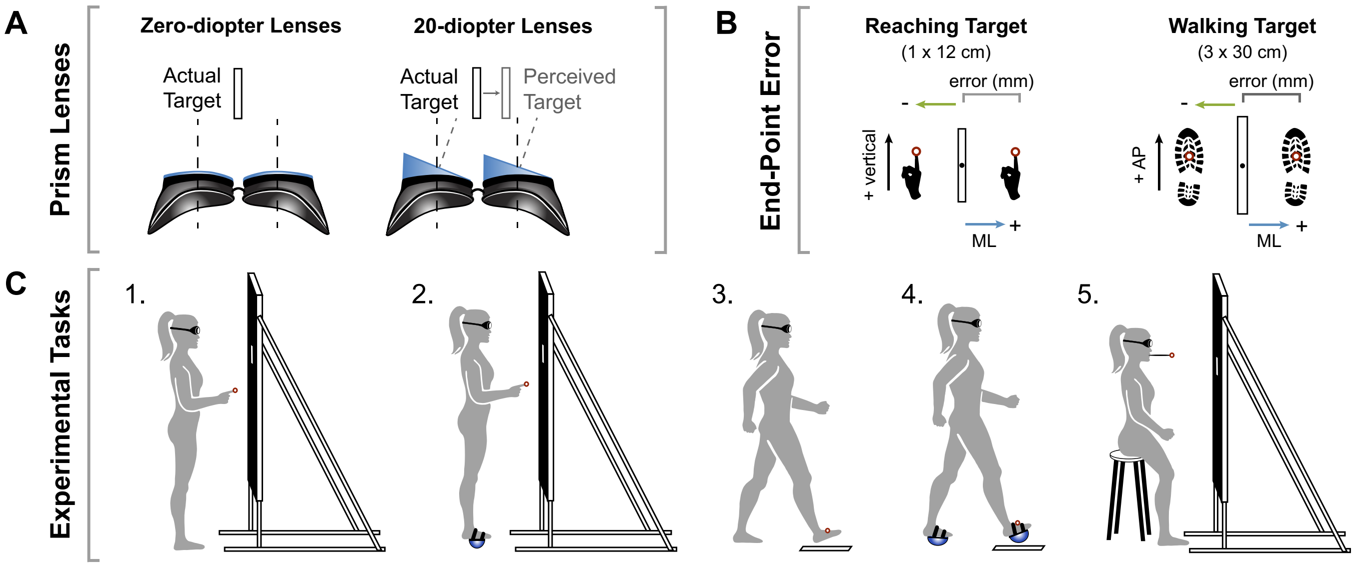

Fig. 1. Experimental tasks. *A*: a simulated view of the target through the goggles coupled with zero-diopter (non-visual field shifting) lenses and 20-diopter prism lenses that shift the perceived location of the target 11.4° to the right. *B*: an illustration showing positive (+) and negative (−) medial-lateral (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 each experimental task performed during the testing session. This includes balance-unchallenged reaching (*1*), balance-challenged reaching (*2*), balance-unchallenged walking (*3*), balance-challenged walking (*4*), and non-limb-based, seated reaching (*5*) tasks.

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. Participants performed this task while balance was challenged or without any additional balance manipulation. For the balance-unchallenged condition, participants performed the task while wearing normal walking shoes (Fig. 1*C3*). For the balance-challenged condition, participants performed the task with the same inflatable rubber hemispheres described above attached to the soles of their shoes (Fig. 1*C4*). An experimenter helped stabilize the participants before the start of each trial. Thereafter, the participant performed the task without assistance. We randomized the participant's AP starting location (between 1.5 and 2.5 m) in all trials to avoid learning of specific walking sequences or timing and to increase the demand for visual feedback during the task.

For the reaching tasks, an LCD projector (Epson EX7200) back-projected the target onto a screen (279 × 218 cm). We aligned the top of the target to the participant's chin. For the walking tasks, a different LCD projector (Epson PowerLight 5535U; brightness of 5,500 lm) displayed the target on a black uniform mat covering the walking path (~6 m long). We configured the target's size and position in MATLAB (The MathWorks, Natick, MA) with the Psychophysics Toolbox, version 3 (Brainard 1997; Kleiner et al. 2007). To diminish the effect of environmental references and increase target visibility, participants performed the tasks under reduced light conditions (~0.9 lx).

We also designed a non-limb-based, seated reaching task to serve as a universal comparison for generalization across adaptation groups. For this task, participants sat on a backless stool at ~90% of their arm's length away from a screen (279 × 218 cm) and reached with their head to the ML center of a back-projected target (1 × 12 cm), using a pointing instrument (tongue depressor, 1.75 × 15.24 cm) placed in their mouth (Fig. 1*C5*). We aligned the top of the target to the participant's chin. The participants used head movements to reach to targets, while in a seated position, to reduce favoring of the limbs involved in either reaching or walking task and to minimize the need to control whole body balance.

For all tasks, we instructed participants to be as accurate as possible when reaching, stepping, or head-pointing to the target. We also instructed participants to perform the tasks at a quick and constant pace. These guidelines minimized online corrections of the finger or leg/foot trajectory to more closely match previous experiments in which the movements are ballistic and emphasize the use of sensory feedback before movement. Participants received visual feedback through the lenses during each task; however, we instructed the participants to have their eyes open only when they were performing the task, to prevent adaptation between trials. To begin a trial, participants opened their eyes once cued by an audible tone and immediately started moving to the target. An experimenter demonstrated each task before the testing.

An Optotrak Certus motion capture camera (Northern Digital, Waterloo, ON, Canada), positioned perpendicular to the walkway, recorded (at 120 Hz) infrared-emitting position markers placed on the participant's midback (in line with the sternum) and index finger of the right hand and bilaterally on the heel, midfoot (second to third metatarsal head), and toe (third metatarsal). Additionally, we attached a position marker to the end of the tongue depressor used during the non-limb-based, seated reaching task. An electromyography (EMG) system (MA300; Motion Laboratory Systems, Baton Rouge, LA), synchronized via the Optotrak data acquisition unit, recorded leg muscle activity at a sampling frequency of 2,040 Hz. Before electrode placement, we cleaned the skin locations with alcohol. We recorded surface EMG from electrodes placed bilaterally over the belly of the tibialis anterior, medial gastrocnemius, vastus lateralis, and biceps femoris muscles.

Experimental protocol. All participants performed baseline, adaptation, generalization, readaptation, and postadaptation phases. During each phase, participants wore goggles coupled with either 20-diopter prism lenses or zero-diopter (non-visual field shifting) lenses (Fig. 2*A*). The 20-diopter prism lenses displaced the perceived location of the target ~11.4° to the right (Fig. 1*A*). This altered the relationship between visual inputs and motor commands and caused errors in the goal-directed limb movements. The goggles blocked a portion of the peripheral visual field, such that the participants had to look through the lenses during the tasks. Figure 2 illustrates an example of the experimental protocol and the predicted end-point error responses for each phase of testing.

Participants performed 20 baseline trials for their respective adaptation tasks as well as 20 baseline trials for each generalization task (100 trials in total) while wearing zero-diopter lenses. Participants performed the baseline trials for the adaptation task last, before the

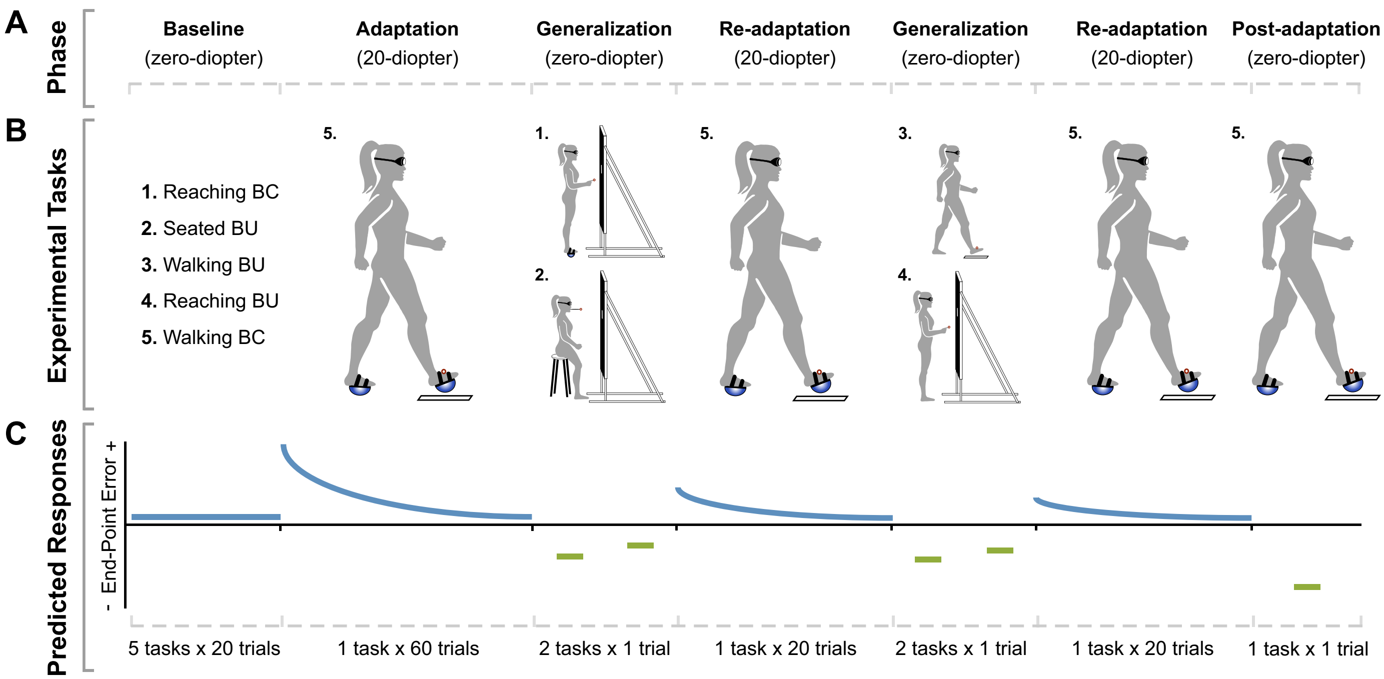

Fig. 2. Experimental protocol. *A*: all participants performed baseline, adaptation, generalization, readaptation, and postadaptation phases. Depending on the phase, participants wore goggles paired with either zero-diopter or 20-diopter lenses. *B*: an example using the balance-challenged walking group of the experimental tasks performed throughout the testing session. Participants performed a total of 5 precision reaching and walking tasks while balance was challenged (balance challenged, BC) or without an additional balance manipulation (balance unchallenged, BU). Participants performed the baseline trials for the adaptation task last, before the adaptation phase. We randomized the order of the remaining baseline conditions and matched this order for the generalization tasks interspersed within the adaptation phase. *C*: an illustration of the predicted end-point error profiles for each phase of testing. See text for details.

adaptation phase. We randomized the order of the remaining baseline conditions and matched this order for the generalization tasks interspersed within the adaptation phase. During the adaptation phase, participants learned the novel visuomotor mapping induced by the 20-diopter prism lenses while performing 60 trials of their assigned adaptation task.

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 groups' adaptation tasks, as well as a non-limb-based, seated reaching task using head movements. For example, the balance-challenged walking group performed the balance-unchallenged walking task, both the balance-challenged and -unchallenged reaching tasks, and the non-limb-based, seated reaching task (see Fig. 2*B*). Participants performed the generalization tasks with the zero-diopter lenses to determine whether the learned mapping was applied to the different, nonadapted task. To mitigate any deadaptation 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 one 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).

Data and statistical analysis. We analyzed data with custom-written MATLAB programs. We used kinematic data (filtered with a 4th-order, 6-Hz low-pass Butterworth algorithm) to calculate movement speed, velocity, and acceleration profiles of the position markers and to determine the end-point position of the finger, foot, and pointing instrument (Maeda et al. 2017b). We used EMG data (full-wave rectified and low-pass filtered at 50 Hz with a 4th-order Butterworth algorithm) to calculate muscle activity during the reaching and walking tasks.

We calculated reaching time and gait speed using the position markers placed on the index finger and the midback infrared marker, respectively. We determined finger and pointing instrument placement on each reaching target as the time at which 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 with the vertical velocity of the midfoot marker on the right foot (Maeda et al. 2017b). The ML distance between the respective position markers and the center of the target at these time points defined the ML end-point error and served to quantify adaptation and generalization. A positive value represents errors in the direction of the prism shift (right), and a negative value represents errors in the direction opposite to the prism shift (Fig. 1*B*).

When balance is challenged, we expect to see greater trunk motion, variability in performance, and increased muscle activity. Therefore, to test whether balance was indeed more challenged in the balance-challenged conditions, we calculated measures of trunk motion (reflected by trunk acceleration root mean square, RMS), performance variability (reflected by end-point error variability), and motor cost (reflected by muscle activity) during the last 10 baseline trials for the standing-based reaching and walking tasks. We quantified trunk motion as the mean AP and ML acceleration RMS of the marker on the midback (in line with the sternum) during specific time intervals, depending on the task. Specifically, for the reaching tasks, we calculated trunk motion during the reach to the target, defined as the period between when the AP velocity of the finger or pointing instrument marker exceeded five standard deviations of the mean (calculated over the first 0.4 s, or 50 frames of motion capture data, before reach initiation) and then stabilized back to zero. For the walking tasks, we calculated trunk motion during one full step cycle, defined as the period from heel strike of the nondominant leg before the target to heel strike of the nondominant leg after the target. We quantified performance variability as the standard deviation of the ML end-point error of the relevant position markers for each task. Finally, we calculated a metric for total muscle activation (TMA) for each task to quantify motor cost (Domínguez-Zamora and Marigold 2019). We reasoned that decreased stability due to the balance challenge requires greater leg muscle activation to control the whole body. We separated the EMG data into the reaching and stepping time intervals mentioned above. We first calculated the muscle activation (MA) for each individual muscle:

$$\mathrm{MA} = \left(\frac{\mathrm{EMG}_{\mathrm{Area}}}{\mathrm{EMG}_{\mathrm{AreaSRT}}}\right) \tag{1}$$

where $\mathrm{EMG}_{\mathrm{Area}}$ is the area under the muscle profile during each time interval and $\mathrm{EMG}_{\mathrm{AreaSRT}}$ is the area under the ensemble-averaged profile, calculated by the trapezoid method, of the non-limb-based, seated reaching task. We reasoned that the seated reaching task would elicit the least amount of lower limb muscle activity and serve as a suitable (common) baseline to compare motor cost across standing-based reaching and walking tasks. To account for differences in muscle volume, we used normalized volume fraction values (see Supplementary Table 1 in Handsfield et al. 2014) to calculate a common weighting factor for each muscle (i) for all participants, such that the sum of the weight factors equated to 1:

$$\text{weight factor}_i' = \frac{\text{muscle volume}_i}{\sum_{i=1}^{8} \text{muscle volume}_i} \tag{2}$$

Finally, we calculated the TMA, using a weighted arithmetic mean:

$$\mathrm{TMA} = \sum_{i=1}^{8} \text{weight factor}_i' \times \mathrm{MA}_i \tag{3}$$

where i is each muscle that is analyzed. We used this method to account for differences in muscle volume and their relative contribution to muscle activity, where high-volume muscles contribute more than low-volume muscles. To determine differences in trunk motion, performance variability, and motor cost, we used separate two-sample t tests to determine the differences in balance measures for the reaching and walking groups.

To determine whether the learned visuomotor mapping generalized to the nonadapted tasks, we performed separate one-tailed, paired t tests to compare the mean end-point error of the last 10 baseline trials of the task to the end-point error of the generalization trial for each nonadapted task. We used a one-tailed test since errors in the direction opposite to the learned prism shift (i.e., a negative aftereffect) indicate generalization. To quantify the magnitude of generalization, we calculated a generalization index:

$$\text{generalization index} = \frac{(G_{i1} - B_{l1})}{(P_{i2} - B_{l2})} \times 100 \tag{4}$$

where i is the initial trial of the particular phase; l is the mean of the last 10 trials of the particular phase; B, G, and P refer to the baseline, generalization, and postadaptation phases; 1 is the task for which transfer is being tested; and 2 is the adaptation task (Savin and Morton 2008). This measure calculates the percentage of learning (normalized by baseline performance) that is transferred to the nonadapted tasks, where 100% represents complete generalization. We used separate independent (2 tailed) t tests to compare the magnitude of generalization between the different balance conditions for the reaching and walking tasks.

We used JMP 14 software (SAS Institute Inc., Cary, NC) with an α level of 0.05 for all statistical analyses. For ANOVAs, we used Tukey's post hoc tests when we found significant main effects of task.

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 assessed how challenging balance during the standing-based reaching and walking tasks affected the generalization of learned sensorimotor mappings across different balance conditions for the same task (e.g., generalization from the balance-unchallenged to the balance-challenged walking task and vice versa). We also tested the generalizability of learning across different tasks (e.g., from balance-unchallenged reaching to balance-unchallenged walking).

Our manipulation successfully challenges balance. To confirm that maintaining balance is more challenging in the balance-challenged conditions, we calculated measures of trunk motion, task performance variability, and motor cost during the last 10 trials of the baseline phases for the standing-based reaching and walking tasks. The results are illustrated in Fig. 3. Separate two-sample t tests showed that the balance-challenged conditions had significantly greater trunk motion in the AP (reaching: $t_{46} = 3.8$, $P = 0.0003$; walking: $t_{46} = 5.3$, $P =$ 3.429e-6) and ML (reaching: $t_{46} = 2.3$, $P = 0.028$; walking: $t_{46} = 5.1$, $P =$ 5.727e-6) dimensions. Similarly, we found significantly greater performance variability (reaching: $t_{46} = 2.8$, $P = 0.007$; walking: $t_{46} = 5.1$, $P =$ 7.399e-6) in the balance-challenged conditions. Finally, the balance-challenged groups showed increased motor cost compared with the balance-unchallenged groups for both tasks (reaching: $t_{46} = 5.8$, $P =$ 5.612e-7; walking: $t_{46} = 3.2$, $P = 0.003$). This is also evident in Figs. 4 and 5. Thus the rubber hemispheres worn under the feet successfully challenged balance during both standing and walking.

Challenging balance does not impair the ability to adapt to the prisms. Participants in all groups performed each task without making online corrections. We verified the absence of sudden changes in marker trajectory by analyzing the displacement and velocity profiles of the markers placed on the finger, midfoot, and pointing instrument (Maeda et al. 2017b). For the standing-based reaching tasks, 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) groups. Similarly, we did not detect a significant difference in average gait speed between walking groups during adaptation (balance unchallenged: 1.33 ± 0.13 m/s; balance challenged: 1.22 ± 0.19 m/s; $t_{22} = 1.6$, $P = 0.133$). Furthermore, we found no significant differences in reaching times ($F_{3,44} = 0.02$, $P =$ 0.996) and gait speeds ($F_{3,44} = 0.8$, $P = 0.155$) between baseline and adaptation phases or balance condition.

Figure 4 illustrates the finger trajectory as well as leg muscle activity during a late baseline trial and the first adaptation phase trial during the standing-based reaching task. Representative participants from the reaching balance-unchallenged and reaching balance-challenged groups are shown. Figure 5 illustrates the foot trajectory as well as leg muscle activity during a late baseline trial and the first adaptation phase trial during the precision walking task. Representative participants from the walking balance-unchallenged and walking balance-challenged groups are shown.

Upon initial exposure to the 20-diopter (rightward shifting) prism lenses, participants showed a large, rightward deviation in limb placement to the target for the reaching (balance unchallenged: 53.5 ± 18.2 mm, balance challenged: 49.9 ± 18.1 mm) and walking (balance unchallenged: 283.6 ± 36.2 mm, balance challenged: 263.5 ± 44.6 mm) tasks. The end-point error gradually returned to near-baseline levels as the participants adapted to the prisms. We found no significant differences in the mean end-point error of the last five trials between

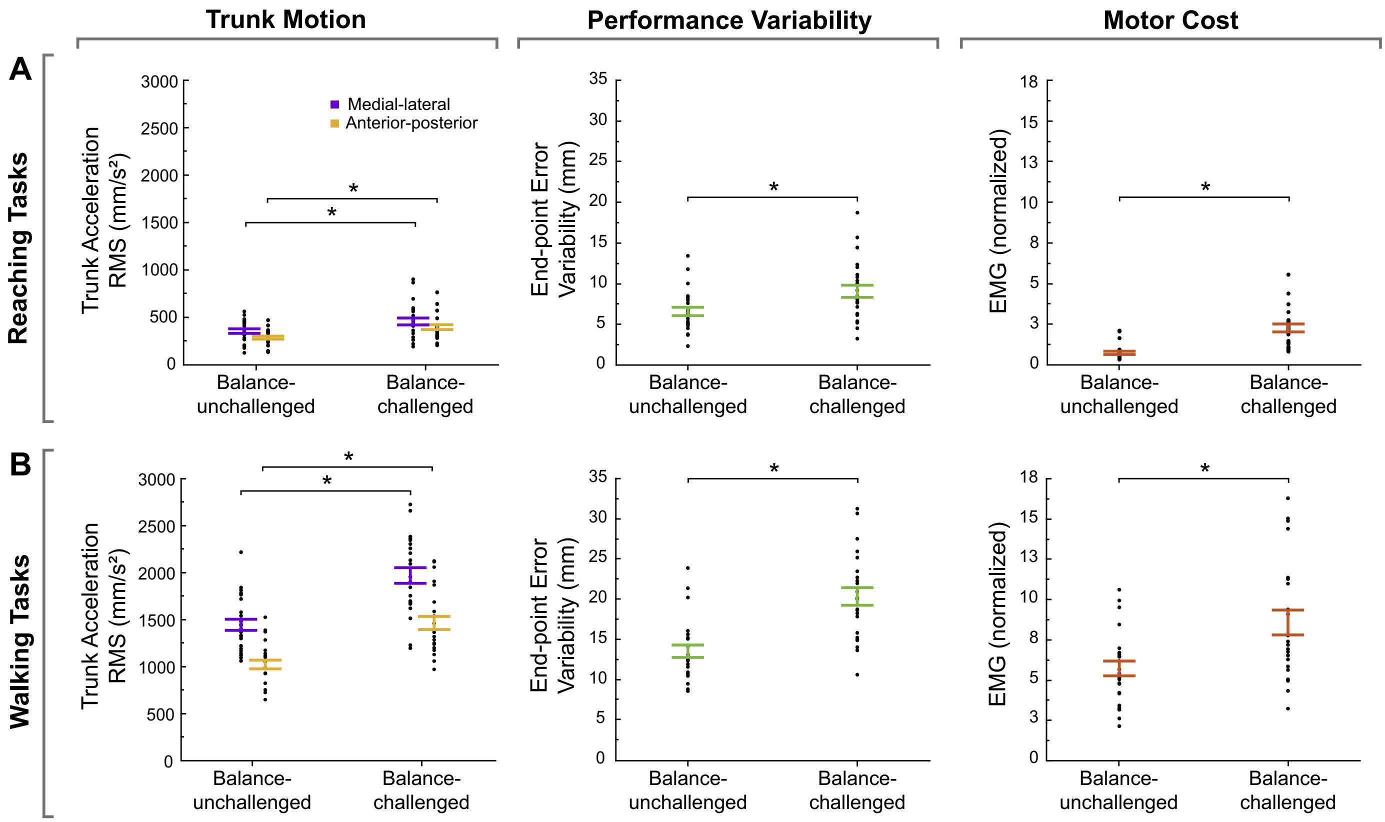

Fig. 3. Balance measures. The effects of our balance manipulation on trunk motion (reflected by trunk acceleration root mean square, RMS), performance variability (reflected by limb end-point error variability), and motor cost (reflected by muscle activity) during the last 10 baseline trials for the standing-based reaching tasks (*A*) and walking tasks (*B*). Data are represented as means ± SE. *Values significantly different from each other ($P < 0.05$).

each adaptation phase for the reaching (balance unchallenged: $F_{2,33} = 0.07$, $P = 0.935$, balance challenged: $F_{2,33} = 0.4$, $P = 0.682$) and walking (balance unchallenged: $F_{2,33} = 0.2$, $P = 0.795$, balance challenged: $F_{2,33} = 0.03$, $P = 0.968$) groups. After the adaptation phases, removal of the prism lenses resulted in a large end-point error to the left of the target (i.e., a negative aftereffect). Finally, we did not detect significant differences in the end-point error for the postadaptation trials between balance conditions for the reaching ($t_{22} = 0.4$, $P = 0.725$) or walking ($t_{22} = 0.3$, $P = 0.779$) task. Taken together, these findings show that our balance manipulation did not impair adaptation to the novel, prism-induced visuomotor mapping.

Challenging balance increases within-task generalization. To determine whether the learned visuomotor mappings generalized within the same reaching task (e.g., from reaching balance-unchallenged to reaching balance-challenged), participants performed a single trial of the nonadapted reaching task with the zero-diopter lenses after adaptation. To assess generalization, we compared the mean end-point error of the last 10 baseline trials to the end-point error of the generalization trial for the nonadapted task. Errors in the direction opposite to the learned prism shift (i.e., a negative value) indicate generalization. We found that the balance-unchallenged reaching group generalized to the (nonadapted) balance-challenged reaching task ($t_{11} = 5.4$, $P = 0.0001$) and the balance-challenged reaching group ($t_{11} = 7.8$, $P = 4.19e{-}6$) generalized to the (nonadapted) balance-unchallenged reaching task (Fig. 6*A*). To assess the effect of challenging balance on generalization, we compared the magnitude of generalization across balance conditions for each reaching task using our generalization index. This measure calculates the percentage of learning that is generalized to the nonadapted tasks, where 100% represents complete generalization. We found that whereas the balance-unchallenged group generalized ~47% to the balance-challenged task, the balance-challenged group generalized ~83% to the balance-unchallenged task. According to the generalization index, the balance-challenged reaching group showed significantly greater percent generalization ($t_{22} = 3.9$, $P = 0.0008$) compared with the balance-unchallenged reaching group (Fig. 6*B*).

The above pattern of generalization also held true for walking, in that both the balance-unchallenged group ($t_{11} = 3.1$, $P = 0.005$) and the balance-challenged group ($t_{11} = 7.9$, $P = 3.52e{-}6$) generalized to the nonadapted walking task (Fig. 7*A*). According to the generalization index, the balance-unchallenged group generalized ~54% to the balance-challenged task, whereas the balance-challenged group generalized ~102% to the balance-unchallenged task. Similar to the reaching groups, the balance-challenged walking group showed significantly greater percent generalization ($t_{22} = 2.6$, $P = 0.018$) (Fig. 7*B*). Thus challenging balance enhanced generalization for both the reaching and walking groups.

The effects of challenging balance on across-task generalization. As a secondary test of our hypothesis, we tested whether learning also generalizes across tasks (e.g., from balance-unchallenged reaching to balance-unchallenged walking). To answer this question, for each of our four groups we

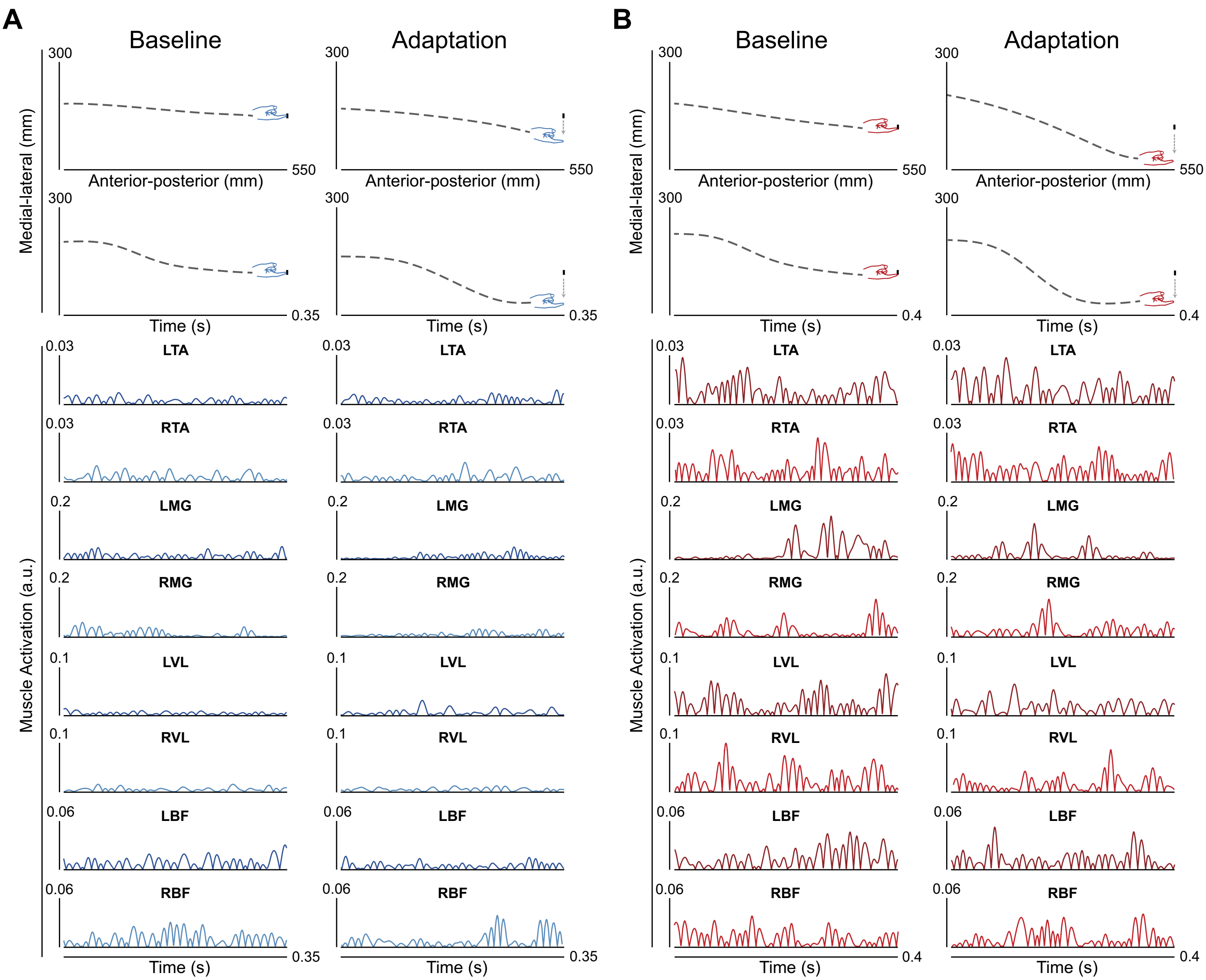

Fig. 4. Participant behavior during reaching. An illustration of finger trajectory (dashed line) and end-point placement relative to the target (black rectangle) as well as leg muscle activity during a late baseline trial and the first adaptation trial for the standing-based reaching tasks. Representative participant data from the balance-unchallenged (*A*) and balance-challenged (*B*) reaching groups are shown. Dashed arrows indicate medial-lateral end-point error during the adaptation trials. Bilateral muscle activity was recorded from the tibialis anterior (TA), medial gastrocnemius (MG), vastus lateralis (VL), and biceps femoris (BF) muscles, where L and R denote the left and right leg, respectively. a.u., Arbitrary units.

compared end-point error between the baseline and generalization phases of their nonadapted tasks. The results are summarized in Table 1 and illustrated in Fig. 8. First, we determined whether this was the case for the balance-unchallenged reaching group. Interestingly, this group was the only one to show significant generalization to the non-limb-based, seated reaching task (t_{11} = 3.2, P = 0.004). However, the balance-unchallenged reaching group did not generalize to the balance-unchallenged (t_{11} = −0.4, P = 0.638) or balance-challenged (t_{11} = −0.3, P = 0.632) walking task. Second, we determined whether the balance-challenged reaching group generalized across tasks. Although this group generalized to the balance-unchallenged walking task (t_{11} = 3.7, P = 0.002), it did not show significant generalization to the seated reaching (t_{11} = 0.5, P = 0.302) or balance-challenged walking (t_{11} = 0.7, P = 0.254) task. Third, we determined whether the balance-unchallenged walking group generalized across tasks. This group generalized to the balance-challenged reaching task (t_{11} = 2.3; P = 0.020) but not to the seated (t_{11} = 1.7, P = 0.063) or balance-unchallenged (t_{11} = −0.2, P = 0.575) reaching task. Finally, we determined whether the balance-challenged walking group generalized across tasks. This group generalized to the balance-challenged reaching task (t_{11} = 2.4, P = 0.018). However, we found no significant generalization to the seated reaching task (t_{11} = 1.6, P = 0.072) or the balance-unchallenged reaching task (t_{11} = −1.1, P = 0.846). In summary, there is mixed evidence that suggests challenging balance increased generalization across the reaching and walking tasks.

DISCUSSION

The ability to generalize movement to novel contexts is an important component of learning and contributes to an array of

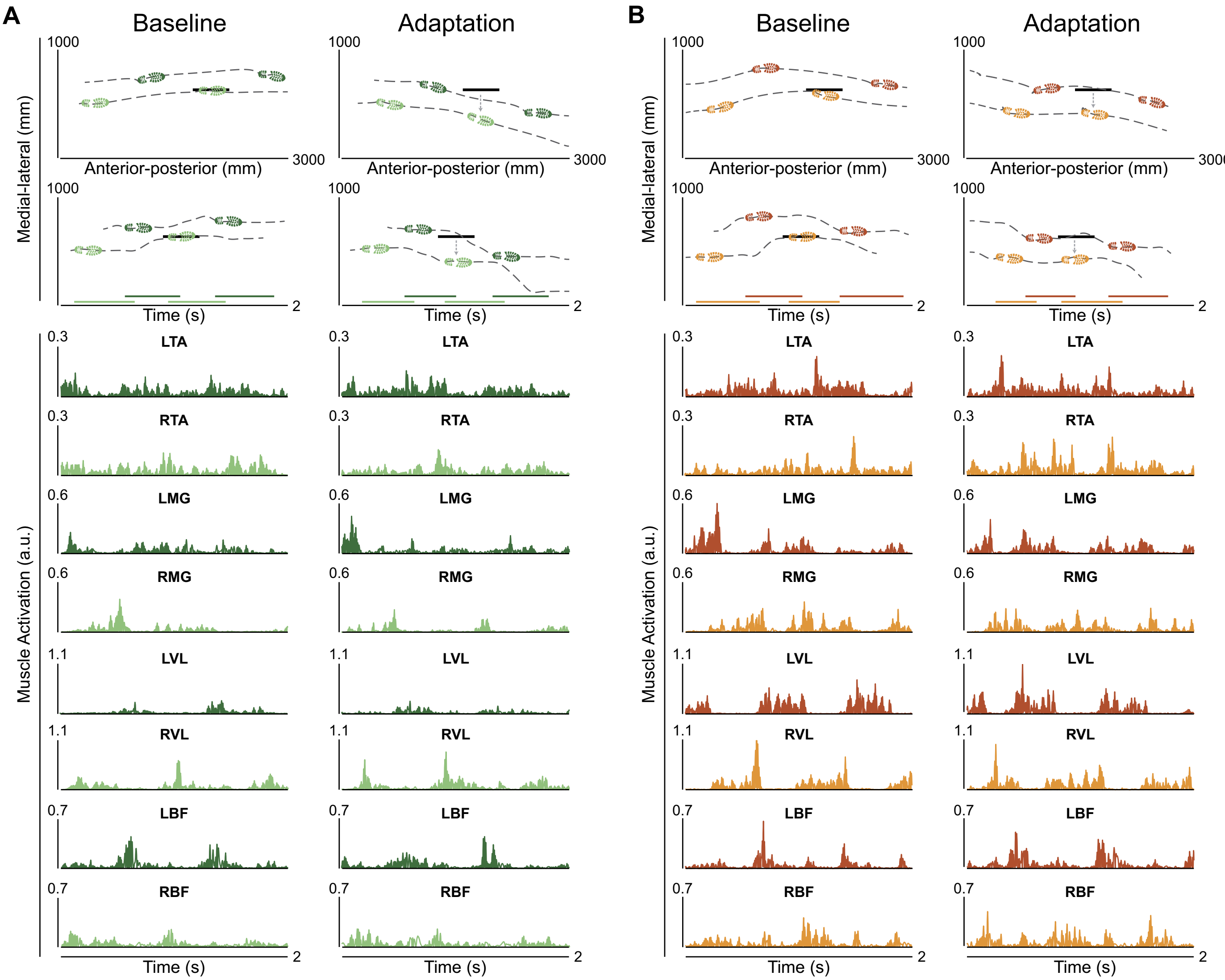

Fig. 5. Participant behavior during walking. An illustration of foot trajectories (dashed lines) and foot placement relative to the target (black bar), as well as leg muscle activity during a late baseline trial and the first adaptation trial for the precision walking tasks. Representative participant data from the balance-unchallenged (*A*) and balance-challenged (B) walking groups are shown. Data are presented over 2 strides (2 steps before the step to the target and 1 step after the target) and depict the moment of heel strike (denoted by the shoeprints) and stance phase for each leg (horizontal lines). Dashed arrows indicate the medial-lateral foot-placement error during the adaptation trials. Bilateral muscle activity was recorded from the tibialis anterior (TA), medial gastrocnemius (MG), vastus lateralis (VL), and biceps femoris (BF) muscles, where L and R denote the left and right leg, respectively. a.u., Arbitrary units.

skilled everyday motor behaviors. Here we tested the hypothesis that challenging balance during adaptation would increase generalization. We found that challenging balance resulted in greater generalization for both the reaching and walking tasks. These results suggest that the effects of challenging balance are not specific to the task but instead apply to motor learning more broadly. Thus it appears that challenging balance leads to a more generalizable model. Although we demonstrate strong evidence for this concept, the explanation for these findings is less clear. We discuss possible reasons below.

Challenging balance may increase the value assigned to the learned internal model. Challenging balance doubled the amount of generalization for both the reaching and walking tasks. One hypothesis for this enhanced generalization is that learning under balance-challenged conditions increases the value (or importance) assigned to the updated internal model. This change in assignment may result from the necessity to control exacerbated motion of the body induced by the rubber hemispheres to maintain balance or may occur because of the perceived threat of falling and causing injury.

When balance is challenged, the effects that the motion of one body segment or limb has on the motion of another become more pronounced because of the interconnected nature of our musculoskeletal system. Consequently, the nervous system requires better control over the body to maintain an upright position and to ensure successful task performance. This may increase the computational demand on the sensorimotor system as well as the mechanical and metabolic demand on the musculoskeletal system. Ultimately, decisions about movement control involve weighing the benefits of potential rewards (or penalties) associated with the task against the effort required to act (Gallivan et al. 2018). These decisions require an estimate of the value associated with allocating control to a given task (i.e., the expected value of control) to determine if

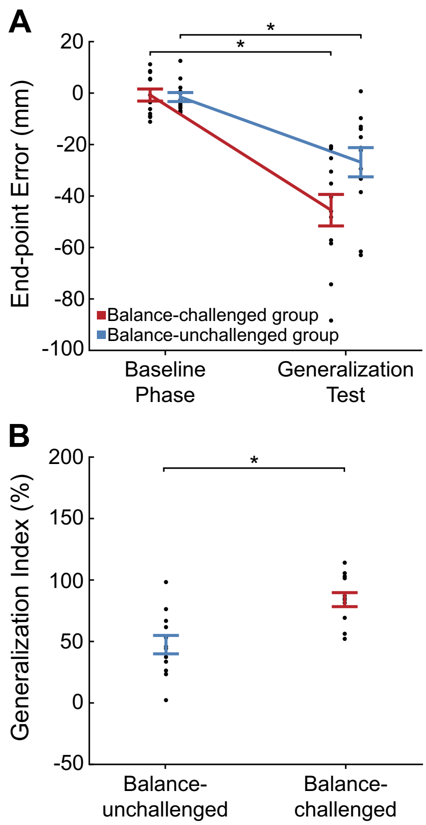

Fig. 6. Generalization within reaching tasks. *A*: the effects of challenging balance on generalization to the nonadapted reaching task. Here we compared the mean end-point error of the last 10 baseline trials to the end-point error of the generalization trial for the nonadapted task. The balance-unchallenged reaching group generalized to the nonadapted, balance-challenged reaching task. Similarly, the balance-challenged reaching group generalized to the nonadapted, balance-unchallenged reaching task. *B*: the magnitude of generalization for the 2 reaching groups, calculated with the generalization index. Data are represented as means ± SE. *Values significantly different from each other ($P < 0.05$).

it is worth pursuing (Rangel et al. 2008; Shenhav et al. 2013). The goal of our tasks was to hit a target with either the finger or the foot. In each case, the inability to minimize unwanted motion of the body would jeopardize the likelihood of success. Thus there is increased value in controlling balance.

Although we did not directly measure fear or anxiety, the increased risk of falling and injury during the balance-challenged tasks may have altered these emotions and thus also contributed to the generalization patterns observed for these groups. Perceived threat and fear of falling can significantly affect balance and gait (Adkin et al. 2002; Adkin and Carpenter 2018). There is also evidence suggesting that colliding with an obstacle during prism adaptation may facilitate subsequent generalization (Alexander et al. 2013). Similarly, Green et al. (2010) argue that arousal level, which reflects perceived risk and task difficulty, affects locomotor aftereffects experienced during walking on a stationary sled that was previously moving (also known as the "broken escalator phenomenon"). These studies suggest that perceived threat can modulate generalization.

In the present study, the perceived threat associated with the risk of falling during the balance-challenged tasks may have modified the value assigned to the model and altered the strategy used during generalization. From a safety perspective, it is more important to get the right strategy when balance is challenged than it is to get the wrong strategy when balance is not challenged. Thus it is better to broadly generalize the learned balance-challenged strategy and not take the risk of selecting the wrong strategy. This is, to some extent, related to statistical decision theory in that our participants might have chosen to adopt a more conservative "just in case" approach to minimize the probability of being penalized for selecting the incorrect strategy (Trommershäuser et al. 2003). In these circumstances, participants are able to leverage their knowledge about a perturbation to consciously modify their motor performance. This notion is supported by recent research demonstrating that generalization is maximized around the intended location of an explicitly accessible motor plan (Day et al. 2016; McDougle et al. 2017). Furthermore, there is evidence to suggest that explicit components of learning generalize broadly across the workspace (Heuer and Hegele 2008, 2011).

Another possible contributing factor for the enhanced within-task generalization observed in our balance-challenged groups is that our balance manipulation might alter the assignment of errors experienced during adaptation. Previous research shows that solving the credit assignment problem is essential for sensorimotor recalibration and that changes in the assignment of errors can modulate generalization (Berniker and Kording

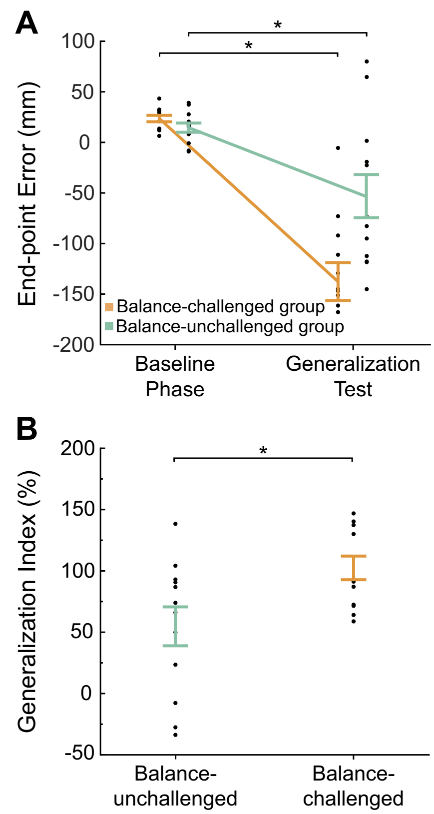

Fig. 7. Generalization within walking tasks. *A*: the effects of challenging balance on generalization to the nonadapted walking task. Here we compared the mean end-point error of the last 10 baseline trials to the end-point error of the generalization trial for the nonadapted task. The balance-unchallenged walking group generalized to the nonadapted, balance-challenged walking task. Similarly, the balance-challenged walking group generalized to the nonadapted, balance-unchallenged walking task. *B*: the magnitude of generalization for the 2 walking groups, calculated with the generalization index. Data are represented as means ± SE. *Values significantly different from each other ($P < 0.05$).

Table 1. *Across-task generalization*

Generalization Task	Balance Unchallenged Baseline, mm	Balance Unchallenged Generalization, mm	Balance Unchallenged GI, %	Balance Unchallenged P	Balance Challenged Baseline, mm	Balance Challenged Generalization, mm	Balance Challenged GI, %	Balance Challenged P
Reaching groups								
Seated, nonlimb reaching	13.6 ± 1.6	4.5 ± 2.5	17.9 ± 7.1	**0.004**	5.9 ± 2.9	4.0 ± 3.0	6.1 ± 9.4	0.302
Balance-unchallenged walking	11.6 ± 2.4	13.9 ± 6.9	−8.3 ± 15.5	0.638	8.1 ± 4.8	−4.9 ± 7.2	24.4 ± 7.6	**0.002**
Balance-challenged walking	15.5 ± 4.2	17.0 ± 6.9	−10.9 ± 15.4	0.632	6.2 ± 5.9	2.1 ± 4.9	10.4 ± 10.3	0.254
Walking groups								
Seated, nonlimb reaching	10.6 ± 1.8	3.0 ± 4.6	3.4 ± 2.6	0.063	12.6 ± 1.5	8.2 ± 2.8	5.4 ± 1.7	0.072
Balance-unchallenged reaching	−4.1 ± 1.6	−3.4 ± 3.4	−0.2 ± 3.2	0.575	−2.8 ± 2.2	−0.3 ± 3.7	−4.2 ± 3.6	0.846
Balance-challenged reaching	−4.8 ± 1.2	−14.8 ± 5.1	8.7 ± 4.2	**0.020**	−3.9 ± 1.8	−12.7 ± 4.1	8.9 ± 3.5	**0.018**

Bold text denotes significant generalization ($P < 0.05$). GI, generalization index; P, P value.

2008; Fercho and Baugh 2014; Kluzik et al. 2008; Torres-Oviedo and Bastian 2012; Wilke et al. 2013). For example, previous research has concluded that errors within the natural range of movement variability are typically assigned to the person (i.e., produced by the body) and generalize beyond training, whereas unusual or abrupt errors are frequently attributed to an external source (i.e., produced by the environment) and are largely context dependent (Torres-Oviedo and Bastian 2012). By this logic, however, our balance-challenged groups should have demonstrated less generalization because they experience exaggerated movements during adaptation that should, in theory, be attributed to an external source (i.e., the rubber hemispheres). In contrast, we demonstrate that our balance-challenged groups exhibit significantly greater generalization compared with their balance-unchallenged counterparts. One possible explanation for our seemingly contradictory findings may relate to the nature of our balance manipulation. During our balance-challenged tasks, the direction and magnitude of the perturbation may be directly associated with the participant's own movement, since the rubber hemispheres are attached to their feet. As a result, this manipulation may shift the assignment of errors experienced during adaptation from the environment to the person, and they may attribute performance errors to their inability to produce accurate movements. Coupled with the increased necessity for greater control, this potential change in credit assignment toward errors in motor execution may favor context-independent adaptation and strengthen generalization across motor behaviors.

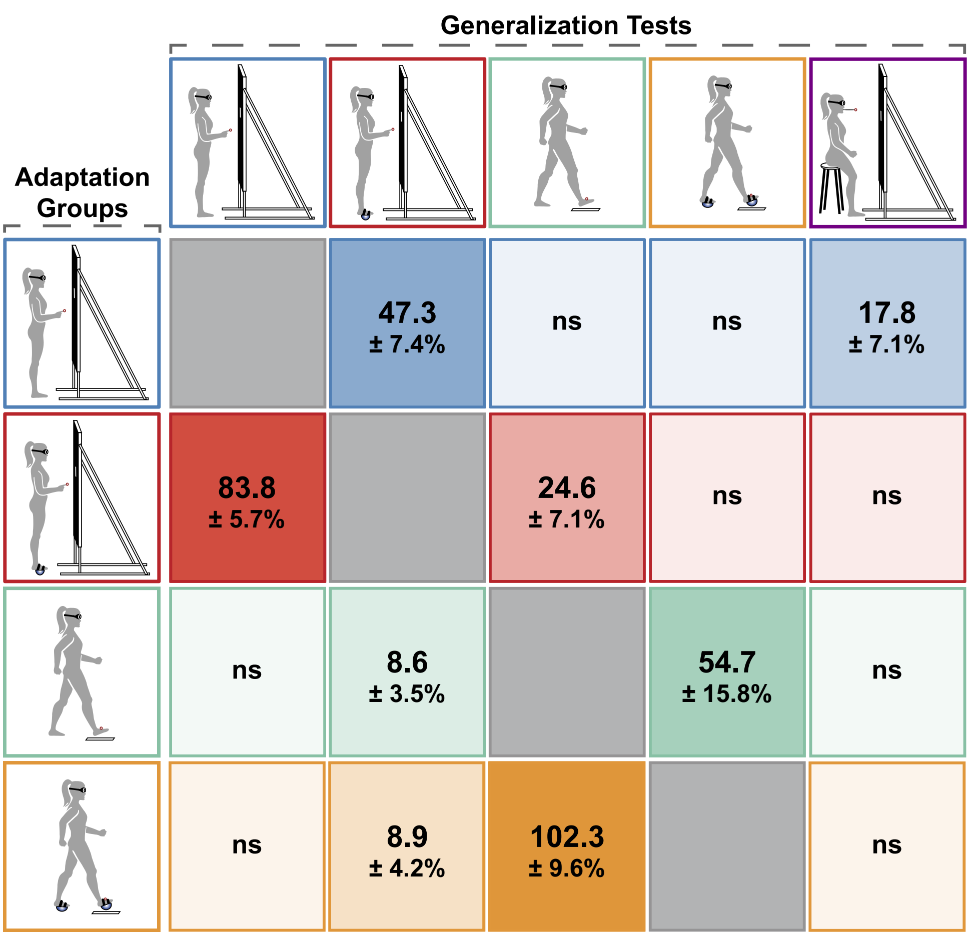

Fig. 8. Generalization summary. A summary diagram of the significant within- and across-task generalization. The % values represent the magnitude of generalization, calculated with the generalization index (means ± SD). ns, Nonsignificant.

Prisms induce a visuo-proprioceptive mismatch, and as such adaptation entails some combination of remapping these sensory signals with motor signals responsible for reestablishing movement accuracy (Hay and Pick 1966; Petitet et al. 2018; Redding and Wallace 1988). What role, if any, does sensory information play in the improved generalization of our balance-challenged groups? Although we did not design our experiment to address this question, we can still speculate as to a possible answer. Our balance manipulation led to greater upper body motion and limb movement variability relative to the balance-unchallenged condition. Increased upper body motion would result in greater optic flow as well as greater activation in vestibular organs. The exaggerated body motion, in conjunction with the increased limb movement variability, would also alter proprioceptive feedback during the adaptation. One future testable hypothesis is that heightened activity in visual, vestibular, and proprioceptive pathways facilitates the formation of a more comprehensive internal model, which in turn enhances generalization.

The greater necessity for control, combined with the greater risk of falling, may increase recruitment of certain brain areas. Indeed, neuroimaging studies show that coordinated movement involves a distributed network of brain activity that may be increased during more complex tasks (Debaere et al. 2001; Hülsdünker et al. 2015, 2016; Swinnen 2002). For example, overall activity in the supplementary motor area, cingulate motor cortex, premotor cortex, primary motor cortex, somatosensory cortex, and cerebellum during tasks that require across-limb coordination exceeds that observed during isolated limb movements (Debaere et al. 2001). Furthermore, challenging balance during standing results in greater electroencephalography spectral power within certain frequencies across many different cortical regions (Hülsdünker et al. 2015, 2016). In conjunction, perceived threat may contribute to broader behavioral generalization through the recruitment of brain areas that mediate negative reinforcers and respond to aversive stimuli, such as the ventral striatum and the amygdala (Armony et al. 1997; Bromberg-Martin et al. 2010; Jensen et al. 2003; Taub and Mintz 2010; Tom et al. 2007). These changes in brain activity may reflect (or serve to reinforce) the value placed on the updated internal model. The anterior cingulate cortex is thought to contribute to the estimated value of control by integrating information about the expected payoff and cost related to allocating control to a given task (Shenhav et al. 2013). Interestingly, this region is one of several that show greater theta band spectral power with a loss of balance during walking (Sipp et al. 2013). One potential future direction of our work is to determine how changes in brain activity during our tasks relates to the observed generalization patterns.

Taken together, the necessity to control exacerbated body motions and the perceived threat associated with the balance-challenged conditions may each contribute—to varying degrees—to generalization. Each of these contributions may accomplish this by altering the learning process and increasing the value assigned to the internal model formed during adaptation. As such, we propose that this greater-valued model increases generalization.

Challenging balance modulates across-task generalization. The reaching and walking groups showed bidirectional, within-task generalization. For example, the balance-challenged reaching group generalized to the balance-unchallenged reaching task, and vice versa. These results are unsurprising and support the substantial amount of evidence demonstrating generalization among tasks that share similar movement characteristics (Carroll et al. 2014; Gandolfo et al. 1996; Ghahramani et al. 1996; Mattar and Ostry 2010; Morton et al. 2001; Thoroughman and Shadmehr 2000). Is there evidence that challenging balance affects generalization across different tasks (e.g., from reaching to walking, and vice versa)?

To compare the magnitude of generalization across tasks, we normalized the generalization trials to the participants' performance during baseline and used the postadaptation trial as an indication of how much each participant learned during adaptation (Savin and Morton 2008). One possible issue with this method is that the postadaptation trial was performed at the end of our protocol, after several adaptation phases, and therefore may not be a true reflection of adaptation. We based our protocol decision on a practical compromise to accommodate multiple across-task generalization trials (randomized) and based our generalization index decision to account for individual differences in learning. There are alternative ways to quantify generalization using the initial and final adaptation error to reflect learning (Carroll et al. 2014; Morton et al. 2001). As an additional test, we quantified generalization with these methods. Although our results are consistent, the percentage values were substantially higher (between 140% and 210%) when the adaptation trials were used to quantify learning. Furthermore, the magnitudes of the postadaptation trials in the present study are comparable to the results from previous studies from our laboratory (Maeda et al. 2017a). Given that our results do not depend on whether we use the postadaptation or adaptation trials as an indicator of learning, we argue that our choice of generalization index is both suitable and appropriate.

We show that challenging balance modulates generalization across reaching and walking tasks. For example, we found that the balance-challenged reaching group generalized to the balance-unchallenged walking task, whereas the balance-unchallenged reaching group did not generalize to either walking task (Table 1; Fig. 8). Both of the walking groups also showed small, but significant, generalization (~8%) to the balance-challenged reaching task. However, we found no difference between the two balance conditions. We reason that the lack of a significant contribution of the upper limbs during the walking tasks may have limited further generalization to the reaching tasks. In contrast, reaching to the target while balance was challenged required rigorous control of the lower limb and trunk muscles to counter this perturbation, maintain balance, and complete the task successfully. Thus the balance-challenged reaching task arguably requires the greatest interdependent control of the upper and lower limbs for task success, the benefits of which are reflected in the noteworthy generalization (~24%) to the balance-unchallenged walking task. We did not find significant generalization between the balance-unchallenged reaching and walking tasks, which contradicts the findings of Morton and Bastian (2004). These conflicting results may relate to the differences between the walking tasks being evaluated. For example, our study assessed adaptation during a precision walking task using end-point error whereas the other study measured the extent of lateral deviation along the walking path. Finally, we show that only the balance-unchallenged reaching group generalized to the non-limb-based, seated reaching task. These findings support the results from Seidler et al. (2001) that showed that arm adaptation generalizes to a head pointing task. However, the reasons for the lack of significant generalization observed by the other groups are unclear. It is possible that our non-limb-based task was suboptimal for the purpose of comparing generalization across groups. Overall, given the pattern and limited extent of generalization across our reaching and walking tasks, it is clear that there are still other non-balance-related factors contributing to the transfer of learning.

Conclusions. Taken together, our results demonstrate that challenging balance enhances the degree to which visuomotor mappings generalize to untrained movements. We propose that challenging balance increases the value assigned to the internal model formed during learning, whether this be from a greater need to control motion at different body segments or from a greater perceived threat, thus making it more generalizable. Overall, our study demonstrates the significance of studying motor learning during unconstrained, natural behaviors.

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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., J.M.D., 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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