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## Transfer of postural adaptation depends on context of prior exposure

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**Pienciak-Siewert A, Barletta AJ, Ahmed AA.** Transfer of postural adaptation depends on context of prior exposure. *J Neurophysiol* 111: 1466–1478, 2014. First published December 26, 2013; doi:10.1152/jn.00235.2013.—Postural control is significantly affected by the postural base of support; however, the effects on postural adaptation are not well understood. Here we investigated how adaptation and transfer of anticipatory postural control are affected by stance width. Subjects made reaching movements in a novel dynamic environment while holding the handle of a force-generating robotic arm. Each subject initially adapted to the dynamics while standing in a wide stance and then switched to a narrow stance, or vice versa. Our hypothesis is that anticipatory postural control, reflected in center of pressure (COP) movement, is not affected by stance width, as long as the control remains within functional limits; therefore we predicted that subjects in either stance would show similar COP movement by the end of adaptation and immediately upon transfer to the other stance. We found that both groups showed similar adaptation of postural control, by using different muscle activation strategies to account for the differing stance widths. One group, after adapting in wide stance, transferred similar postural control to narrow stance, by modifying their muscle activity to account for the new stance. Interestingly, the other group showed an increase in postural control when transferring from narrow to wide stance, associated with no change in muscle activity. These results confirm that adaptation of anticipatory postural control is not affected by stance width, as long as the control remains within biomechanical limits. However, transfer of control between stance widths is affected by the initial context in which the task is learned.

neuromechanics; anticipatory postural adjustment; stance width; motor learning; transfer

WHEN WE MAKE FAMILIAR MOVEMENTS, anticipatory control allows us to predict and compensate for changing dynamics. Familiar and predictable movements are usually preceded by anticipatory postural adjustments (APAs), which involve the activation of postural muscles and resultant center of pressure (COP) movement initiated prior to onset of the focal movement. APAs act to control the whole body center of mass (COM) against the impending shift in dynamics caused by the movement, thus helping to maintain postural equilibrium; they can also aid in generating the desired movement (Bouisset et al. 2000; Bouisset and Zattara 1987; Stapley et al. 1998, 1999). These adjustments are frequently taken for granted as we pursue our daily activities, but they are a fundamental component of our ability to make effective movements.

All of the movements we make while standing are subject to varying constraints dependent on the postural base of support (BOS), but the effect of BOS size on postural control remains something of an enigma. If the size of the BOS is reduced, the

minimum distance between the COP and the edges of the BOS, called the “stability margin,” is also reduced; this results in a reduced capacity to recover from a postural perturbation (that is, to recover without taking a step, grasping an external supporting object, or otherwise altering the postural configuration) (Holbein-Jenny et al. 2007; Koozekanani et al. 1980; Patton et al. 1999; Patton and Pai 1997; Schulz et al. 2006). To generate an APA that is appropriate for a given movement or perturbation, one must make an accurate prediction about the impending dynamics; if that prediction is not accurate, the APA will be too large or too small for the actual dynamics, and some reactive or corrective control action will be required in order to recover postural equilibrium. Therefore, decreasing BOS size and thus stability margins could theoretically lead to reduced APAs because of the reduced capacity to recover. However, increasing BOS size could also lead to reduced APAs if the capacity to recover is sufficiently large that APAs are no longer needed to maintain postural equilibrium.

Studies have examined anticipatory postural control with various manipulations of BOS, such as adding postural supports or changing the size of the BOS by having subjects stand with their feet in different configurations or stand on wobble boards, with ambiguous results. Aruin et al. (1998) used wobble boards to manipulate BOS and found that APAs were reduced in the direction of the narrower BOS. However, in this study, APAs may have been reduced simply because the reduced BOS imposed by the wobble board was so narrow that it biomechanically constrained the COP movements. Two other studies found that APAs were also reduced, but in various upper body-supported conditions of very large BOS, where smaller APAs were sufficient or no APAs were required to help maintain balance (Cordo and Nashner 1982; Hall et al. 2010). In all of these studies, however, the forms of postural support used (a balance board or a trunk support) were not very representative of normal daily activities but rather induced “extreme” BOS conditions—namely, either very large BOS (trunk support), where APAs were supplanted by other means of maintaining postural equilibrium, or very small BOS (wobble board), where APAs may have been physically limited by the small BOS. Therefore it is not entirely clear how BOS size influences APAs.

To address certain aspects of this issue, we investigated the effects of BOS size on adaptation and transfer of a novel postural control strategy, using different stance widths to vary BOS size. In standing posture, when the distance between the feet is varied in the mediolateral direction the width of the base of support and thus the stability limits are increased. Both narrow and wide stances are familiar and everyday postures, making this an ideal way to manipulate BOS without reducing the familiarity of the support or constraining COP movements

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biomechanically. Furthermore, we wished to examine a novel task. Previous studies used tasks such as reaching or pulling on a handle, but in such an overly familiar task preference for previously established control strategies may have taken precedence over those more appropriate to the specific postural context (de Rugy et al. 2012). Therefore, to better address the question of how BOS size affects postural control, we considered the adaptation of control strategies for a novel task (where adaptation is defined as an error-driven gradual modification of movement parameters for a given task) (Bastian 2008). We also sought to determine how the postural context in which the task was adapted initially would affect the transfer of the adapted control strategy to a different postural context. Such transfer of adapted control is of significant interest, especially in rehabilitation, where it is desirable for adaptation that is acquired in a training context to be generalized beyond that context. In light of studies that question the idea of whether learning in a more challenging environment is beneficial to adaptation and/or transfer (Domingo and Ferris 2009; Wulf et al. 1998), we hope this investigation will lead to a better understanding of how the postural context in which a movement is adapted may influence the strength of adaptation as well as how well the adaptation generalizes to other postures.

We used a well-studied force field learning experimental paradigm in which subjects make arm reaching movements while holding the handle of a robotic arm that generates forces perpendicular to the reaching direction and with practice they adapt their arm control to compensate for those forces. In this paradigm, it has also been shown that adaptation occurs in the postural control system; when subjects perform the same arm reaching experiment while standing, their postural control as well as their arm control show adaptation to the robot forces (Ahmed and Wolpert 2009; Manista and Ahmed 2012). Ahmed and Wolpert (2009) also showed that in this arm reaching experimental paradigm subjects adapt an appropriate arm control strategy and can then transfer that strategy between different postural contexts, namely from sitting to standing. In addition, they found that upon switching from sitting to standing subjects immediately demonstrated perturbation-specific anticipatory COP movements appropriate to the novel posture. This indicates that the postural control system can anticipate the effects of movement dynamics on a novel posture and will control COP movement accordingly.

In the present study, subjects first adapted to the forces while standing in a wide stance and then transferred to a narrow stance, or vice versa. In both stance widths, the same mechanical perturbation was applied to the arm; based on a quasi-static model of standing posture, the same anticipatory COP movement should be biomechanically sufficient to maintain equilibrium, regardless of stance width. Importantly, these postures are familiar and do not biomechanically constrain the required COP movement, and therefore they should not inhibit APAs (unlike the extremely narrow BOS when standing on a wobble board as in Aruin et al. 1998). Our hypothesis is that anticipatory postural control, reflected in COP movement, is not affected by stance width, as long as the control remains within functional limits.

On the basis of our hypothesis, we made several predictions specific to this experiment, regarding the adaptation and transfer of COP movements and related muscle control. We predicted that subjects in either wide or narrow stance would show

similar COP movements by the end of the adaptation period; however, because of the difference in biomechanical configuration between stance widths, the anticipatory muscle activity required to generate this COP movement would differ (Bingham et al. 2011). We also predicted that subjects would transfer similar COP movements from one stance to another, with appropriate changes in anticipatory muscle activity to account for the change in configuration. We made two additional predictions about the adaptation and transfer of anticipatory muscle activity related to these anticipatory COP movements; generally, we expected that different muscle activation strategies would be used in each stance width to account for the difference in biomechanical configuration. In adaptation, we predicted that anticipatory COP movements of the same magnitude would require lower levels of anticipatory muscle activity in wide stance compared with narrow stance, and that subjects in wide stance would rely more on hip muscles than subjects in narrow stance (Bingham et al. 2011; Henry et al. 2001; Torres-Oviedo and Ting 2010). In transfer, we predicted that each group would modify their anticipatory muscle activity appropriately in order to transfer the same COP movement between stance widths (e.g., if similar COP movements were transferred from wide to narrow stance, we would predict an increase in anticipatory muscle activity levels as well as a shift from a hip muscle strategy to an ankle strategy).

## MATERIALS AND METHODS

Twelve young adult subjects (age  $22.1 \pm 1.7$  yr; height  $1.7 \pm 0.1$  m; mass  $68.4 \pm 13.0$  kg) participated in the study. All subjects were screened with a health questionnaire and the Edinburgh Handedness Inventory test (Oldfield 1971). Inclusion criteria included right-hand dominance, normal or corrected-to-normal vision, and no reported history of neurological or upper limb musculoskeletal disorders. The University of Colorado at Boulder Human Research Committee approved all experimental procedures.

### *Apparatus and Data Collection*

Subjects made forward-reaching movements in the horizontal plane with their right hand while grasping the handle of a two-degree-of-freedom planar robotic arm (InMotion2 Shoulder-Elbow Robot, Interactive Motion Technologies) and while standing barefoot on a six-axis force plate (AMTI LG-6-4-1, Advanced Mechanical Technology) (Fig. 1A). We defined stance width as the distance between the lateral edges of the feet. Subjects stood in either a wide stance width (150% of hip width, mean  $38.6 \pm 2.6$  cm across all subjects) or a narrow stance width (feet placed together, mean  $19.6 \pm 1.3$  cm across all subjects). These stance widths are comparable to those used in previous studies. Winter et al. (1998) tested stance widths (distance between ankles, measured from joint centers) of 50%, 100%, and 150% of hip width (measured as distance between right and left anterior superior iliac spine); using the same measures, Bingham et al. (2011) tested a range of stance widths from 50% to 200%. Henry et al. (2001) tested stance widths (distance between centers of heels) of 10 and 32 cm, and, using the same measure, Torres-Oviedo and Ting (2010) tested 9, 19, and 30 cm (as well as a 60-cm "extreme" stance width). Subjects were asked to keep their feet flat on the ground, to ensure that the BOS size was not affected by lifting or rotation of the feet. The subject's forearm was supported against gravity by a rigid cradle attached to the handle. The height of the robot was adjusted for each subject so that the robot arm and handle were level with the shoulder joint of the subject's reaching arm. A computer monitor, vertically suspended in front of the subject, displayed visual feedback

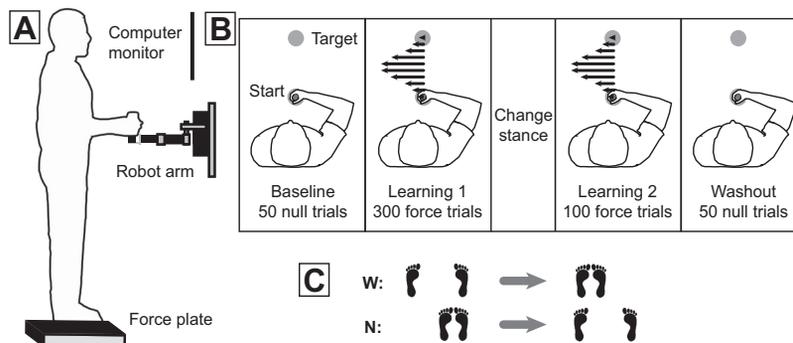


Fig. 1. *A*: apparatus. *B*: experimental protocol. *C*: subject groups: W group begins in wide stance and changes to narrow; N group begins in narrow stance and changes to wide.

of hand, start, and target positions throughout the movement. Visual feedback about movement duration was provided to ensure that it stayed within a certain range (450–600 ms).

Position, velocity, and force data from the robot handle were sampled at 200 Hz. Three-dimensional ground reaction forces ( $F_x$ ,  $F_y$ ,  $F_z$ ) and moments ( $M_x$ ,  $M_y$ ,  $M_z$ ) from the force plate were also sampled at 200 Hz and then low-pass filtered at 10 Hz.

Surface EMG data were collected with a wireless electrode system (Trigno Wireless System, Delsys) with a fixed interelectrode distance of 1 cm on each sensor and a signal bandwidth of 20–450 Hz. EMG data were sampled at 2,000 Hz from six right-left pairs of postural muscles: tensor fascia latae (TFL), rectus femoris (RF), biceps femoris (BF), tibialis anterior (TA), peroneus longus (PL), and soleus (Sol). Electrodes were placed according to SENIAM guidelines (Surface Electromyography for the Non-Invasive Assessment of Muscles, <http://www.seniam.org/>).

#### Experimental Protocol

Before the experiment began, a “start” circle and a cursor representing COP location were shown on the screen, with a 1:1 scaling between COP movement and cursor movement. Subjects were asked to stand such that their COP was centered in the start circle when they were standing comfortably straight. Their foot positioning was marked on the force plate to ensure that they always stood in the same location.

After this, subjects played a brief COP game for the purpose of measuring their functional BOS, or the limits of the area within the BOS that a person is willing to extend their COP (Holbein-Jenny et al. 2007; King et al. 1994; Lee and Lee 2003). This game was also used to obtain data for EMG normalization. In this game, they controlled the cursor with their COP to make a series of 24 “reaching” movements from the start circle toward 8 randomized targets located in different directions, evenly spaced around a 360° circle at 45° angles, and at a distance of 10 cm from the central start position. This game was first played with feet placed in the wide stance and then repeated with feet in the narrow stance.

After playing the COP game, subjects started the experiment. In the experiment, subjects were asked to make 15-cm reaching movements straight ahead, using the robot handle to control the cursor on the screen, with a 1:1 scaling between hand movement and cursor movement. At the start of each trial, subjects were required to hold the 0.6-cm-diameter hand cursor inside the 1-cm start circle and to maintain their COP location (represented by a separate cursor with a different color) within a second, larger 1.6-cm-diameter start circle centered at the same location. Both the cursor and start circle for the hand were filled in, while for COP only the outlines of the cursor and start circle were displayed. After a short time delay, the COP circles disappeared and a 1.6-cm target circle appeared, and subjects moved the hand cursor toward the target. At the end of the movement, subjects were required to remain within the target circle for 50 ms, after which the robot moved the subject’s hand back to the start position to begin the next trial. The desired movement time, measured

from the time the hand left the start position to the time at which the 50-ms target requirement was fulfilled, was  $525 \pm 125$  ms (desired range 450–600 ms).

All subjects encountered the same sequence of trials throughout the experimental protocol (Fig. 1*B*). The protocol consisted of 500 trials and was divided into four blocks: baseline (50 trials), *learning 1* (300 trials), *learning 2* (100 trials), and washout (50 trials). Subjects were randomly assigned into one of two groups, “W” or “N.” The W group stood in a wide stance throughout the baseline and *learning 1* blocks and then switched to a narrow stance for the *learning 2* and washout blocks; the N group stood in a narrow stance throughout the baseline and *learning 1* blocks and then switched to a wide stance for the *learning 2* and washout blocks (Fig. 1*C*).

The baseline block consisted of null trials, in which robot forces were turned off, to familiarize the subject with the robot and to measure baseline performance. Null trials were also used in the washout block at the end of the experiment to allow the subject to deadapt the previous dynamic environment. The *learning 1* and *learning 2* blocks consisted of curl trials, in which a viscous curl field was simulated such that the robot exerted a force  $F$  on the hand that was proportional to the magnitude and perpendicular to the direction of the instantaneous velocity  $V$  of the robot handle:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = k \begin{bmatrix} 0 & -1 \\ 1 & 0 \end{bmatrix} \begin{bmatrix} V_x \\ V_y \end{bmatrix} \quad (1)$$

where  $k = -20$  N-s/m. One trial in every batch (5 trials) was chosen randomly to be a channel trial. In channel trials, the robot generated a force channel that restricted the subject’s hand trajectory to a straight path between the start position and the target; the robot could then measure the perpendicular force that the subject was exerting into the channel. Stiffness and damping for the channel were 6,000 N/m and 250 N-s/m, respectively. Channel trials were used to quantify subjects’ predictive, feedforward control. These trials have been shown to have a minimal effect on adaptation or deadaptation (Scheidt et al. 2001). The sequence of trial types was identical for all subjects.

#### Data Analysis

All data were aligned to movement onset, such that time zero represents movement onset of the arm, and truncated at movement end. Movement onset was defined as when the cursor left the start circle. Movement end was defined as when the cursor reached the target circle. All data were taken from movement onset to movement end, unless otherwise noted. Data from channel trials were analyzed separately from all other trials.

*Arm control.* To confirm adaptation and transfer in the arm, arm control was quantified with two metrics: hand error and anticipatory force. Hand error for each trial (excluding channel trials) was defined as the maximum absolute value of the perpendicular deviation of the handle trajectory from a straight path between the start and target positions. Anticipatory force was taken from channel trials only and was calculated as the mean of the perpendicular force exerted into the channel over the duration of the movement.

**Postural control.** Postural control was reflected in COP movement. COP data were calculated from filtered force-plate data as  $COP_x = (-M_y - F_x \times r_z)/F_z$  and  $COP_y = (M_x - F_y \times r_z)/F_z$ , where  $x$  and  $y$  subscripts denote mediolateral and anteroposterior axes, respectively, and  $r_z$  represents the distance from the top of the force plate to its origin. All COP data for each subject were normalized to foot length. Subsequently, COP velocity was calculated with a five-point differentiation algorithm. COP movement in the direction of the force perturbation is considered evidence of postural control, as it provides a measure of the net external moment generated about the ankle to control for the perturbation. Specifically, COP movement initiated prior to the movement is considered anticipatory control, and subsequent COP movement is considered reactive control. Postural control was quantified for each trial (excluding channel trials) with two COP movement metrics: anticipatory postural adjustment (COP-APA) and reactive postural adjustment (COP-RPA). Both of these metrics were based on the normalized COP velocity perpendicular to the direction of reaching movement (where all COP data were normalized to foot length). Horak and Nashner (1986) investigated postural control responses to unexpected backward sway perturbations and observed reactive response latencies in the TA varying from 73 to 110 ms; this was after repeated exposure, which is known to reduce the latency of automatic postural responses. Therefore, as a conservative measure of anticipatory control, the COP-APA was calculated as the mean velocity from 50 ms before movement onset to 100 ms after movement onset. The COP-RPA was calculated as the maximum positive value of velocity throughout the remaining duration of the movement (following the COP-APA time period). (Positive movement is leftward, in the direction of the perturbation.) This is a useful paradigm for studying adaptation of postural control because the component of postural control that is adapted in response to the force field is perpendicular to, and thus not confounded by, the tangential component required for the focal movement (normal unperturbed reaching). We chose to quantify postural control by using COP rather than COM movement because while COP movement provides a measure of active control, COM movement is a controlled outcome variable. Previous studies have shown that COP displacement (horizontal difference between COP and COM locations) drives horizontal acceleration of the COM for quiet standing (Winter et al. 1998), gait initiation and termination (Jian et al. 1993), and balance recovery after a perturbation (Rietdyk et al. 1999).

**Muscle activity.** EMG data were high-pass filtered at 20 Hz to remove movement artifact, full-wave rectified, and then low-pass filtered at 50 Hz, with a zero-phase fourth-order Butterworth filter. EMG data from one subject in the N group were excluded from analysis on account of excessive noise. For each subject included in the analysis, EMG data were normalized by dividing by the maximum observed activity for each muscle, taken as the maximum filtered EMG activity observed during the preexperiment COP game in either stance. Anticipatory muscle activity for each trial (excluding channel trials) was quantified as the root-mean-square value of the normalized EMG trace from 100 ms before movement onset to 50 ms after movement onset (50 ms earlier than the time period sampled for COP data, offset to account for the time lag between recorded EMG activity and corresponding COP movement).

### Statistics

Data were compared between groups and across seven phases of the protocol: late baseline, first *learning 1*, late *learning 1*, first *learning 2*, late *learning 2*, first washout, and late washout. The “first” phases of a trial block consisted of one trial only; for anticipatory force, the “first” phases consisted of the first channel trial. For “late” phases, data were averaged over the last two batches (8 nonchannel trials or 2 channel trials) of the trial block.

Hand error, anticipatory force, COP-APA, and COP-RPA data were analyzed by repeated-measures ANOVAs, with phase as a

within-subjects factor and group as a between-subjects factor. To test for adaptation, we performed planned comparisons on the within-subjects results between the late baseline, first *learning 1*, and late *learning 1* phases. To compare adaptation between groups, we made a planned comparison in the late *learning 1* phase. To test for initial transfer, we performed planned comparisons on the within-subjects results between the late *learning 1* and first *learning 2* phases. To examine the time course of transfer, we performed additional planned comparisons on the within-subjects results for each group between the first *learning 2* and late *learning 2* phases. Planned comparisons were also made between groups at specific phases of interest. All planned comparisons were made with independent two-sample *t*-tests.

On the basis of previous studies, we made specific predictions about changes in activity for individual muscles that might be involved in development of the anticipatory COP movement (specifically, leftward COP movement): increased activity in the right TFL and/or decreased activity in the left TFL (Leonard et al. 2009), increased activity in the left TA (Gefen 2001) and/or decreased activity in the right TA (Hopkins et al. 2012) (with similar changes in PL activity, because the PL activates with the TA in order to maintain foot-on-ground contact), and also increased activity in the right Sol (Leonard et al. 2009). Directional changes in muscle activity were examined with one-sided paired *t*-tests ( $\alpha = 0.05/2$ ). To test for differences between groups, we made planned comparisons with independent two-sample *t*-tests.

ANOVAs were performed with SPSS, and *t*-tests were performed with the appropriate built-in MATLAB functions. For all statistical analyses the criterion for significance was set at the level of  $\alpha = 0.05$  unless otherwise noted. Mean values are reported as means  $\pm$  SD.

## RESULTS

Both groups displayed similar arm movement characteristics and also showed similar adaptation of arm control. Across all subjects, similar arm control was transferred between stance widths. Both groups showed similar adaptation of COP movements, by using different anticipatory muscle control strategies to account for the differing stance widths. In transfer, the W group transferred similar COP movements, by modifying their anticipatory muscle activity to account for the new stance. However, the N group showed an increase in COP movements when transferring, related to no change in anticipatory muscle activity.

Results are presented below for movement characteristics (reaching velocity, field force, and COP displacement), arm control (hand error and anticipatory force), COP movements (COP-APA and COP-RPA), and anticipatory muscle activity.

### Arm Movement Characteristics

To compare performance between groups, we had to be sure that both groups made hand reaching movements with similar velocities and experienced similar forces. Average velocities for the reaching movement ranged from 0.31 to 0.36 m/s throughout the experiment; average and maximum velocities were not significantly different between groups at all phases (all  $P \geq 0.133$ ). During *learning 1* and *learning 2*, average and maximum forces were not significantly different between groups at all phases (all  $P \geq 0.133$ ).

### Arm Control

Hand error and anticipatory force data (Fig. 2A) show that subjects adapted to the field during the *learning 1* trial block, transferred this adaptation to the *learning 2* block with no

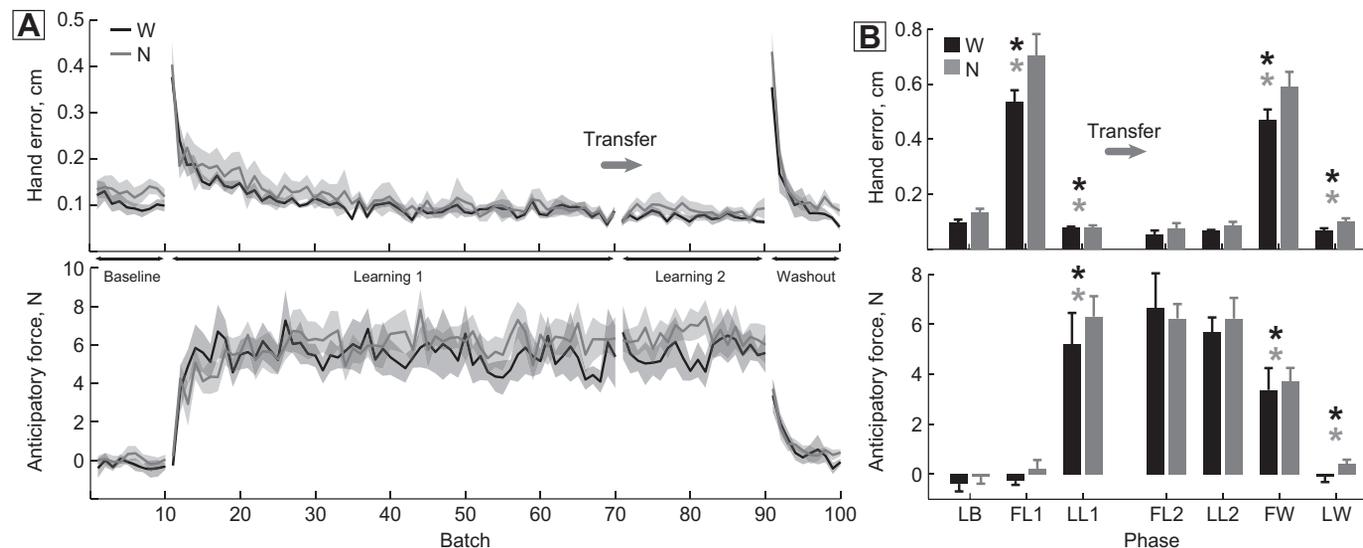


Fig. 2. *A*: hand error (*top*) and anticipatory force (*bottom*) vs. batch (5 trials); in each plot, 2 traces show group means (solid lines)  $\pm$  SE (shading) for W group and N group. *B*: hand error (*top*) and anticipatory force (*bottom*) at the late baseline (LB), first learning 1 (FL1), late learning 1 (LL1), first learning 2 (FL2), late learning 2 (LL2), first washout (FW), and late washout (LW) phases for W group vs. N group, with error bars showing SE. \*Statistically significant differences ( $P < 0.050$ ) for a change from the previous phase (black for W group, gray for N group).

changes, displayed aftereffects at the start of the washout block, and then deadadapted during the remainder of the washout block. The ANOVA revealed a main effect of phase (hand error  $P < 0.001$ ,  $F = 139.0$ ; anticipatory force  $P < 0.001$ ,  $F = 46.36$ ) but showed no main effect of group ( $P = 0.261$ ) and no interaction effect of phase  $\times$  group ( $P = 0.261$ ).

**Adaptation.** To test for movement adaptation in the arm, we focused on hand error and anticipatory force in the late baseline, first learning 1, and late learning 1 phases (Fig. 2*B*). We found that subjects adapted as expected, and we found no differences between groups. Across all subjects, hand error was significantly increased from late baseline to first learning 1 and reduced from first learning 1 to late learning 1 (all  $P < 0.001$ ). Anticipatory force was not significantly different from late baseline to first learning 1 ( $P = 0.380$ ) and significantly increased from first learning 1 to late learning 1 ( $P < 0.001$ ). Additionally, deadadaptation was evident in that hand error was significantly different from late learning 2 to first washout and from first washout to late washout (all  $P < 0.001$ ), and anticipatory force was significantly different from first washout to late washout ( $P < 0.001$ ). It should be noted that we did see a significant decrease in anticipatory force from late learning 2 to first washout ( $P = 0.001$ ); however, the “first washout” channel trial followed two null trials, and from previous experience we know that subjects deadadapt very quickly. Planned comparisons at the late baseline, first learning 1, and late learning 1 phases revealed no significant differences between groups (all error  $P \geq 0.101$ , all force  $P \geq 0.268$ ).

**Transfer.** To test for transfer of arm control, we focused on the late learning 1 and first learning 2 phases (Fig. 2*B*). We found no differences between these phases or between groups. Hand error and anticipatory force did not significantly differ from late learning 1 to first learning 2 (error  $P = 0.504$ , force  $P = 0.610$ ) and did not significantly differ from first learning 2 to late learning 2 (error  $P = 0.402$ , force  $P = 0.341$ ). Planned comparisons at the first learning 2 and late learning 2 phases revealed no significant differences between groups (all error  $P \geq 0.185$ , all force  $P \geq 0.587$ ).

#### Postural Control

We compared maximum lateral COP displacements during the experiment, in both wide and narrow stance, to those measured during the COP game (which established the lateral dimensions of the functional BOS). (All COP data were measured from the “start” location and normalized by foot length.) This was done to verify that the COP movements executed during the experiment were within the limits of the functional BOS (see Fig. 3*A*). Across all subjects, mean foot length was  $24.0 \pm 2.0$  cm, mean wide stance width was  $38.6 \pm 2.6$  cm, and mean narrow stance width was  $19.6 \pm 1.3$  cm. In the COP game, averaged across all subjects, the maximum normalized lateral displacement was  $0.48 \pm 0.09$  cm/cm in wide stance and  $0.26 \pm 0.06$  cm/cm in narrow stance, or a lateral functional BOS limit (measured from center) of  $11.4 \pm 1.6$  cm in wide stance and  $6.2 \pm 1.4$  cm in narrow stance; this was significantly different between stance widths ( $P < 0.001$ ). In the experiment, maximum COP displacements did not exceed  $\sim 0.15$  cm/cm, or 3.6 cm, in either group. In COP-APAs, COP displacements ranged from  $\sim 0.01$  to 0.03 cm/cm in the W group and from 0.02 to 0.06 cm/cm in the N group; in COP-RPAs, they ranged from  $\sim 0.02$  to 0.11 cm/cm in the W group and from 0.02 to 0.15 cm/cm in the N group. This confirms that the COP-APAs and COP-RPAs developed in response to the force field were well within the limits of the functional BOS for both stance widths.

COP-APAs that developed to anticipate the force field were in the same direction as the field, perpendicular to the direction of the hand reaching movement. In the direction tangential to the reaching movement, COP-APAs related to the reaching movement itself were observed consistently on all trials (Fig. 3*B*); specifically, the COP moved away from the target prior to hand movement onset, as has been observed previously (Manista and Ahmed 2012). Across all subjects the magnitude of the tangential COP-APA did not significantly differ between phases (all  $P \geq 0.198$ ), and at all phases magnitudes did not significantly differ between groups (all  $P \geq 0.263$ ). Hereafter,

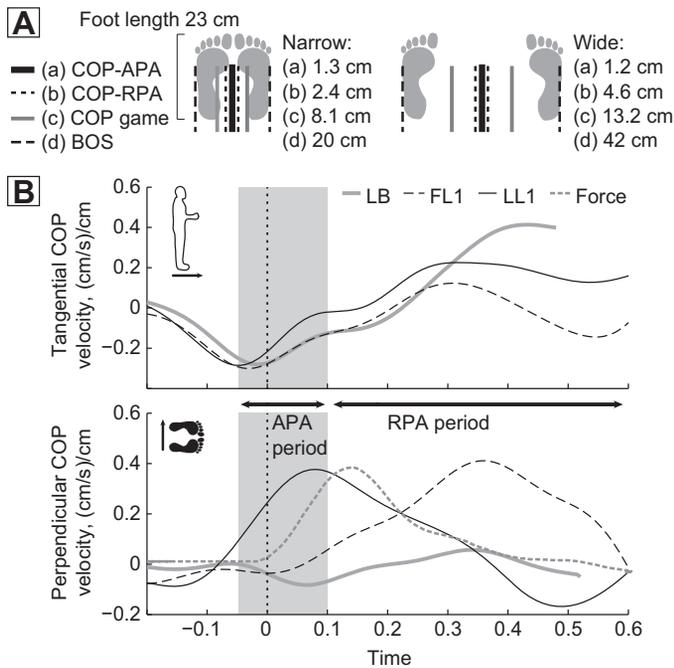


Fig. 3. *A*: center of pressure (COP) limits and movements for 1 representative subject; base of support (BOS) width is shown for each stance width, along with maximum lateral COP excursion measured during the COP game and maximum lateral COP excursion observed during COP-anticipatory postural adjustment (APA) and COP-reactive postural adjustment (RPA) movements in the experiment. *B*: representative tangential (*top*) and perpendicular (*bottom*) COP velocity traces (normalized by foot length) vs. time for the late baseline (LB), first learning 1 (FL1), and late learning 1 (LL1) phases, taken from 1 subject in the W group. Time 0 represents movement onset of the arm. Note that for the perpendicular direction, positive is leftward (same direction as force field); for the tangential direction, positive is forward (same direction as reaching movement).

all COP-APA and COP-RPA results are based on the perpendicular COP velocity.

COP movement data (Fig. 4*A*) show that all subjects adapted to the field during the *learning 1* trial block, displayed after-effects at the start of the washout block, and then deadadapted

during the remainder of the washout block; however, the groups showed differences in transfer. ANOVA revealed a main effect of phase on both metrics (COP-APA  $P < 0.001$ ,  $F = 21.0$ ; COP-RPA  $P < 0.001$ ,  $F = 22.5$ ), with significant interaction effect of group  $\times$  phase (COP-APA  $P = 0.007$ ,  $F = 3.4$ ; COP-RPA  $P = 0.001$ ,  $F = 4.4$ ) and with a main effect of group on COP-RPA ( $P = 0.019$ ,  $F = 8.1$ ) but not on COP-APA ( $P = 0.087$ ,  $F = 3.7$ ).

*Adaptation.* To test for adaptation of COP movements, we focused on COP-APAs and COP-RPAs in the late baseline, first *learning 1*, and late *learning 1* phases (Fig. 4*B*). We found that subjects adapted as expected and the groups showed similar adaptation. For both groups, COP-APAs were not significantly different from late baseline to first *learning 1* (W group  $P = 0.248$ , N group  $P = 0.406$ ) and significantly increased from first *learning 1* to late *learning 1* (all  $P < 0.001$ ). COP-RPAs were significantly increased from late baseline to first *learning 1* (W group  $P = 0.010$ , N group  $P < 0.001$ ) and reduced from first *learning 1* to late *learning 1* (W group  $P = 0.034$ , N group  $P = 0.017$ ). Deadadaptation was evident in the washout block for both groups, in that COP-APAs were not significantly different from late *learning 2* to first washout (W group  $P = 0.546$ , N group  $P = 0.270$ ) and were significantly different from first washout to late washout (all  $P \leq 0.009$ ); COP-RPAs were significantly different from late *learning 2* to first washout (W group  $P < 0.001$ , N group  $P = 0.009$ ) and from first washout to late washout (all  $P \leq 0.002$ ). Planned comparisons between groups showed that COP-RPAs were higher for the W group than for the N group in late baseline ( $P = 0.036$ ); otherwise, COP-APAs and COP-RPAs were not significantly different between groups in late baseline (COP-APA  $P = 0.512$ , first *learning 1* (COP-APA  $P = 0.583$ , COP-RPA  $P = 0.617$ ), and late *learning 1* (COP-APA  $P = 0.067$ , COP-RPA  $P = 0.789$ ).

*Transfer.* To test for transfer of COP movements, we focused on the late *learning 1* and first *learning 2* phases (Fig. 4*B*). We found that the W group transferred similar COP movements but the N group did not; we also found differences

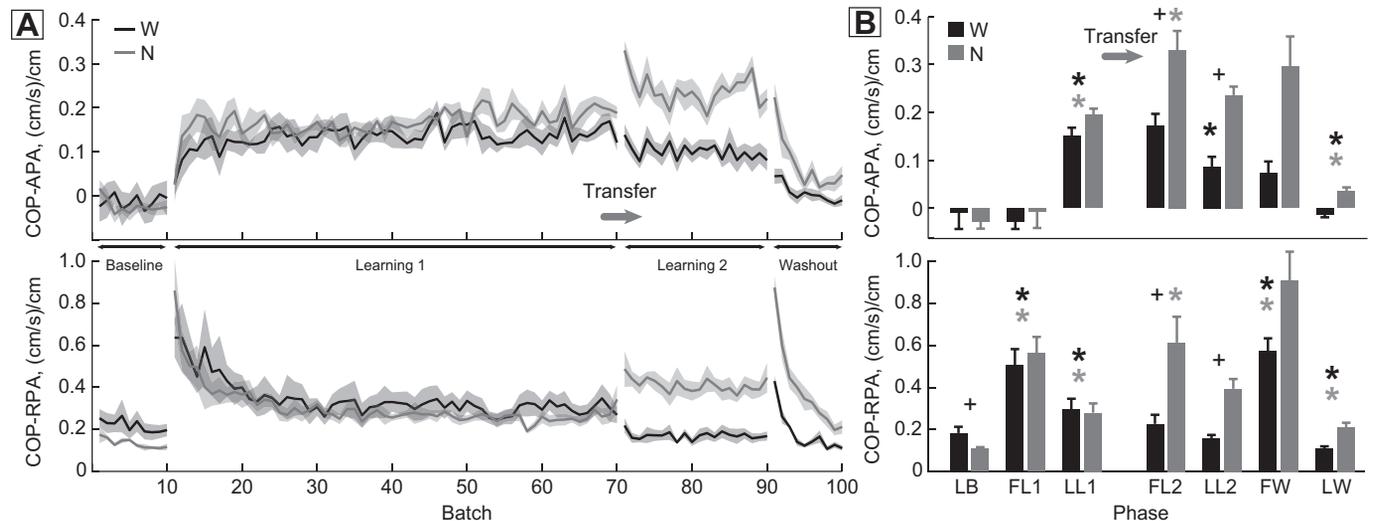


Fig. 4. *A*: COP-APA (*top*) and COP-RPA (*bottom*) vs. batch (5 trials); in each plot, 2 traces show group means (solid lines)  $\pm$  SE (shading) for W group and N group. *B*: COP-APA (*top*) and COP-RPA (*bottom*) at the late baseline (LB), first *learning 1* (FL1), late *learning 1* (LL1), first *learning 2* (FL2), late *learning 2* (LL2), first washout (FW), and late washout (LW) phases, for W group vs. N group, with error bars showing SE. Statistically significant differences ( $P < 0.050$ ): \*change from the previous phase (black for W group, gray for N group); +between groups.

between groups related to the amount of transfer. The W group transferred COP-APAs and COP-RPAs that were not significantly different from late *learning 1* to first *learning 2* (COP-APA  $P = 0.203$ , COP-RPA  $P = 0.108$ ) but then decreased from first *learning 2* to late *learning 2* (COP-APA  $P = 0.039$ , COP-RPA  $P = 0.185$ ), with both metrics in late *learning 2* being significantly lower than in late *learning 1* (COP-APA  $P = 0.041$ , COP-RPA  $P = 0.034$ ). In the N group, COP-APAs and COP-RPAs significantly increased from late *learning 1* to first *learning 2* (COP-APA  $P = 0.040$ , COP-RPA  $P = 0.012$ ) and then numerically decreased, although not significantly, from first *learning 2* to late *learning 2* (COP-APA  $P = 0.109$ , COP-RPA  $P = 0.062$ ), with COP-APAs in late *learning 2* not significantly different from late *learning 1* ( $P = 0.298$ ) and with COP-RPAs in late *learning 2* remaining significantly higher than in late *learning 1* ( $P = 0.004$ ). (Note that the N group showed high intertrial variability in late *learning 2*.) Planned comparisons at the first *learning 2* and late *learning 2* phases showed significantly higher COP-APAs and COP-RPAs in the N group than in the W group (first *learning 2*: COP-APA  $P = 0.018$ , COP-RPA  $P = 0.024$ ; late *learning 2*: COP-APA  $P = 0.002$ , COP-RPA  $P = 0.004$ ).

### Anticipatory Muscle Activity

To determine which muscles were involved in the tangential COP-APA related to the reaching movement, we focused on anticipatory muscle activity in the late baseline phase. As shown in Fig. 5, the TA and PL muscles showed anticipatory activity bilaterally in this phase and the Sol muscles showed inhibition, indicating a normal APA for forward reaching. This is consistent with previous findings (Leonard et al. 2009; Manista and Ahmed 2012).

Anticipatory muscle activity data pertaining to adaptation and transfer are shown in Fig. 6. Bar plots are included for all muscles that showed relevant differences (Fig. 6A). Plots of anticipatory activity vs. batch (Fig. 6B), as well as group average traces for the late baseline and late *learning 1* phases (Fig. 6C), are shown for the left and right TA, as these muscles are exemplary of the differences between groups and across phases. To examine adaptation and transfer of anticipatory muscle activity, we limited our focus to the late baseline, late *learning 1*, first *learning 2*, and late *learning 2* phases.

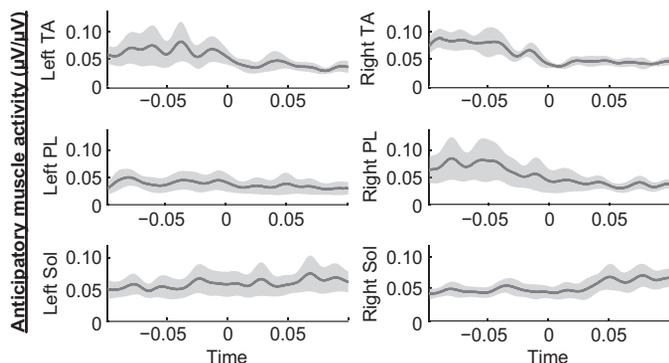


Fig. 5. Average time traces of anticipatory muscle activity (mean normalized EMG) for the tibialis anterior (TA), peroneus longus (PL), and soleus (Sol) muscles in the late baseline phase for the N group. Each plot shows group average trace (solid line)  $\pm$  SE (shading). Time 0 represents movement onset of the arm.

**Adaptation.** To determine how muscle activity led to the changes in COP-APAs after adaptation, we focused on changes in anticipatory muscle activity from late baseline to late *learning 1* (Fig. 6, A and C). As expected, we found changes in anticipatory activity in the TA, PL, and Sol across all subjects and changes in the TFL in the W group; also as expected, we observed higher levels of anticipatory activity in the N group. Across all subjects, anticipatory muscle activity from late baseline to late *learning 1* was significantly decreased in the right TA ( $P = 0.018$ ) and right PL ( $P = 0.039$ ) and significantly increased in the right Sol ( $P = 0.036$ ). The W group showed a significant decrease in left TFL activity ( $P = 0.037$ ) and also showed a significant decrease in right RF activity ( $P = 0.020$ ). Activity was higher for the N group than for the W group in the right TA and left RF in late baseline (right TA  $P = 0.016$ , left RF  $P = 0.036$ ) and late *learning 1* (right TA  $P = 0.052$ , left RF  $P = 0.038$ ); the same trends were also seen in the left TA and right RF, but with no significance. The BF muscles showed no significant differences across phases or between groups.

**Transfer.** To test for transfer of EMG strategies, we focused on changes in anticipatory muscle activity from late *learning 1* to first *learning 2* (Fig. 6A). We found a significant change in anticipatory activity in the W group and no significant changes in the N group. In the W group, left TA activity significantly increased from late *learning 1* to first *learning 2* ( $P = 0.024$ ) and right TA activity did not significantly change ( $P = 0.405$ ), adding to the asymmetry caused by the decrease in right TA activity from late baseline to late *learning 1*. This increased left TA activity was maintained from first *learning 2* to late *learning 2*, with late *learning 2* significantly higher than late *learning 1* ( $P = 0.036$ ). Small, nonsignificant increases were also observed from late *learning 1* to first *learning 2* in the right PL ( $P = 0.147$ ) and right Sol ( $P = 0.190$ ), but that activity then decreased and was not significantly different between late *learning 2* and late *learning 1* (all  $P \geq 0.423$ ). In the N group, no significant changes in anticipatory muscle activity were observed from late *learning 1* to first *learning 2* (all  $P \geq 0.112$ ). However, activity slightly decreased in the left TA ( $P = 0.068$ ) and left PL ( $P = 0.056$ ) and then decreased further, with activity being significantly lower in late *learning 2* than in late *learning 1* (left TA  $P = 0.042$ , left PL  $P = 0.043$ ).

### DISCUSSION

The results of this study partially support our hypothesis that anticipatory postural control, reflected in COP movement, is not affected by stance width, as long as the control remains within functional limits. Specifically, we found that adaptation of novel anticipatory postural control is not affected by stance width. However, the transfer of adapted anticipatory postural control between stance widths is affected by the biomechanical context of prior exposure.

#### Adaptation of Postural Control

The results confirmed our prediction that subjects in either wide or narrow stance would show similar COP movements by the end of the adaptation period. As expected, lateral functional BOS limits were increased from narrow to wide stance, and COP-APAs and COP-RPAs were well within these limits for

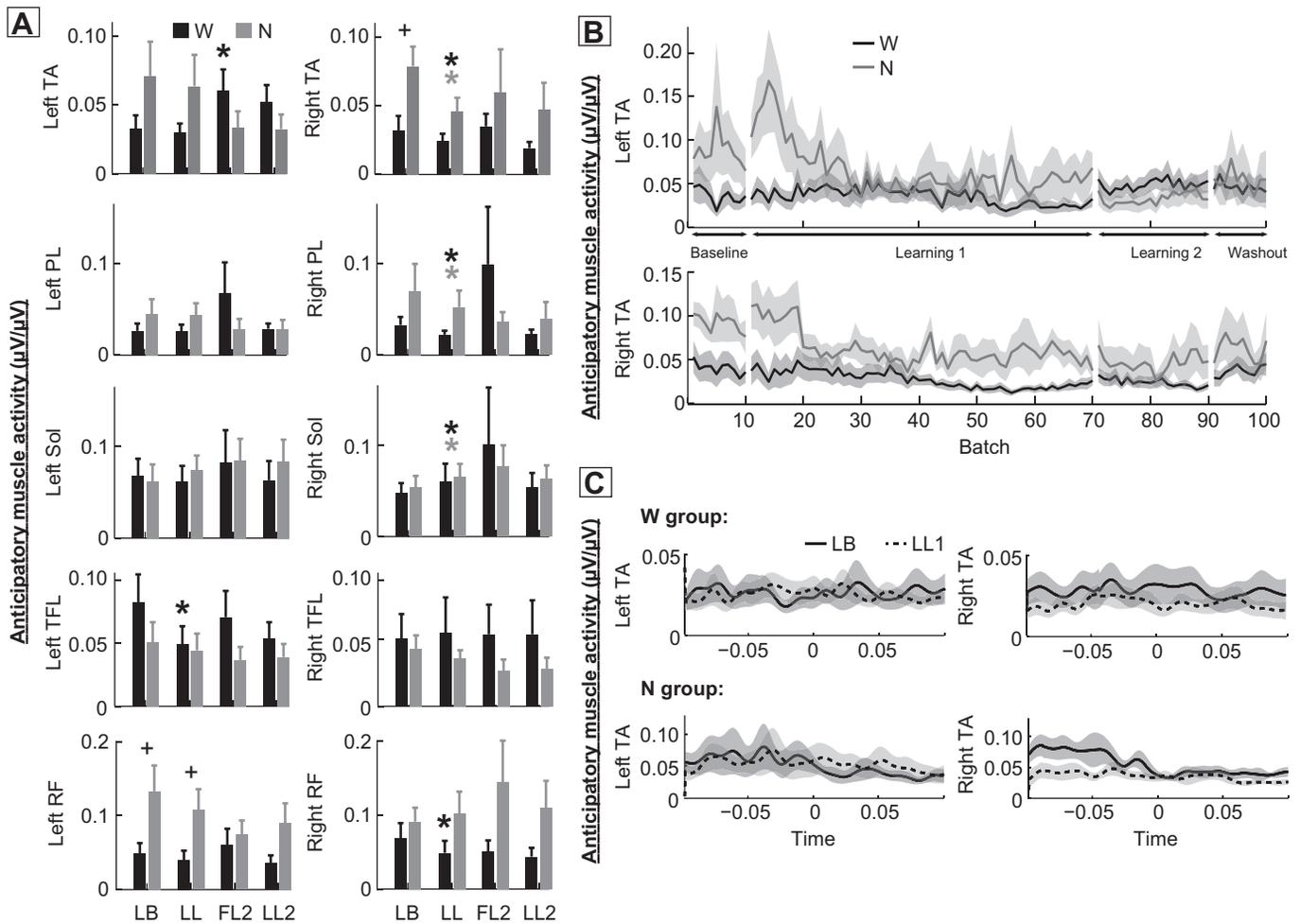


Fig. 6. A: anticipatory muscle activity (mean normalized EMG) for muscles at the late baseline (LB), late *learning 1* (LL1), first *learning 2* (FL2), and late *learning 2* (LL2) phases, for W group vs. N group, with error bars showing SE. Statistically significant differences ( $P < 0.025$ ): \*change from the previous phase (black for W group, gray for N group); + between groups. B: batch plots show anticipatory muscle activity for the left and right TA vs. batch (5 trials); in each plot, 2 traces show group means (solid lines)  $\pm$  SE (shading) for W group and N group. C: average time traces of anticipatory muscle activity for the left and right TA in the late baseline (LB) and late *learning 1* (LL1) phases. In each plot, 2 traces show group mean for LB phase (solid line) and LL1 phase (dashed line)  $\pm$  SE (shading). Time 0 represents movement onset of the arm.

both stance widths. Combined, these results indicate that the same COP strategy was sufficient for both stance widths and that adaptation of COP control was not affected by the difference in stance width.

While the N group did show nonsignificantly higher COP-APAs than the W group in late *learning 1*, we interpreted this result as “similar” for several reasons. First, the difference between group means in late *learning 1* was small and statistically insignificant. More importantly, there is no reason to expect larger COP-APAs in narrow stance, based on previous studies that found that anticipatory COP movements were reduced with smaller BOS size (Kaminski and Simpkins 2001; Manista and Ahmed 2012; Yiou et al. 2007).

The results also confirmed our prediction that because of the difference in biomechanical configuration between stance widths, the anticipatory muscle activity required to generate the same COP movement would differ. In late baseline and *learning 1*, activity levels were higher in the N group compared with the W group. Previous experimental studies found that, in general, muscle activity in response to a perturbation is decreased with increasing stance width (Henry et al. 2001; Torres-Oviedo and Ting 2010; Winter et al. 1998). Initially,

this was thought to be due to greater passive stiffness in wide stance, which would provide more passive control of COM movement and thus require less active muscle control (Henry et al. 2001). However, an experimentally validated model demonstrated that the body’s frontal plane inertia actually decreases with wider stance, meaning that a given joint torque will generate larger COM movement in wider stance; therefore, to generate the same COM movement, joint torques (and muscle activity) must be decreased in wider stance (Bingham et al. 2011).

Both groups adapted their COP-APAs in *learning 1*, specifically adapting COP-APAs in a leftward direction, by reducing anticipatory muscle activity in the right TA and right PL and increasing activity in the right Sol. Results from several previous studies indicate similarly that higher activity in the left TA relative to the right TA will generate leftward COP movement (Gefen 2001; Hopkins et al. 2012). Anatomically, the PL acts directionally opposite the TA; however, we believe that here the TA muscles were activated as the primary controlling muscles to move the COP, and the PL muscles were activated to stabilize the ankles and keep the feet flat on the ground. This is supported by our data, which show that changes in left and

right PL activity accompany changes in left and right TA activity. Our finding of increased right Sol activity is supported by results from Leonard et al. (2009), who observed anticipatory activity in the right Sol for leftward arm reaching movements.

Additionally, we found that the W group adapted by also reducing anticipatory activity in the left TFL and right RF. Similarly, Leonard et al. (2009) found that anticipatory activity decreased in the left TFL and increased in the right TFL as reach direction changed from forward to leftward. In a study of reactive postural control, Henry et al. (2001) found that left RF activity was associated with leftward COP movements; it follows that decreased activity in the right RF relative to the left RF should also be associated with leftward COP movements. We observed these strategies in the W group but not in the N group, which agrees with the idea that hip muscles are more effective in wide stance than in narrow stance. Bingham et al. (2011) demonstrated that hip muscle torques have greater leverage on the COM moment in wide stance than in narrow stance, and are therefore more effective in responding to a perturbation.

It is noteworthy that the batch plots for the TA muscles (Fig. 6B) show that anticipatory activity increased bilaterally early in the *learning 1* block; a similar pattern was seen in other muscle pairs as well. These increases occurred after the initial exposure trial (first *learning 1*) and may be indicative of a “stiffness” strategy using muscle coactivation to help reject the perturbation caused by the force field. Such a strategy has been observed in adaptation to novel arm reaching dynamics (Franklin et al. 2003b; Hinder and Milner 2007; Katayama et al. 1998; Milner and Franklin 2005; Osu et al. 2002) but has not been directly observed in postural adaptation. However, Ahmed and Wolpert (2009) did observe a difference in adaptation rates between COP-APAs and COP-RPAs, suggesting that subjects used a postural coactivation strategy to reduce the need for RPAs while APAs were still being adapted.

### *Transfer of Postural Control*

We predicted that subjects would transfer similar COP movements from one stance to another, with appropriate changes in anticipatory muscle activity to account for the change in configuration. The fact that both groups showed similar COP-APAs in late *learning 1* confirms that similar COP-APAs were appropriate for either stance; therefore, this was a reasonable prediction. The W group did transfer similar COP movements, increasing their anticipatory muscle activity to account for the change to narrow stance, which confirms our prediction. However, contrary to our prediction, the N group significantly increased their COP movements upon transfer; this was related to a lack of sufficient modulation of muscle activity. To account for the change to wide stance and transfer similar postural control, a decrease in muscle activity would have been required. This group showed only small, nonsignificant changes in anticipatory muscle activity upon transfer; thus the high levels of muscle activity caused an increase in COP-APA magnitudes, and COP-RPAs were also increased.

The observed transfer in the W group suggests that the postural control system can control for movement dynamics based on the known properties of the body and the environment, rather than learning to control a specific movement in the

form of a specific muscle activation pattern. Previous studies have shown that subjects can control movement dynamics for arm reaching in unstable environments (e.g., divergent force fields) partially by taking advantage of the inherent mechanical properties of the arm relative to the properties of the environment. Trumbower et al. (2009) found that when reaching in unstable environments subjects chose to reach using arm postures that maximized end-point stiffness in the direction of environmental instability. This allowed subjects to minimize energetically costly muscle coactivation that is employed to increase end-point stiffness and simultaneously provide stability when reaching in unstable environments (Burdet et al. 2001; Franklin et al. 2003a, 2003b, 2007). In a similar experiment with fixed arm postures, Krutky et al. (2010) found that subjects preferentially increased stretch reflexes to perturbations applied in the same direction as the environmental instability only when the magnitude of the instability exceeded end-point stiffness in that direction. This showed that stretch reflexes were specifically modulated for the properties of the environment relative to the inherent properties of the arm. These prior results further support the idea that movements can be controlled based on the known dynamics of the body and the environment.

However, this behavior was not observed in the N group. What could be the potential mechanism underlying such asymmetric transfer? One possible explanation relates to the manner in which the task was initially adapted. It is possible that the N group initially adapted to the task in terms of muscle activity rather than COP movement. As this would result in identical COP movement, differences in the representation of the task would not emerge unless upon transfer. The fact that the N group transferred similar muscle activity to the wide stance width therefore suggests that this may reveal the hidden representation of motor adaptation. Other motor learning studies have found similar results. A study of adaptation to a visuomotor rotation found that adaptation in reaching transferred to walking, but transfer was not observed in the opposite direction, likely because of differences in how the visuomotor rotation was represented in the different contexts of walking and reaching (Morton and Bastian 2004). Another study demonstrated that object dynamics are represented along a continuum from object-space to muscle-space, with the least familiar objects represented in muscle-space (Ahmed et al. 2008). Thus it is possible that the unfamiliarity or reduced BOS of narrow stance may have influenced the representation of the learned task.

There is another possible explanation for the observed asymmetric transfer. The N group may have simply chosen not to change their strategy because it was not required to maintain balance upon transfer to wide stance. Indeed, the larger COP movements observed in the N group upon transfer were acceptable within the larger functional BOS of wide stance. Even after transfer, the N group did not significantly alter their control. These results may be indicative of “good enough” control strategies, as described by Loeb (2012); in the face of increased functional BOS limits upon transfer from narrow to wide stance, despite the fact that the transferred postural control was overly large and clearly nonoptimal, that strategy persisted because it was “good enough.” Similarly, de Rugy et al. (2012) found that habitual patterns of muscle coordination in wrist movements were robust to various physical and virtual

manipulations of biomechanics, despite the fact that these habitual patterns were not optimal in the face of the altered biomechanics.

Results from a previous study suggest that postural control may be transferred differently between postural contexts, depending on whether the level of postural threat is increased or decreased. Jeka et al. (2008) investigated changes in the amplitude of compensatory postural sway in response to abrupt changes in visual environmental motion. They found that when an experimentally induced change in visual motion threatened balance, subjects responded rapidly with a compensatory change in postural sway to maintain upright stance. However, when the change in visual motion did not threaten balance, subjects responded more slowly, presumably because a rapid adjustment was not required. This is analogous to the behavior observed in the present study, where an increase or decrease in BOS size causes a change in the postural threat level. The W group experienced an increase in postural threat during transfer and immediately modulated their muscle control in order to maintain appropriate COP movements. In contrast, the N group experienced a decrease in threat and did not alter their muscle control, because their existing strategy was sufficient, or “good enough.”

With regard to reactive postural control, several other studies have reported findings indicating that the initial postural context in which a task is performed can affect transfer to other contexts. Horak and Nashner (1986) studied reactive postural control in response to a sagittal-plane platform perturbation in two different BOS conditions, with subjects standing on a beam that was wide or narrow in the direction of the perturbation. They found that subjects used a characteristic control strategy in each condition; interestingly, they also found that when subjects transferred from one condition to the other, they initially used an intermediate control strategy before adapting the characteristic strategy of the new condition. In two other studies, de Lima-Pardini et al. (2012) and Papegaaij et al. (2012) studied the effects of voluntary task stability constraints on reactive postural control. Subjects stood on a platform and held a tray (voluntary task) with a half-cylinder placed flat side down (low stability constraint) or round side down (high stability constraint) and were perturbed with backward surface translations (postural task). They found that the constraint condition (low or high stability) in the initial trial block affected transfer of postural control strategy to subsequent trial blocks. In these studies it was suggested that subjects chose to use their prior postural control strategy in the new context, where the prior strategy remained “good enough,” rather than generate a new control strategy, which would require more attention.

An intriguing implication of the present study is that the postural control system may not always choose to control for movement dynamics or have the ability to do so, as when the N group failed to modulate their muscle activity in transfer. An interesting question for future investigation is what might drive this change in strategy and whether it represents a control choice or a constraint.

#### *Effects of BOS Size, Uncertainty, and Threat on Postural Control*

Several earlier studies investigated the effects of postural BOS size on APAs and reported that APAs were reduced in the

direction of smaller BOS size and/or increased in the direction of larger BOS size. However, for various reasons, these studies did not clearly demonstrate that APAs were affected by BOS size alone. In a load-release task performed while standing on a wobble board, Aruin et al. (1998) found that anticipatory muscle activity was reduced with narrower beam widths. However, COP movements may have been biomechanically constrained by the very small BOS of the wobble boards. In the present study, we ensured that both anticipatory and reactive COP movements were not biomechanically constrained but were well within the functional BOS for both stance widths. Kaminski and Simpkins (2001) asked subjects to make forward-reaching arm movements to a target while standing normally or with one foot placed farther forward (thus extending BOS in that direction); they found that anticipatory COP movement amplitude was increased in the foot-forward condition. Similarly, Yiou et al. (2007) also asked subjects to make forward-reaching arm movements, while standing with their two feet perpendicular to each other, and BOS was varied by increasing the distance between the heels in the forward direction; they also found that anticipatory COP movement amplitude was increased in the direction of the extended BOS. However, Yiou et al. further reported that the velocity of the focal reaching movement was also increased with extended BOS size, which itself would require an increased anticipatory COP movement, thus obscuring the effect of BOS size on COP movements alone. In the present study, we ensured that the characteristics of the focal arm movement were similar between stance widths, and thus the same COP-APA could be expected. Our adaptation results clearly show that anticipatory postural control is not affected by BOS size, even in a novel task, as long as the COP movement remains within the functional BOS.

Our adaptation results help to further explain the findings of a recent study by Manista and Ahmed (2012). They performed a force field adaptation experiment, in which subjects reached in multiple directions while standing and adapted to a curl field similar to that used in this study. While the same magnitude of COP-APA was required for a forward vs. a backward force field perturbation, and the required COP-APA was within the BOS in both directions, they found that COP-APAs were significantly reduced in the backward direction. However, it was not possible to determine whether the reduced APAs resulted from the reduced length of the BOS in the backward direction or the increased threat associated with a recovery step in the backward direction compared with a step in the forward direction. A recent study demonstrated that the cost, or threat, associated with an error could indeed modify adaptation, independent of the magnitude of the error (Trent and Ahmed 2013). Taken together, the results of Trent and Ahmed (2013) and the present findings suggest that the reduced APAs observed by Manista and Ahmed (2012) were not due to the reduced BOS length but rather to the increased threat associated with backward perturbations.

Other studies have shown that COP-APAs are reduced in conditions of increased threat or uncertainty. Adkin et al. (2002) asked subjects to stand on a platform and rise to their toes; they found that anticipatory COP movement amplitude and velocity were reduced with greater threat, e.g., when subjects stood on a high vs. a low platform, where the potential consequences of an incorrect APA are greater. Toussaint et al.

(1998) asked subjects to lift several boxes repeatedly; they found that anticipatory COP movement amplitude was reduced when the boxes had a less predictable weight (identical boxes of different masses), i.e., when subjects could not accurately predict the required APA and were therefore more likely to make an inappropriate APA that would require a corrective control action. We suggest that in such cases subjects choose to compensate for the increased threat or uncertainty by decreasing their anticipatory COP movements and thus maintaining a safe stability margin within their existing BOS (Koozekanani et al. 1980).

In the present study, our transfer results support this idea as well. When the W group transferred to narrow stance, they initially modulated their muscle control in order to maintain appropriate COP movements and then chose to reduce their COP movements, avoiding their functional BOS limits. Interestingly, reduced COP movements in narrow stance were not observed in the subjects who initially adapted in a narrow stance (N group). We suggest that this strategy emerged only after transfer from wide to narrow stance because of the increase in postural threat. It is also notable that COP-RPAs were greater for the N group in wide stance (late *learning 2*) than for the W group in wide stance (late *learning 1*), indicating that the N group tolerated larger COP movements after they transferred to wide stance than the W group initially tolerated in wide stance. This suggests that for the N group excessively large COP movements were acceptable after changing to wide stance because of the decrease in postural threat.

#### *Implications for Training and Rehabilitation*

Our results demonstrate that the postural context in which initial adaptation or training occurs can influence transfer to other contexts. Assuming that the control strategies that were adapted at the end of *learning 1* were appropriate strategies for this dynamic task, it would appear that the W group were better at transferring their adapted control to the second stance, because the N group, in contrast, showed excessively large COP movements (both COP-APAs and COP-RPAs) as well as high variability in *learning 2*. This would seem to indicate that it is beneficial to train in a less challenging context. Similarly, Wulf et al. (1998) found that when learning to use a ski simulator subjects performed better when they trained with ski poles for increased support; furthermore, in subsequent practice sessions without poles better performance was seen in subjects who had trained initially with poles than in those who had trained initially without poles. However, another study reported differing results. Domingo and Ferris (2009) found that when subjects were trained to walk on a balance beam either wearing a stabilizing harness or not, performance improvements were greater for subjects who trained without the harness; this result would seem to indicate that it is beneficial to train in a more challenging context.

Taken together with the results of the present study, these findings suggest that in training and rehabilitation it is important to consider the postural context in which task learning or relearning occurs, as well as the context in which the task will be performed in the future. However, it remains unclear whether it is beneficial for initial training to take place in a more challenging or less challenging context. Furthermore, these findings demonstrate that the postural context of initial

training can influence transfer in healthy young adults; future research directions should expand to include clinical populations.

#### *Limitations*

One limitation of this study is that it is possible that other muscles, especially the gluteus medius and the gastrocnemius, could have been active in adapting to this force perturbation (Imagawa et al. 2013; Leonard et al. 2009). However, we were only able to collect EMG data from a limited number of muscles, and these were not included.

Another issue is the time window over which COP movement was averaged for COP-APAs. To be conservative, we took a time window of 50 ms before onset to 100 ms after onset. Figure 3B shows that in late *learning 1* the anticipatory COP movement reaches its velocity peak just before the end of the APA time window; therefore, extending the window would capture more of that COP movement. However, the major reason we did not extend the window was to avoid capturing COP movement caused by the force perturbation. When robot forces are on, the force at the hand and thus the perturbation to the COM begin to develop immediately at the start of movement. This is also shown in Fig. 3B; on the first *learning 1* trial, the COP starts to move almost immediately after time zero (hand movement onset). In response to perturbations, muscle activity has been observed as early as 90–100 ms after perturbation onset (Diener et al. 1988; Horak et al. 1990); therefore, this early COP movement is occurring earlier than any active control response could begin. Neither would it be possible for the subject to be anticipating the force perturbation, because this is the first trial on which the perturbation is experienced. If the APA window were extended, this early COP movement would cause the data to show a false COP-APA. Therefore, because of our chosen time window, our COP-APA results in late *learning 1* are likely underestimated. However, if we had extended the window COP-APAs would be overestimated at the start of *learning 1* because of how the force perturbation influences COP movement immediately after hand movement onset.

#### *Conclusions*

The results of this study demonstrate that initial adaptation of anticipatory postural control, reflected in COP movement, is not affected by stance width. However, transfer of COP control to another stance width is affected by the context of prior exposure. Generally, these results support the idea that the context in which a task is initially introduced should be taken into consideration, as it can have an effect on the transfer or generalization of the adapted control strategy.

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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

## AUTHOR CONTRIBUTIONS

Author contributions: A.P.-S., A.J.B., and A.A.A. conception and design of research; A.P.-S. analyzed data; A.P.-S. and A.A.A. interpreted results of experiments; A.P.-S. prepared figures; A.P.-S. drafted manuscript; A.P.-S. and A.A.A. edited and revised manuscript; A.P.-S., A.J.B., and A.A.A. approved final version of manuscript; A.J.B. performed experiments.

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