RESEARCH ARTICLE

Control of Movement

Whole body adaptation to novel dynamics does not transfer between effectors

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Abstract

How does the brain coordinate concurrent adaptation of arm movements and standing posture? From previous studies, the postural control system can use information about previously adapted arm movement dynamics to plan appropriate postural control; however, it is unclear whether postural control can be adapted and controlled independently of arm control. The present study addresses that question. Subjects practiced planar reaching movements while standing and grasping the handle of a robotic arm, which generated a force field to create novel perturbations. Subjects were divided into two groups, for which perturbations were introduced in either an abrupt or a gradual manner. All subjects adapted to the perturbations while reaching with their dominant (right) arm and then switched to reaching with their nondominant (left) arm. Previous studies of seated reaching movements showed that abrupt perturbation introduction led to transfer of learning between arms, but gradual introduction did not. Interestingly, in this study neither group showed evidence of transferring adapted control of arm or posture between arms. These results suggest primarily that adapted postural control cannot be transferred independently of arm control in this task paradigm. In other words, whole body postural movement planning related to a concurrent arm task is dependent on information about arm dynamics. Finally, we found that subjects were able to adapt to the gradual perturbation while experiencing very small errors, suggesting that both error size and consistency play a role in driving motor adaptation.

NEW & NOTEWORTHY This study examined adaptation of arm and postural control to novel dynamics while standing and reaching and subsequent transfer between reaching arms. Neither arm nor postural control was transferred between arms, suggesting that postural planning is highly dependent on the concurrent arm movement.

anticipatory postural adjustment; interlimb; motor adaptation; motor error; transfer

INTRODUCTION

The ability to maintain stable, upright standing while carrying out other physical tasks is required for many of our daily activities. This ability requires that we generate appropriate postural control when making voluntary movements or compensating for an external perturbation. A common measure of postural control is center of pressure (COP), defined as the application point of the net ground reaction force vector (1). COP provides a measure of the net torque at the ankle (an active control variable) and thus represents the active control being generated to control the movement of the whole body center of mass (COM) (2, 3). Of particular interest is anticipatory postural control, which involves the activation of postural muscles and resultant COP movement initiated before onset of the focal movement or perturbation.

That anticipatory control helps to maintain postural equilibrium by controlling the COM against the impending shift in body mass and other movement dynamics (3–6); it can also aid in generating the desired movement (7–10). To generate anticipatory control 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 anticipatory control will be inappropriate for the actual dynamics, and some reactive or corrective control action will be required. Upon correction, we can then adapt our anticipatory control for subsequent movements to better compensate for internal and external dynamics. These abilities to anticipate and adapt our movement control are frequently taken for granted as we pursue our daily activities, but they are a fundamental component of our ability to maneuver effectively in different environments.

An extant question in the field of motor control is how the central nervous system represents and coordinates the concurrent adaptation of focal movements and whole body posture. A body of previous studies have investigated concurrent adaptation of arm reaching and standing postural control, using an experimental paradigm in which subjects make arm reaching movements while holding the handle of a robotic manipulandum that can generate perturbing forces. With repeated exposure to a given perturbation, subjects learn to anticipate the perturbation and adapt both their arm control and their postural control to compensate (11–14). Theoretically, in this dual-modality task, whole body standing posture is controlled secondary to (i.e., in support of) the focal arm movement; even the postural perturbations are induced via the arm perturbations. However, the whole body posture experiences a perturbation due to the external forces at the hand, and postural control is adapted to minimize overall the whole body effects of that perturbation. Ahmed and Wolpert (11) showed that after subjects adapted their arm reaching movements to novel dynamics while sitting, they were able to generate appropriate postural control immediately upon standing. This indicates that the postural control system can use information about arm movement dynamics to plan appropriate postural control, even though the whole body postural system did not directly experience the novel dynamics during adaptation. However, even when the perturbation was explicitly linked between arm and posture with a perturbation to the arm while standing, all of the studies referenced above showed specific differences in adaptation between the two modalities, suggesting that adaptation occurs via a similar but independent mechanism in each form of movement. Most notably, another study used a similar paradigm with a range of perturbation magnitudes; they found that although arm control was adapted in response to all perturbation magnitudes, postural control was not adapted to the smallest perturbations (15). This supports the idea that postural control may be adapted independently or partially independently in this dual-modality task, rather than being adapted dependent on adaptations in arm control. In other words, whereas some components of postural control are specifically linked to control of the focal reaching movement, other components may be adapted independently in response to the whole body postural perturbation.

In this study, therefore, we sought to answer the question of whether postural control can be adapted and transferred independently, or partially independently, of arm control in this dual-modality task, or if postural control is completely dependent on the adapted arm control. Subjects adapted their arm and postural control to a novel force field while standing and reaching with their dominant (right) arm and then switched to standing and reaching in the same force field with their nondominant (left) arm. The postural control required to support a left-handed versus right-handed reaching movement is slightly different, and similarly the specific control required to counter the force perturbation at the left versus the right hand is slightly different; however, the net force perturbation imparted from the robot arm to the whole body COM is similar, and the COP control required to counteract the perturbation is similar. Therefore, if the postural control system can adapt to, anticipate, and control for the force field dynamics independent of the arm controller, there should be minimal change in the perturbation-specific postural control when subjects switch arms, regardless of whether or not the adapted arm control is transferred.

To investigate that possibility, we sought to control whether or not arm control would be transferred between reaching arms. Two previous studies of arm reaching adaptation found that when subjects adapted their arm reaching movements (while seated) to an "abrupt" perturbation, where the force field was introduced abruptly and experienced at a constant strength throughout the adaptation period, the adapted arm control was transferred from the dominant to the nondominant arm (16, 17). However, when subjects experienced a "gradual" perturbation, where the force field gradually increased in strength from zero over many trials, they showed no transfer from the dominant to the nondominant arm (17). So an abrupt introduction to the force field leads to transfer of learning from right to left in seated reaching movements, but a gradual introduction does not. In the present study, we leveraged these findings to probe the dependence of postural control on arm control.

We tested two groups of subjects, who adapted their arm and postural control to a novel force field with either an abrupt or a gradual development. We then examined the arm and postural behavior upon initial transfer to the nondominant arm, to gain insight into whether postural control can be adapted and transferred independently of arm control. When subjects switched arms, they experienced the same force field and a similar postural perturbation; thus, the change in reaching arm should have a minimal effect on the associated postural control. Based on this, we formed two separate hypotheses about how subjects might transfer their adapted control. First, if the postural control system can independently adapt to, anticipate, and control for the novel dynamics, there should be no change in the perturbation-specific postural control when subjects switch arms, regardless of whether or not the adapted arm control is transferred. Conversely, if the gradual group shows no transfer of either arm or postural control, this would suggest that in this task not only is the postural control system able to generate predictive control based on information from the arm but planning of postural control is also dependent on information about the planned arm movement.

Importantly, the results of this study demonstrate the extent to which postural control is informed by the planned arm control in a concurrent reaching task. This gives us information about how postural control is coordinated with concurrent movement tasks and can provide greater insight into the underlying mechanisms of whole body movement planning.

METHODS

Fourteen healthy young adult subjects (age 24.6 ± 5.1 yr; height 171.7 ± 11.5 cm; mass 68.9 ± 12.4 kg; 7 male, 7 female) participated in the study. All subjects were screened with a health questionnaire and the Edinburgh Handedness Inventory test (18). All subjects were right-handed, had normal or corrected-to-normal vision, and reported no recent musculoskeletal injuries or history of neurological or

musculoskeletal disorders. The University of Colorado Boulder Human Research Committee approved all experimental procedures, and all participants gave written informed consent.
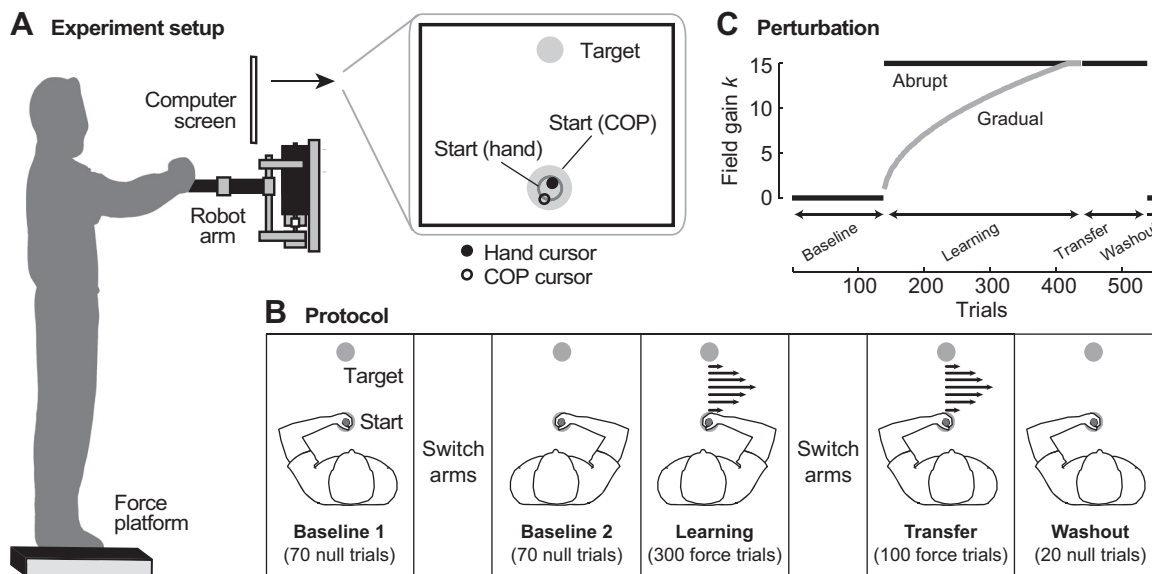
Experimental Apparatus and Setup

Subjects made forward reaching movements in the horizontal plane while grasping the handle of a two-degree-of-freedom planar robotic arm (InMotion2 Shoulder-Elbow Robot, Interactive Motion Technologies Inc.) and standing barefoot on a six-axis, dual-plate force platform (AMTI Dual-Top AccuSway, Advanced Mechanical Technology Inc.) (Fig. 1A). A rigid cradle was attached to the handle to support the arm if needed (separate right- and left-handed cradles were used during reaching with right and left arms), but subjects were instructed not to lean on the handle or cradle. The height of the robot was adjusted for each subject so that the robot arm and handle were level with the subject's sternum (mean height 127.7 ± 7.4 cm across subjects). A computer monitor, vertically suspended in front of the subject, displayed visual feedback of hand, start, and target positions throughout the movement.

Before the experiment began, a "start" circle and a cursor representing COP location were shown on the screen. Subjects were asked to stand such that their COP was centered in the start circle when they were standing comfortably upright and holding the robot handle. Their exact foot position was marked on the force platform to ensure that they always stood in the same location. Subjects were asked to keep their feet flat on the ground throughout the experiment, to ensure that the size of the base of support (BOS) was not affected by lifting or rotation of the feet. They were also explicitly instructed not to lean on the handle of the robot arm for support. To ensure that they were not leaning on the handle, we measured the vertical forces exerted on the handle during the experiment with a force transducer in the handle.

In the experiment, subjects were asked to make 15-cm reaching movements straight ahead ($+y$), using the robot handle to control the cursor on the screen (Fig. 1A). At the start of each trial, subjects were required to hold the 0.6-cm-diameter hand cursor in the center of the 1.6-cm start circle and to maintain their COP location (represented by a separate 0.6-cm cursor of a different color) anywhere within the same start circle. Along with the centering exercise described in the previous paragraph, this ensured that they returned to a neutral position at the beginning of every trial. After a short time delay, the COP cursor 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. After each movement, subjects also received visual feedback about the movement duration, measured from the time at which the hand left the start position to the time at which the 50-ms target requirement was fulfilled. This was to encourage subjects to complete the reaching movements within a duration window of 450–550 ms.

Experimental Protocol

The protocol consisted of 560 trials and was divided into five consecutive blocks: baseline 1 (70 null trials, left arm), baseline 2 (70 null trials, right arm), learning (300 force trials, right arm), transfer (100 force trials, left arm), and washout (20 null trials, left arm) (Fig. 1B). The baseline blocks 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 block consisted of force 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

Figure 1. Experimental setup and protocol. *A*: experimental apparatus and setup; visual feedback is provided on computer screen. *B*: experimental protocol. *C*: force field gain *k* vs. trial; subjects experienced either the Abrupt or Gradual perturbation during the learning block. COP, center of pressure.

perpendicular to the direction of the instantaneous velocity V of the robot handle, with field strength dependent on the gain k (Eq. 1). Thus, for a forward reaching movement (in the anterior direction, $+y$) and a positive value of k, the robot generated rightward perturbing forces ($+x$).

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

Subjects were randomly assigned into one of two groups, Abrupt and Gradual, with $n = 7$ per group. In the learning block, the force field was introduced in either an abrupt or a gradual manner, depending on group (Fig. 1C). The Abrupt group experienced force trials with a constant gain of $k = 15$ N-s/m. For the Gradual group, force field gain k was increased gradually over the first 280 learning trials, with the remaining learning trials at the maximum field strength of $k = 15$ N-s/m. The gradual increase in gain k was dictated by the equation $k = t^a$, where t is learning trial number (excluding channel trials) and $a = \log(15)/\log(T)$; 15 is the maximum final value of k, and T is the learning trial number (excluding channel trials) at which k reaches its maximum (17, 19).

Every trial block began with a null or force trial, immediately followed by a channel trial, with the exception of the transfer block; in that block, the first trial was a channel trial. In the rest of each block, one trial in every batch (5 trials) was chosen randomly to be a channel trial. Channel trials were used to quantify subjects' predictive, feedforward arm control. In channel trials, the robot generated a force channel that restricted the hand trajectory to a straight path between the start position and the target; the robot could then measure the amount of perpendicular force that the subject was exerting into the channel. Stiffness and damping for the channel were 2,000 N/m and 50 N-s/m, respectively. These trials have been shown to have a minimal effect on adaptation or deadaptation (20). The sequence of trial types was identical for all subjects.

After the experiment, subjects played a brief COP game for the purpose of measuring the size of their functional BOS (fBOS), or the limits of the area within the BOS that a person is willing to extend their COP (21–23). In this game, they controlled the cursor with their COP to make a series of 24 leaning movements from the start circle toward eight randomized targets located in different directions, evenly spaced around a 360° circle at 45° angles and at a distance of 13 cm from the central start position (this distance was chosen to encourage subjects to move their COP out as far as possible).

Data Collection and Analysis

Position, velocity, and force data from the robot handle were sampled at 200 Hz. Center of pressure (COP) position data were calculated from force platform data, which were also sampled at 200 Hz. For each side of the dual-plate platform (right and left), eight voltage signals were collected and converted into three-dimensional ground reaction forces (F_x, F_y, F_z) and moments (M_x, M_y, M_z), which were then low-pass filtered at 10 Hz. COP position data for each force plate (right and left) were calculated from these filtered data, relative to the center of the platform $[C_x\ C_y]$, as $[COP_x\ COP_y] = [C_x\ C_y] + [M_y\ M_x]/F_z$, where x and y subscripts denote mediolateral and anteroposterior axes, respectively. The net COP was

then calculated as a weighted average of the COP for each plate by the method described by Winter et al. (24). COP velocity was calculated from net COP position with a five-point differentiation algorithm. All COP data for each subject were normalized to foot length (mean 25.7 ± 2.2 cm across subjects).

All data were aligned to movement onset, such that *time 0* represents movement onset of the arm, and truncated at movement end. Movement onset was defined as 50 ms before the time when tangential hand position and velocity exceed threshold values of 0.25 cm and 2 cm/s, respectively. Movement end was defined as the time 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. Note that for forward reaching movements ($+y$), the force perturbation is in the rightward direction ($+x$).

Trials were excluded from analysis if the movement onset criterion was inaccurate (by visual inspection) or if the data were corrupted. A total of eight trials were rejected, out of the entire data set, with five trials excluded for the Abrupt group and three trials for the Gradual group (out of 3,920 total trials per group, with 560 trials per subject). These were all channel trials. On average, less than one trial was rejected per subject.

Arm control.

Arm control was quantified with two metrics: hand error and anticipatory force. Hand error was calculated for each trial, excluding channel trials, as the peak signed value of the perpendicular deviation of the handle trajectory from a straight path between the start and target positions. Anticipatory force was calculated, for channel trials only, as the perpendicular channel force at the time of peak tangential hand velocity. This was therefore a measure of the amount of force being exerted by the subject at the time when peak perturbation force would be experienced in the force field. As a measure of forces experienced in the force field, we quantified field force as the peak signed value of perpendicular force (exerted by the robot arm) on force trials.

Postural control.

The rightward ($+x$) force perturbation in this experiment exerts a net rightward torque on the COM, causing the COM to be perturbed to the right. To recover, subjects activate postural muscles to generate a leftward torque on the COM, which is represented by rightward COP movement. This may be viewed colloquially as the COP moving to the right to "catch" the COM, to recover from the perturbation. This recovery action is termed a "reactive postural adjustment" and can serve as a measure of postural error, somewhat analogous to hand error. When subjects have adapted to the force perturbation, they generate anticipatory control to counter the predicted perturbation, represented by rightward COP movement that begins near movement onset; this early COP movement is termed an "anticipatory postural adjustment" and serves as a measure of anticipatory postural control, analogous to anticipatory force at the hand.

Postural control was quantified for each trial, excluding channel trials, with three COP movement metrics: reactive postural adjustment (RPA$_d$) based on COP displacement,

reactive postural adjustment (RPA_a) based on COP acceleration, and anticipatory postural adjustment (APA) based on COP displacement. All of these metrics were based on the normalized COP displacement or acceleration in the direction of the force perturbation ($+x$, perpendicular to the direction of reaching movement). We observed that COP velocity responses on force trials began no earlier than 100 ms after movement onset, and COP displacement responses occurred later than that. Therefore, as a conservative measure of anticipatory control, APA was calculated as the peak signed value of COP displacement observed between 50 ms before movement onset and 100 ms after movement onset. Over the remaining duration of the movement (after the APA time period), RPA_d was calculated as the peak signed value of COP displacement and RPA_a was calculated as the peak value of COP acceleration.

RPA_d and similar metrics using COP velocity are typical measures of postural error used in this experimental paradigm (11–15). However, by the end of learning, these metrics remain elevated relative to baseline because of the fact that subjects anticipate a perturbation by initiating COP movement near arm movement onset and that COP displacement is then propagated into the reactive portion of the movement. Therefore, we included the additional RPA_a metric as a way to measure the quickness of the COP movement. When subjects experience a large unexpected perturbation, COP acceleration will be high, reflecting a quick COP movement made in reaction to the perturbation. However, when subjects are correctly anticipating the perturbation and/or the relative perturbation is small (as with the gradual perturbation), COP movements are slower and smoother, and COP acceleration and thus RPA_a will remain low.

Statistics

Data were compared between groups and across eight phases of the protocol: late baseline 1 and 2 (LB1, LB2), first learning (FL), late learning (LL), first transfer (FT), late transfer (LT), first washout (FW), and late washout (LW). The "first" phases consisted of one trial only; for anticipatory force these phases consisted of the first channel trial in the block, and for all other metrics these phases consisted of the first force or null trial in the block. One exception is that for both anticipatory force and APA the first transfer phase consisted of the first trial (channel trial) in the transfer block. For all metrics, the "late" phases consisted of the last four batches (16 null or force trials, or 4 channel trials) of the trial block.

Hand error, anticipatory force, RPA_d, RPA_a, and APA data were analyzed with repeated-measures ANOVAs, with phase as a within-subject factor and group as a between-subjects factor. To test for adaptation during right-handed reaching, we made planned comparisons on the within-subject results for each group between the late baseline 2, first learning, and late learning phases (all 3 phases are from right-handed movement blocks). To compare adaptation between groups, we made a planned comparison in the late learning 1 phase. When testing for transfer, we included comparisons for right- and left-handed phases to respective right- and left-handed baseline, to control for differences in reaching-specific control versus perturbation-specific control. To test for

initial transfer of adaptation to left-handed reaching, we made planned comparisons on the within-subject results for each group between the late learning and first transfer phases (right-handed vs. left-handed phases) and between the late baseline 1 and first transfer phases (both are left-handed phases). To examine transfer behavior more closely, we also made planned comparisons within each individual subject between the late baseline 1 and first transfer trials, using independent two-sample t tests. To examine the time course of transfer, we made additional planned comparisons on the within-subject results for each group between the first transfer and late transfer phases. Planned comparisons were also made between groups at specific phases of interest. Unless otherwise noted, we used paired t tests for within-subject planned comparisons between phases and independent two-sample t tests for planned comparisons between groups.

All data analyses were performed with MATLAB. For all statistical tests, the criterion for significance was set at the level of $\alpha = 0.05$. Mean values are reported in the text as mean ± standard deviation.

RESULTS

Both groups adapted their arm and postural control as expected while reaching with the right arm (Fig. 2, *A–D*). When initially exposed to the force field, the Abrupt group showed large rightward movement errors, in the same direction as the perturbing forces, but the Gradual group did not. With practice, however, both groups increased their anticipatory control to counter the force field. Despite the difference in the abrupt versus gradual force field introduction, and the corresponding differences in initial movement errors, both groups showed similar adaptation of arm and postural control by the end of learning. Interestingly, neither group showed evidence of transferring the adapted control of arm or posture from right-handed to left-handed reaching, but both groups subsequently adapted their control in left-handed reaching and showed similar control by the end of the transfer block. This is illustrated in the transfer trajectories of Fig. 2, *E–H*, where upon switching to the left arm both groups initially showed anticipatory control similar to late baseline 1 (left-handed reaching) and showed large rightward movement errors, but with practice they increased their anticipatory control.

Results are presented below for adaptation and transfer of arm control (hand error and anticipatory force) and postural control (RPA_d, RPA_a, and APA) as well as movement characteristics (reaching velocity, field force, and COP displacements).

Arm Control in Adaptation and Transfer

As expected, both the Abrupt and Gradual groups adapted similarly to the reaching dynamics by the end of the learning block. Hand error and anticipatory force were similar between groups in late baseline 1 and late baseline 2 (all P values ≥ 0.281). In the first learning phase, peak velocities were similar between groups ($P = 0.814$); as expected, peak field forces were significantly different ($P < 0.001$) because of the difference in field gains. By late learning, peak
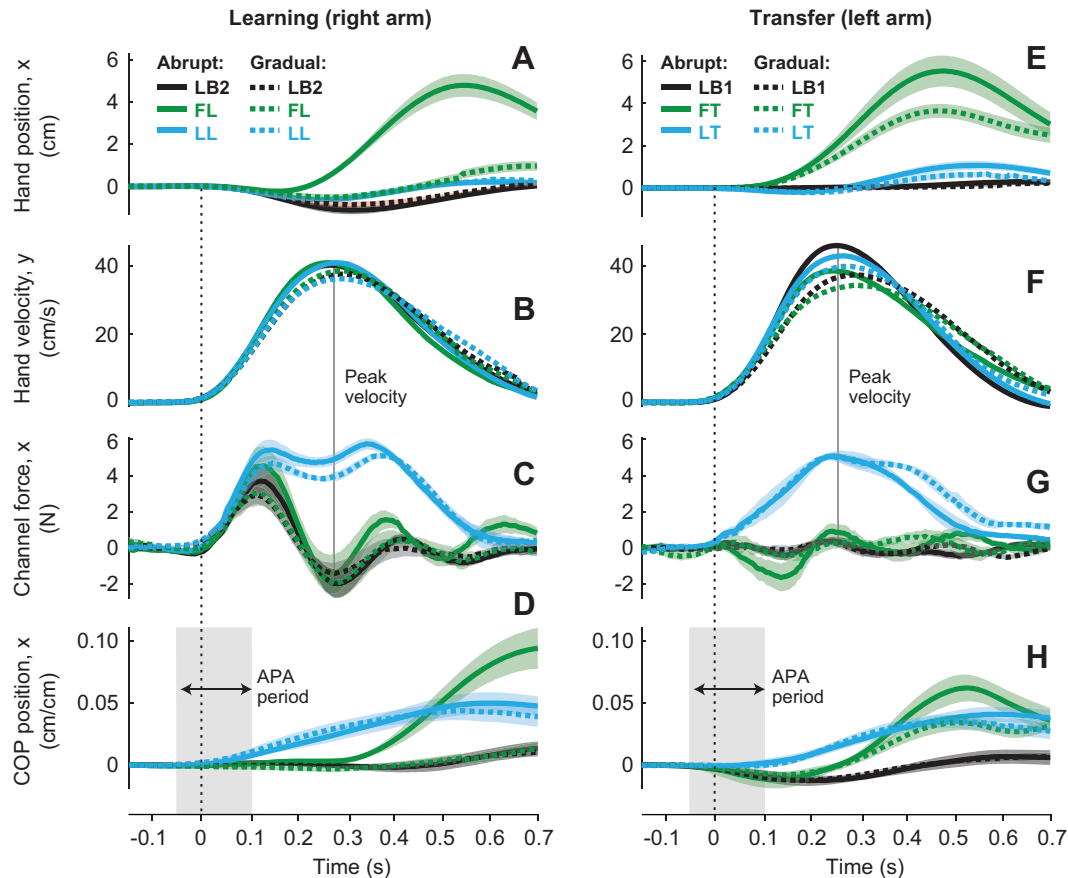
Figure 2. Group mean trajectories (Abrupt: $N = 7$; Gradual: $N = 7$). Mean trajectory data are shown for perpendicular hand position (force trials only), tangential reaching velocity and channel force (channel trials only), and perpendicular center of pressure (COP) position (force trials only). Data for Abrupt group are plotted with solid lines; data for Gradual group are plotted with dashed lines. A–D: data for right-handed reaching phases: late baseline 2 (LB2), first learning (FL), and late learning (LL). E–H: data for left-handed reaching phases: late baseline 1 (LB1), first transfer (FT), and late transfer (LT). Note that trajectories were averaged across trials in each phase for each subject, then averaged across subjects in each group. Shading indicates SE across subjects. Time 0 represents movement onset of the arm. APA, anticipatory postural adjustment.

velocities and field forces were again similar between groups (both P values $\geq$ 0.289).

In the first transfer phase, peak velocities and field forces in the force trial (second trial in transfer block) were significantly lower in the Gradual group compared with the Abrupt group (P = 0.018), despite the same field gain. However, in the channel trial, which was the very first trial in the transfer block, peak velocities were similar between groups (P = 0.202); therefore, there should be no difference in the magnitude of the anticipated perturbation (proportional to reaching velocity). In late transfer, peak velocities and field forces were similar between groups (both P values $\geq$ 0.360).

Hand error and anticipatory force data (Fig. 3) show that both groups adapted to the field with the right arm during the learning block. Interestingly, both groups then failed to transfer this adaptation to the left arm initially but subsequently showed further adaptation with the left arm throughout the rest of the transfer block. For hand error, the ANOVA revealed main effects of phase (P < 0.001, F = 148.54) and group (P < 0.001, F = 80.32) as well as an interaction effect of phase × group (P < 0.001, F = 13.35). For anticipatory force, the ANOVA revealed a main effect of phase (P < 0.001, F = 75.54) but did not show a main effect

of group (P = 0.106, F = 3.06) or an interaction effect (P = 0.465, F = 0.96).

Adaptation.

To test for movement adaptation in the right arm, we focused on hand error and anticipatory force in the late baseline 2, first learning, and late learning phases (Fig. 3, C and E). In the Abrupt group, hand error significantly increased from late baseline 2 to first learning and then decreased from first learning to late learning (both P values < 0.001). In the Gradual group, hand error did show a relatively very small, but significant, increase from late baseline 2 to first learning (P < 0.001); however, hand error then showed no change from first learning to late learning (P = 0.429). Anticipatory force was significantly different from late baseline 2 to late learning in both groups (both P values < 0.001), demonstrating that both groups adapted to the novel dynamics. To compare the extent of adaptation of arm control between groups, we made planned comparisons between the changes in hand error and anticipatory force from late baseline 2 to late learning (Fig. 3, D and F). These changes were similar between groups (hand error P = 0.473; anticipatory force P = 0.227), indicating that the groups adapted similarly in the right arm by the end of the learning block.
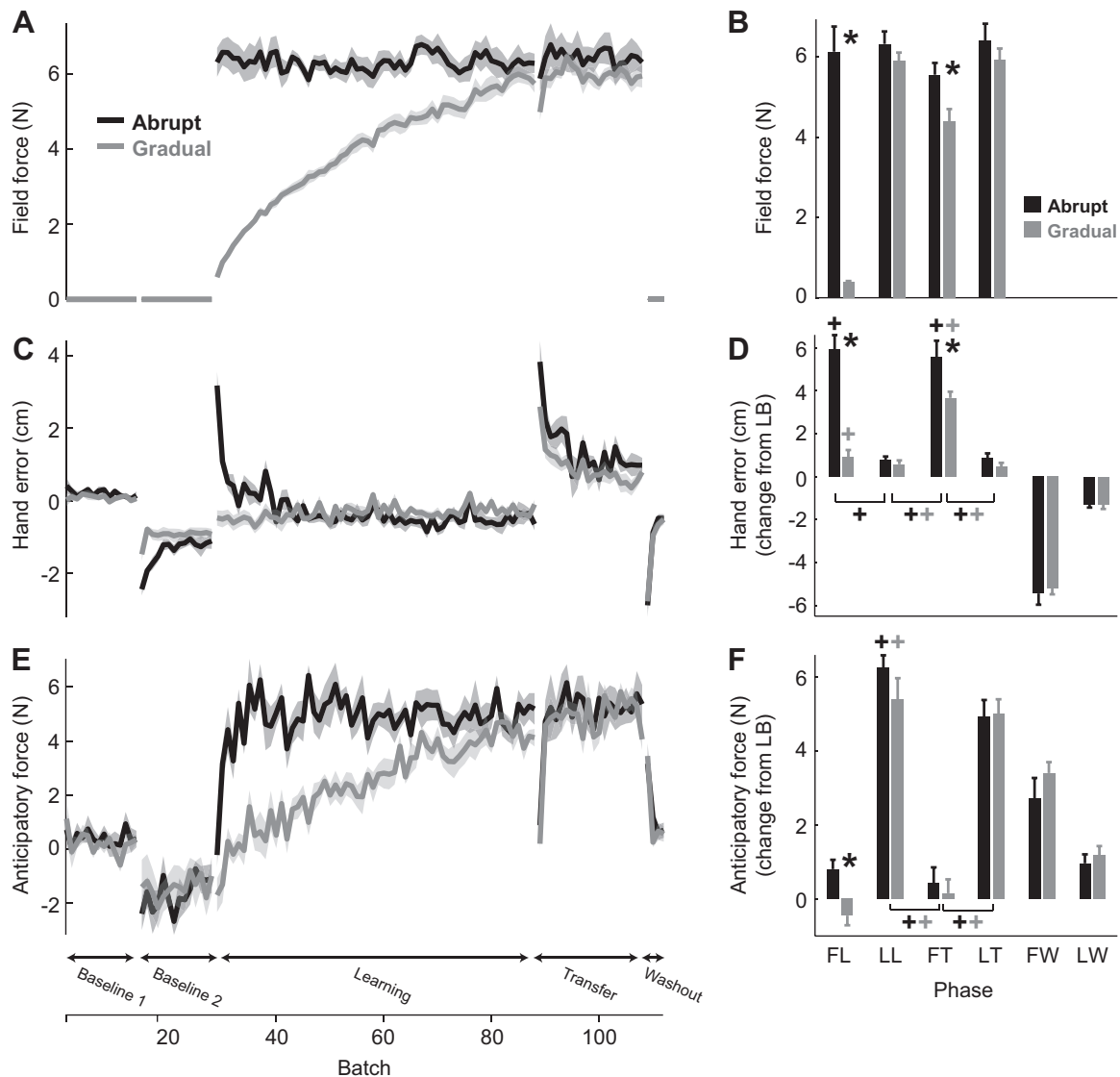
Figure 3. Arm control metrics. Data shown are peak field force (*A* and *B*), hand error (*C* and *D*), and anticipatory force (*E* and *F*). Black, Abrupt group (*N* = 7); gray, Gradual group (*N* = 7). *A*, *C*, and *E*: each metric vs. batch (5 trials); in each plot, 2 traces show group means (solid lines) ± SE (shading). *B*, *D*, and *F*: the change from respective late baseline (LB) to first learning (FL, from LB2), late learning (LL, from LB2), first transfer (FT, from LB1), late transfer (LT, from LB1), first washout (FW, from LB1), and late washout (LW, from LB1), with error bars showing SE. (*B* shows actual peak force values, because field force is 0 in baseline.) *Statistically significant differences between groups (*P* < 0.050). +Statistically significant difference within group in change from respective baseline or between other phases where indicated (*P* < 0.050).

Transfer.

To test for transfer of adapted arm control from the right to the left arm, we focused on the late baseline 1, late learning, and first transfer phases (Fig. 3, *C* and *E*). From late learning to first transfer, both groups showed significant reductions in anticipatory force and increases in hand error (all *P* values < 0.001), indicating a lack of transfer to reaching with the left arm. We next compared initial transfer performance to baseline performance, before any exposure to the novel dynamics. From late baseline 1 to first transfer, both groups showed no significant change in anticipatory force (both *P* values ≥ 0.342) and a significant increase in hand error (both *P* values < 0.001), indicating that when subjects switched to the left arm they used arm control that was similar to left-handed baseline; they did not anticipate the perturbation in

the left arm and thus experienced large errors as a consequence. Subsequently, both groups adapted to the perturbation in the left arm, showing significant decreases in hand error and significant increases in anticipatory force from first transfer to late transfer (all *P* values < 0.001).

To compare the degree of transfer between groups, we made planned comparisons between the changes in hand error and anticipatory force from late baseline 1 to first transfer and late transfer (Fig. 3, *D* and *F*). The changes in anticipatory force from late baseline 1 to first transfer were similar between groups (*P* = 0.628), indicating that the groups showed a similar lack of transfer. The Gradual group did show a smaller change in hand error from late baseline 1 to first transfer compared with the Abrupt group (*P* = 0.035); however, this is likely due to the fact that the Gradual group

reached with a smaller peak velocity and experienced a smaller peak field force than the Abrupt group ($P = 0.018$) (Fig. 3B). The changes in hand error and anticipatory force from late baseline 1 to late transfer were similar between groups (both P values ≥ 0.184), indicating that the groups adapted similarly in the left arm by the end of the transfer block.

Postural Control in Adaptation and Transfer

RPA and APA data (Fig. 4) show that both groups adapted their postural control to the field during the learning block when reaching with the right arm; both groups then failed to transfer this adaptation when they switched to the left arm initially but subsequently showed further adaptation throughout the rest of the transfer block. For RPA_d, the ANOVA revealed main effects of phase ($P < 0.001$, $F = 28.04$) and group ($P = 0.016$, $F = 7.91$) as well as an interaction effect

of phase × group ($P < 0.001$, $F = 5.39$). For RPA_a, the ANOVA revealed a main effect of phase ($P < 0.001$, $F = 8.31$) but did not show a main effect of group ($P = 0.328$, $F = 1.04$) or an interaction effect ($P = 0.328$, $F = 1.17$). For APA, the ANOVA revealed a main effect of phase ($P < 0.001$, $F = 8.97$) but did not show a main effect of group ($P = 0.935$, $F = 0.01$) or an interaction effect ($P = 0.947$, $F = 0.31$). We expand upon these results below.

Adaptation.

To test for postural adaptation while reaching with the right arm, we focused on RPA_d, RPA_a, and APA in the late baseline 2, first learning, and late learning phases (Fig. 4, A, C, and E). In the Abrupt group, RPA_d and RPA_a significantly increased from late baseline 2 to first learning (both P values ≤ 0.018) and then decreased from first learning to late learning (RPA_d $P = 0.055$; RPA_a $P = 0.008$). In the Gradual group, RPA_a
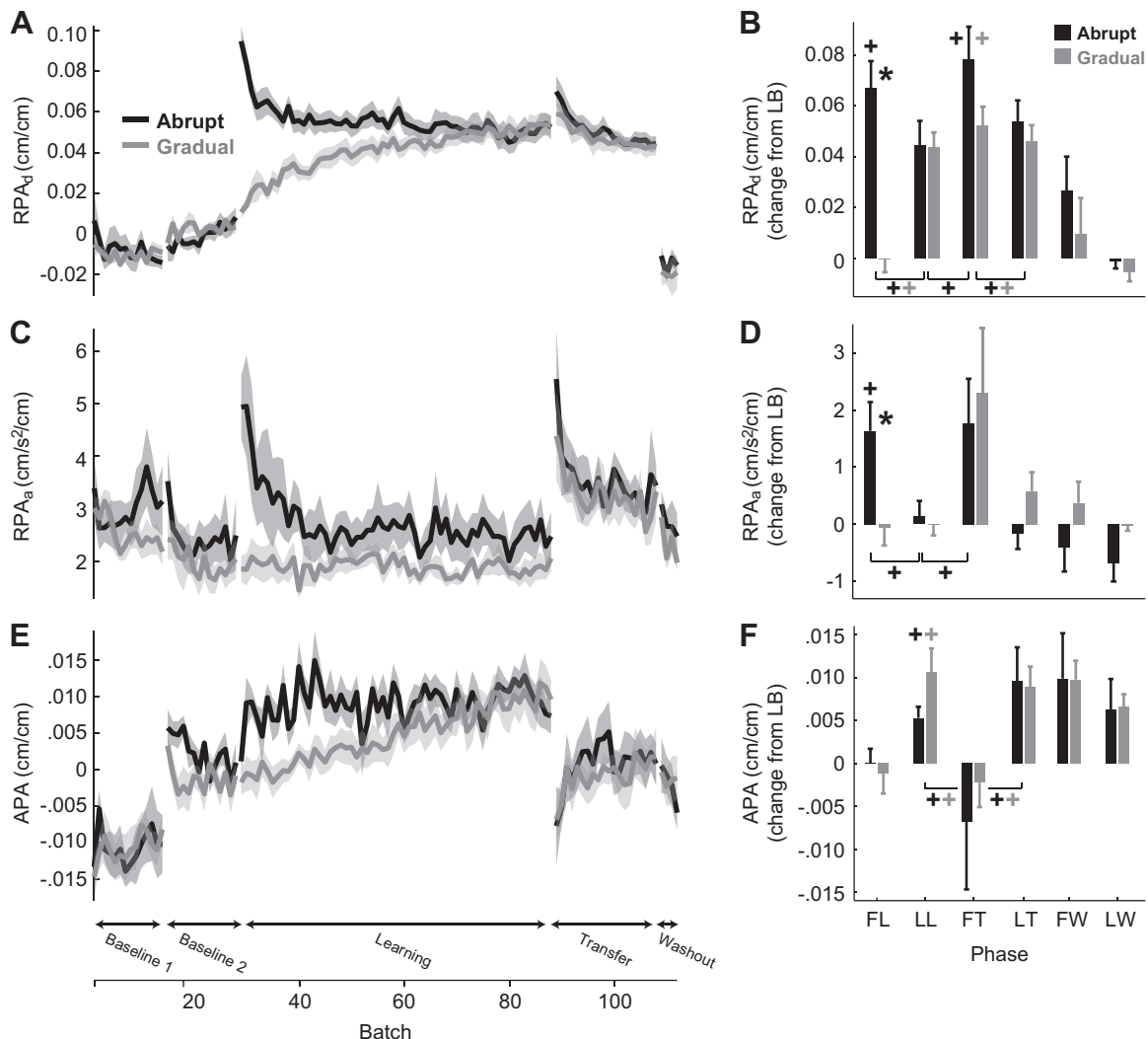
Figure 4. Postural control metrics. Data shown are reactive postural adjustment based on center of pressure (COP) displacement (RPA_d; A and B), reactive postural adjustment based on COP acceleration (RPA_a; C and D), and anticipatory postural adjustment (APA; E and F). Black, Abrupt group ($N = 7$); gray, Gradual group ($N = 7$). A, C, and E: each metric vs. batch (5 trials); in each plot, 2 traces show group means (solid lines) ± SE (shading). B, D, and F: the change from respective late baseline (LB) to first learning (FL, from LB2), late learning (LL, from LB2), first transfer (FT, from LB1), late transfer (LT, from LB1), first washout (FW, from LB1), and late washout (LW, from LB1), with error bars showing SE. *Statistically significant differences between groups ($P < 0.050$). +Statistically significant difference within group in change from respective baseline or between other phases where indicated ($P < 0.050$).

showed no significant change from late baseline 2 to first learning or from first learning to late learning (both P values $\geq$ 0.870). Similarly, RPA_d did not show a significant change from late baseline 2 to first learning (P = 0.963), but then it significantly increased from first learning to late learning (P = 0.001). However, that increase over the learning block was related to adaptation of APA, which significantly increased from late baseline 2 to late learning in both groups (both P values $\leq$ 0.009). (As discussed in METHODS, in the Gradual group RPA_a was expected to remain low because of the incremental perturbation and RPA_d was expected to increase throughout learning because the COP movement that is initiated in the APA is propagated into the reactive time period.) To compare adaptation of postural control between groups, we made planned comparisons between the changes in RPA_d, RPA_a, and APA from late baseline 2 to late learning (Fig. 4, B, D, and F). These changes were similar between groups (RPA_d P = 0.940; RPA_a P = 0.668; APA P = 0.113), indicating that the groups adapted their postural control to the same extent by the end of the learning block.

Transfer.

To test for transfer of adapted postural control from the right to the left arm, we focused on the late baseline 1, late learning, and first transfer phases (Fig. 4, A, C, and E). From late learning to first transfer, both groups showed a significant reduction in APA (both P values $\leq$ 0.011), indicating reduced anticipatory control for the novel dynamics. Accordingly, the Abrupt group showed significant changes in RPA_d and RPA_a (both P values $\leq$ 0.018), indicating a greater corrective response to the unanticipated dynamics. However, although RPA_d and RPA_a corrective responses increased in the Gradual group, the changes did not reach significance (RPA_d P = 0.275; RPA_a P = 0.052).

Anticipatory control in both groups upon first transfer was also similar to baseline performance, before exposure to the novel dynamics. From late baseline 1 to first transfer they showed no significant change in APA (both P values $\geq$ 0.421). Accordingly, there was a significant increase in RPA_d (both P values $<$ 0.001) and an increase in RPA_a (Abrupt P = 0.066; Gradual P = 0.091). This indicates that when subjects switched to the left arm they used postural control that was similar to left-handed baseline reaching; they did not anticipate the perturbation and thus needed to compensate with large reactive COP movements. Subsequently, both groups adapted to the perturbation while reaching with the left arm, showing significant decreases in RPA_d (both P values $\leq$ 0.029), slight decreases in RPA_a (Abrupt P = 0.058; Gradual P = 0.086), and significant increases in APA (both P values $\leq$ 0.035) from first transfer to late transfer.

To compare transfer between groups, we made planned comparisons between the changes in RPA_d, RPA_a, and APA from late baseline 1 to first transfer and late transfer (Fig. 4, B, D, and F). The changes in all three metrics from late baseline 1 to first transfer were similar between groups (all P values $\geq$ 0.111), indicating that the groups showed a similar lack of transfer. The Gradual group did show a trend toward a smaller change in RPA_d from late baseline 1 to first transfer compared with the Abrupt group (P = 0.111); however, as we observed with hand error, this is likely due to the fact that the Gradual group reached with a smaller peak velocity and

experienced a smaller peak field force than the Abrupt group (Fig. 3B).The changes from late baseline 1 to late transfer were also similar between groups (all P values $\geq$ 0.105), indicating that the groups adapted their postural control similarly by the end of the transfer block.

Alternative Metrics and Additional Transfer Analyses

To ensure that our findings were not dependent on a specific choice of metrics, we performed additional analyses using alternative measures of anticipatory force and APA. These included a metric termed the anticipatory force coefficient, taken as the regression coefficient of the channel force profile onto the ideal force profile (where ideal force is the product of tangential hand velocity and the gain of the force trial immediately preceding the channel trial), and APA, taken as mean COP velocity or as peak signed COP velocity during the APA period. With these alternative measures our findings remained similar. For anticipatory force coefficients, the ANOVA showed a main effect of phase (P < 0.001, F = 32.66) but did not show a main effect of group (P = 0.279, F = 1.28) or an interaction effect (P = 0.754, F = 0.60). For the alternative measures of APA, ANOVAs showed a main effect of phase (mean COP velocity P < 0.001, F = 9.35; peak signed COP velocity P < 0.001, F = 9.98) but did not show a main effect of group (mean COP velocity P = 0.556, F = 0.37; peak signed COP velocity P = 0.782, F = 0.08) or an interaction effect (mean COP velocity P = 0.972, F = 0.25; peak signed COP velocity P = 0.990, F = 0.17). From late baseline 1 to first transfer, all three alternative metrics showed no significant change in either group (anticipatory force coefficient both P values $\geq$ 0.411; mean COP velocity both P values $\geq$ 0.412; peak signed COP velocity both P values $\geq$ 0.666). Similar to our original metrics, these results indicate that when subjects switched from right-handed to left-handed reaching they used anticipatory arm and postural control that was similar to left-handed baseline.

We wished to further confirm our finding that learned control was not transferred from right-handed to left-handed reaching. To do so, we performed additional analyses on anticipatory force and APA data, including the above alternative metrics. First, we quantified transfer as the percentage of anticipatory control transferred from late learning to the initial transfer trial (i.e., we quantified control on the first transfer trial as a percentage of mean control in the late learning phase) for each metric of anticipatory control (25). For anticipatory force and anticipatory force coefficients, this transfer percentage was not significantly different from zero in either group (all P values $\geq$ 0.398). Similarly, for all measures of APA (original and alternative), this percentage was not significantly different from zero in either group (all P values $\geq$ 0.495). These results confirm our original findings of no transfer. Second, we compared the trials in late baseline 1 and first transfer within each individual subject. Anticipatory force was similar between late baseline 1 and first transfer for six of seven subjects in the Abrupt group (P values $\geq$ 0.146; for remaining subject P = 0.029) and all seven subjects in the Gradual group (P values $\geq$ 0.122). (This analysis was not performed for the alternative metric, anticipatory force coefficients, because it would involve comparing a set of zero values in late baseline to a single nonzero value on

the first transfer trial.) APAs, quantified with our original metric, were similar between late baseline 1 and first transfer for six of seven subjects in the Abrupt group (P values $\geq$ 0.221) and six of seven subjects in the Gradual group (P values $\geq$ 0.061). Using the alternative APA metrics, we found comparable results: APAs were similar between late baseline 1 and first transfer for six of seven subjects in the Abrupt group (using mean COP velocity) or five of seven subjects in the Abrupt group (using peak signed COP velocity) and all seven subjects in the Gradual group (using both alternative metrics). These results show that in initial transfer the majority of individual subjects used anticipatory arm and postural control that was similar to left-handed baseline. Thus, this also confirms our finding that subjects did not transfer their learned control.

Postural Adaptation Is Sensitive to Small Errors

With this data set we can also ask the question of whether postural adaptation can be driven by very small errors. A previous study, using a trial-to-trial adaptation paradigm in which perturbations of randomly varying strengths were applied to the hand while subjects stood and made arm reaching movements, found that although arm adaptation was sensitive to small error magnitudes, postural adaptation seemingly was not (15). That study compared those small error magnitudes to errors experienced in unperturbed baseline movements and found that small hand error magnitudes were significantly different from baseline; importantly, however, small postural error magnitudes were indistinguishable from baseline. To make a similar comparison, we compared error magnitudes for the Gradual group in first learning and late learning to error magnitudes in late baseline 2. Hand error magnitudes in both phases were similar to late baseline 2 (first learning P = 0.415; late learning P = 0.172). RPA_a magnitudes were also similar to late baseline 2 (first learning P = 0.827; late learning P = 0.110). RPA_d magnitudes in first learning were similar to late baseline 2 (P = 0.617). RPA_d magnitudes in late learning were significantly increased from late baseline 2 ($P < 0.001$), but, as we discussed above, this was related to APA adaptation. Thus, our results show that error magnitudes experienced by the Gradual group during learning were similar to those experienced in unperturbed baseline movements. Despite this, adaptation was able to occur in both arm and posture.

For reference, we also wished to compare initial adaptation of anticipatory control between arm and posture. For each subject, we found the learning batch at which anticipatory force and APA significantly diverged from late baseline 2 values, using independent t tests to compare for statistically significant differences between trials in late baseline 2 and each subsequent batch. Group mean results are shown in Fig. 5. We then compared between metrics within each group, using one-tailed paired t tests. In both groups, anticipatory force diverged faster than APA (Abrupt P = 0.016; Gradual P = 0.018), indicating that anticipatory learning progressed faster in the arm than in posture.

Control Analyses

Subjects were explicitly instructed not to lean on the handle of the robot arm for support. To ensure that they were not leaning on the handle, we measured the vertical forces
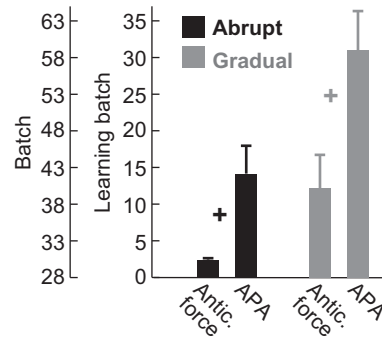
Figure 5. Initial adaptation. Bar plot showing group mean value of learning batch (where learning batch 1 is the first batch of learning trials, or *batch 29* overall) at which anticipatory force and anticipatory postural adjustment (APA) significantly diverge from late baseline 2 values. Black, Abrupt group (N = 7); gray, Gradual group (N = 7). Error bars show SE. +Statistically significant difference within group ($P < 0.050$).

exerted on the handle during the experiment with a force transducer in the handle. The average peak vertical forces were 1.14 ± 0.28 N for the Abrupt group and 1.04 ± 0.28 N for the Gradual group ($<1\%$ of body weight); this suggests that the forces were sufficiently low to indicate they were not leaning on the handle.

We compared maximum lateral COP displacements during the experiment, in both groups, 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. Across all subjects, mean foot length was 25.7 ± 2.2 cm. In the COP game, averaged across all subjects, the maximum normalized lateral displacement was 0.42 ± 0.12 cm/cm, or a lateral functional BOS limit (measured from center) of 10.8 ± 2.9 cm. In the experiment, maximum lateral COP displacements in the Abrupt group were 0.12 ± 0.02 cm/cm (normalized), or 3.1 ± 0.5 cm; in the Gradual group they were 0.08 ± 0.03 cm/cm (normalized), or 2.2 ± 0.5 cm. COP displacements in the experiment did not meet or exceed the limits of the functional BOS in any subject. These results confirm that, for both groups, COP movements developed in response to the force field were well within the limits of the functional BOS.

The type of perturbation used in our experiment is particularly useful for studying adaptation of postural control, because the components of COP movement that are specific to the perturbation are perpendicular to components related to the focal reaching movement and therefore can be clearly isolated (11–13, 15). In this experiment, the perturbation acted in the rightward ($+x$) direction because subjects reached forward to the target (along the $+y$-axis), and the force field acted at a 90° angle in a clockwise direction. Thus, the components of COP movement that were specific to the perturbation were along the x-axis and could be examined without the confounding effect of the reaching movement along the y-axis. Related to the reaching movement itself, y-axis APAs were observed consistently on all trials; specifically, the COP moved away from the target before hand movement onset, as has been observed previously (12, 13, 15). However, the requirements in this direction did not change

whether the force field was active or not, and as there were no perturbations in this direction, these were simply prelearned APAs that were not relevant to the experiment. To confirm that these reaching-specific *y*-axis APAs were not affected by the perturbing forces and related adaptation in the perpendicular direction (along the *x*-axis), we examined *y*-axis APAs between phases and between groups. Reaching-specific APAs were measured in the direction of reaching as the peak signed value of COP displacement, similar to perturbation-specific APAs, but taken between 100 ms before movement onset and 50 ms after movement onset (11, 12, 26). Across all subjects, the magnitude of the reaching APA showed no significant differences between phases (all *P* values ≥ 0.053), except for a reduction in APA magnitude in both groups from late learning to first transfer (Abrupt *P* = 0.036; Gradual *P* = 0.049). However, this was likely related to the drop in peak forward reaching velocity that was observed concurrently (Abrupt *P* = 0.087; Gradual *P* = 0.002). Magnitudes did not significantly differ between groups at any phase (all *P* values ≥ 0.072). It should be noted that, even in the direction of the perturbation, the dynamics related to the arm movement and forces at the arm do have an impact on COP movements, independent of active postural control. Experimentally, it is not possible to completely separate out the components of postural movement that are attributable to anticipatory control, reactive control, and arm movement. In the future, modeling work could help to disambiguate the contributions of these factors.

DISCUSSION

In this study we sought to answer the question of whether postural control can be adapted and transferred independently or partially independently of arm control in a dual-modality standing-and-reaching task, or if postural control is completely dependent on the adapted arm control. Using a dynamic force learning paradigm with concurrent arm and postural adaptation, we found that when subjects switched to the nondominant arm after adapting with the dominant arm, neither arm nor postural adaptation was transferred. Thus we found no evidence that postural control was adapted or transferred independently of arm control. Rather, considered together with previous findings, our results suggest that predictive postural control in this task is generated secondary to the focal arm movement, while allowing for some posture-specific modulation within those constraints.

The lack of arm transfer was an unexpected result compared with previous studies of seated reaching. This may have been caused by the addition of the standing component of the task, which could theoretically interfere with transfer because of adverse effects on uncertainty and/or attentional processing. We also uncovered a novel finding in the Gradual group, where adaptation was able to occur in both arm and posture despite subjects experiencing very small errors with magnitudes within the range of inherent baseline variability. This suggests that error consistency as well as error size play a role in driving motor adaptation.

Postural Control Was Not Transferred in Either Group

We found that both groups failed to transfer their adapted postural control from right-handed to left-handed reaching, even though they adapted their arm and postural control by the end of learning. When subjects switched arms, they were still holding the same robotic arm and reaching in the same force field; thus, the expected postural perturbation caused by the force field, and the associated postural control, should remain the same. Whereas any learned arm control would need to be transferred from one arm to the other, postural control requires no transfer except that which is linked to the specific reaching arm; if any components of postural control were adapted independently from the arm, no transfer of those components would be required. However, we found that the adapted control was not transferred in either arm or posture. When subjects switched arms, they defaulted to baseline left-handed reaching patterns, and their postural control also defaulted to baseline left-handed patterns. Therefore, our results show no evidence that postural control was adapted or transferred independently of arm control.

Ahmed and Wolpert (11) showed that after subjects adapted their arm reaching movements to novel dynamics while sitting, they were able to generate appropriate postural control immediately upon standing, even though the postural system did not directly experience the novel dynamics during adaptation. This indicates that the postural control system can plan appropriate postural control based on information about arm movement dynamics; i.e., the postural controller can learn from the arm controller. But is the inverse true—can the arm controller learn from the postural controller? If that were possible, the arm controller could theoretically incorporate additional information from the postural controller when transferring control between arms. Our findings did not support this idea; rather, our findings suggest that the arm controller planned its movement independently and the postural controller planned its control according to the arm controller's anticipated movement dynamics. In two previous adaptation studies using the same standing-and-reaching task, differing postural conditions (change in BOS size) led to differences in postural control but did not affect control of the focal arm reaching task (13, 14). In another study by Patron et al. (27), subjects made arm reaching movements while standing in microgravity and adapted their arm and postural control in response to the microgravity environment. Note that in this case the "perturbation" was purely environmental and acted equally on the entire body, rather than a force that is applied directly to the arm and is thus applied indirectly to the whole body posture. Even in that case, they found that posture was not controlled over and above the focal arm movement but rather postural control was highly correlated with arm control. Thus it seems that the arm controller does not learn from the postural controller, at least when the arm movement is focal, but further research is needed to provide a more conclusive answer.

Overall, our findings suggest that in a combined postural and arm movement task, not only is the postural control system able to generate predictive control based on information from the arm but postural planning is also dependent on information about the planned arm movement. Furthermore, whether or not appropriate postural control is adapted independently, those adaptations can be overwritten by arm control upon transfer to a new context. This is because predictive postural control is generated secondary to (i.e., in

support of) the focal arm movement and is based on the brain's prediction of how whole body dynamics will be affected by arm movement dynamics. Therefore, because the brain did not predict novel dynamics at the arm, predictive postural control was not generated for those dynamics. Where previous studies observed specific differences in adaptation between the two modalities (11–15), this may point to a kind of limited autonomy rather than fully independent adaptation: the postural controller can modulate its control to suit the known postural conditions, within the constraints dictated by the planned arm movement and its associated dynamics.

Arm Control Was Not Transferred in Either Group

Both groups failed to transfer their adapted arm control from right-handed to left-handed reaching. When we compare these findings to previous studies involving seated arm reaching, the results are mixed. Two previous studies examined adaptation of seated arm reaching to a similar gradual force perturbation, using the same number of adaptation trials (160) and a similar trial sequence, and subsequently also examined transfer from the dominant to the nondominant arm. Findings differed between the two studies. Malfait and Ostry (17) found no transfer between arms, but, using different data analysis methods, Joiner et al. (25) found small but significant transfer. Our Gradual group results agree with the finding of no transfer, despite the use of similar methods and analyses.

Interestingly, however, our Abrupt group results differ from all previous findings. Three studies found that when subjects adapted their seated arm reaching to a similar abrupt force perturbation, they transferred their adapted control from the dominant to the nondominant arm (16, 17, 25). In contrast, we found that subjects in the Abrupt group showed no transfer between arms. In those previous studies, subjects adapted to a force field gain of 13 or 15 N-s/m, over training periods of 450, 160, and 15 trials; in the present study, subjects adapted to the same type of force field with a similar gain of 15 N-s/m, over a period of 300 trials. Therefore, the difference in our findings was not due to perturbation strength or training duration. We also ensured that our findings were robust to alternative data metrics and additional analyses.

In each of these previous studies, at least one condition led to some transfer from the dominant to the nondominant reaching arm. However, we clearly showed that neither group transferred their learned arm control. It seems likely, therefore, that the lack of transfer can be attributed to the major unique feature of our experiment: the addition of the standing component. In all of the previously mentioned studies, subjects performed reaching movements while seated; in our experiment, they reached while standing. This could have adversely affected uncertainty and/or attentional processing, both of which are influential factors in adaptation and transfer. However, we did not directly compare adaptation between seated and standing conditions; this is an area for possible further research.

Movement complexity and variability, and thus overall uncertainty, are greater in a standing reaching task compared with a seated reaching task; these factors could have led to a change in error assignment that thus contributed to the lack of arm transfer. When Malfait and Ostry (17) found no transfer between arms, they suggested that this was because the very small error sizes experienced during adaptation to the gradual perturbation led to a lack of higher cognitive information about the force field, and thus inhibited transfer. A modeling study by Berniker and Kording (28) supported this explanation. Their model indicated that during adaptation to novel dynamics the brain prefers to attribute motor errors to a misestimate of body properties (e.g., reaching arm) rather than to a change in environmental properties (e.g., robotic training device). Thus, the brain will assume the misestimate is mostly localized to the first arm and will not transfer that control to the other arm. When errors are small and/or uncertainty is high, errors are even more likely to be attributed to the arm than to the environment (19, 29), and control that is adapted in response to those errors is less likely to be transferred to the other arm (16, 28). Similar to this idea, Werner et al. (30) found that in adaptation to visuomotor perturbations, awareness of the nature of the perturbation (i.e., awareness of what is causing movement errors) was correlated with transfer between reaching arms; stronger perturbations with an abrupt introduction (compared to smaller perturbations and/or gradual introduction) led to greater awareness and greater transfer. However, others have found that awareness has little effect on transfer (31). Nonetheless, this "awareness" may be related to uncertainty about the source of movement errors, which can negatively affect error assignment and thus transfer.

The standing component of this task likely also had an adverse cognitive effect on the reaching task compared with a seated reaching task. This effect was further exacerbated by the presence of postural perturbations. Several studies have shown that when postural control is more attentionally demanding because of decreased BOS and/or increased postural threat (e.g., standing vs. sitting, standing with a narrow vs. normal BOS, or standing on a high vs. low platform), performance on a concurrent mental task is negatively affected (e.g., reaction times are slowed in an auditory reaction time task) (32–35). Evidence from studies of brain activity suggests that this is a direct result of competing demands on attentional resources in the brain (36, 37). Other studies have shown that responding to a postural perturbation can also draw attentional resources away from a concurrent visual or mental task (38–40). These findings suggest that attentional resources, and thus cognitive processing, may be reduced for the arm reaching task when performed concurrently with a standing postural task compared with a simple seated reaching task. Theoretically, this might interfere with storage and transfer of motor memories, which could result in reduced transfer of motor control. More specifically, the additional cognitive demands may also have a deleterious effect on how the brain processes and assigns motor errors.

It is also possible that the added postural component of this task had a negative effect on adaptation overall due to increased uncertainty and attentional demands. One previous study provides support for this idea: Manista and Ahmed (12) used a similar experimental paradigm, in which subjects adapted their arm reaching to novel dynamics while standing and reaching in multiple directions. They found that subjects adapted their postural control less for a

backward perturbation than for a forward perturbation, correlating with reduced BOS and greater postural threat in the backward direction. It is possible that adaptation was negatively affected by the greater attentional demands of those conditions. Another study found that postural threat also can lead to changes in movement decision-making (41). When choosing between target-directed whole body leaning movements of varying risk (probability of target success vs. monetary reward), subjects chose less risky movements in a condition of greater postural threat. That condition did not have a similar effect on decisions about arm reaching movements, but subjects did restrict their arm movement variability as well as whole body movement variability. These findings may indicate more complex effects of postural threat or difficulty on the attentional demands and cognitive processing of movement control, especially in more complex movement situations such as responding to external perturbations.

Arm and Postural Control Were Adapted in Both Groups

We found that the groups adapted similarly by the end of learning, in both arm and posture. Several earlier studies found that in arm reaching with a visuomotor or dynamic perturbation, adaptation was similar or greater when the perturbation was introduced gradually rather than abruptly (17, 19, 25, 42, 43). For example, Kagerer et al. (42) found that in visuomotor adaptation the gradual group exhibited smaller errors at the end of adaptation than the abrupt group, indicating that they had adapted to a greater extent. However, the duration of adaptation in these studies varied between 84 and 180 trials, with the initial period of gradual increase ranging from 57 to 145 trials. In our experiment the groups adapted over 300 trials, with the final 20 trials at full perturbation strength. Our findings indicate that, given a sufficiently long adaptation period, subjects will adapt similarly whether the perturbation is abrupt or gradual.

This experiment also allows us to address the question of how error size affects adaptation. In general, adaptation of arm reaching movements is found to increase with error size and/or perturbation size (44–49). Interestingly, in an earlier study with a similar standing-and-reaching adaptation paradigm, Pienciak-Siewert et al. (15) found that although subjects did show increasing adaptation with increasing error sizes, they did not adapt their postural control in response to small error magnitudes that fell within the range of inherent movement variability. As mentioned above, smaller errors in dynamic learning are more likely to be attributed to the body, whereas larger errors will be attributed to the environment (e.g., robotic training device) (19, 28, 29). For example, Torres-Oviedo and Bastian (29) found that in adaptation to a locomotor perturbation on a treadmill, smaller errors induced by a gradual perturbation led to improved transfer to overground walking; however, those small error sizes were significantly larger than errors experienced in preperturbation baseline conditions and thus could serve as a distinct error signal to drive adaptation. Similarly, two studies found that when arm reaching was adapted to a gradual visuomotor or dynamic perturbation, subjects experienced errors that were small but still larger than baseline (19, 42). Based on the idea that smaller errors are more likely to be

attributed to the body, Pienciak-Siewert et al. (15) suggested that very small postural errors were small enough to be attributed to inherent postural variability rather than to external forces and thus could not serve as an error signal to drive adaptation. However, the randomly varying perturbation strengths in that experiment likely contributed a high degree of uncertainty, which also may have led to reduced adaptation. Wei and Kording (49) found that in an arm reaching task with visuomotor perturbations, subjects adapted more slowly when the uncertainty of visual feedback was increased via noise added to the cursor position. Stevenson et al. (50) tested a standing task in which subjects controlled their COP position in the presence of random visual perturbations to COP cursor feedback; similar to Wei and Kording, they found that perturbation responses were reduced when noise was added to the cursor position.

In the present experiment, uncertainty was reduced; both groups experienced errors that were consistently biased in a single direction rather than randomly varying. In the Gradual group, the postural error magnitudes (RPA_a) experienced during learning were very small, within the range of movement variability experienced in unperturbed baseline movements; however, adaptation still occurred to a similar extent as in the Abrupt group. Our results show conclusively that subjects can adapt their postural control to very small errors, if those errors are consistently biased so as to minimize uncertainty. Despite being unrelated to our main experimental question, this is nonetheless a novel finding and suggests that both error size and consistency play a role in driving adaptation.

Our adaptation results also showed that anticipatory force diverged from late baseline faster than APA in both groups, indicating that anticipatory learning progressed faster in the arm than in posture. In a similar dynamic adaptation experiment, Ahmed and Wolpert (11) found that anticipatory learning in the arm progressed at a faster rate than anticipatory postural control. These results might be explained as an effect of error uncertainty in arm versus posture. In both experiments, uncertainty may have been greater for postural error than for arm error because subjects received explicit visual feedback about hand movements (via the hand position cursor) in addition to proprioceptive feedback but did not receive explicit visual feedback about posture during movement. However, it is also possible that anticipatory learning in the arm was faster because of the focal nature of the arm movement. This aligns with the idea, discussed above, that in this standing-and-reaching task, planning and adaptation of anticipatory postural control are dependent on the dynamics of the arm movement. If that is the case, it follows that anticipatory learning in posture would lag behind anticipatory learning in the arm.

Clinical Implications

In general, it is desirable for learning acquired in one context to be transferred to other contexts. In this study we found that in a standing-and-reaching task, neither arm nor postural learning was transferred when subjects switched reaching arms. The addition of the standing component of the task (compared to a seated reaching task), as well as postural perturbations, may have led to greater uncertainty

about task performance and error assignment. In addition, those elements may have drawn increased attentional resources to postural control, thus reducing the amount of resources available for arm control (33–40). Theoretically, any of those factors could have interfered with storage and/or transfer of the learned dynamics. Therefore, when designing training and rehabilitation paradigms, it is important to consider the possible effects of performing concurrent tasks.

This would be especially important in clinical populations who exhibit poor motor performance in some areas. For example, older adults can demonstrate reduced postural stability (21, 51–56), reduced mobility (57–59), and reduced ability to recover from perturbations (60–63). These may be related to the fact that postural tasks can be more attentionally demanding in older adults than in young adults (34, 38, 64, 65). Another study showed that when older adults experienced a postural perturbation they exhibited delayed attentional switching between postural control and a concurrent visuomotor task (39). This suggests that older adults may have impaired attentional dynamics, which could exacerbate the deleterious effects of concurrent task performance, especially when adapting to novel dynamics, which requires additional cognitive resources.

Our adaptation results suggest that both error size and consistency play a role in driving motor adaptation. Therefore, both of these factors should be considered in the design of training and rehabilitation paradigms. Some clinical populations make larger and more variable baseline errors in their postural control, such as older adults (52, 54–56) and stroke survivors (66). Because of their larger baseline errors, it is possible that they might be unable to respond to a greater range of "small" errors, compared with healthy individuals, if they are unable to distinguish those errors from their natural errors. However, in light of our present findings, a highly consistent error signal could help to reduce uncertainty and could thus improve adaptation.

Conclusions

The results of this study suggest that in a dynamic force learning paradigm with concurrent adaptation of arm reaching and standing posture, learned postural control can be overwritten by planned arm dynamics. In other words, postural movement planning related to a concurrent focal arm task is dependent on information about arm dynamics, but not vice versa. Taken together with previous findings, this supports the idea that predictive postural control is generated secondary to the planned arm dynamics, with limited autonomy for posture-specific modulation within those constraints.

Generally, our findings demonstrate that although postural control is a separate process from arm control it is nonetheless dependent on arm control. Furthermore, it is important to consider the possible effects of performing concurrent tasks in rehabilitation and training regimens, especially when transfer is of concern.

We highlight one other "small" but notable finding. Subjects were able to adapt their movement control while experiencing only very small errors with magnitudes within the range of inherent baseline variability, when those errors were consistently biased so as to minimize uncertainty.

Therefore, both error size and consistency should be considered in the design of training and rehabilitation regimens.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

A.P.-S. and A.A.A. conceived and designed research; A.P.-S. performed experiments; 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. and A.A.A. approved final version of manuscript.

REFERENCES

1. **Murray MP**, **Seireg A**, **Scholz RC.** Center of gravity center of pressure and supportive forces during human activities. *J Appl Physiol* 23: 831–838, 1967. doi:10.1152/jappl.1967.23.6.831.

2. **Morasso P**, **Casadio M**, **De Santis D**, **Nomura T**, **Rea F**, **Zenzeri J.** Stabilization strategies for unstable dynamics. *J Electromyogr Kinesiol* 24: 803–814, 2014. doi:10.1016/j.jelekin.2014.10.006.

3. **Winter DA**, **Patla AE**, **Frank JS.** Assessment of balance control in humans. *Med Prog Technol* 16: 31–51, 1990.

4. **Belen'kiĭ VE**, **Gurfinkel' VS**, **Pal'tsev EI.** [Control elements of voluntary movements]. *Biofizika* 12: 135–141, 1967.

5. **Massion J.** Movement, posture and equilibrium: interaction and coordination. *Prog Neurobiol* 38: 35–56, 1992. doi:10.1016/0301-0082(92)90034-c.

6. **Traub MM**, **Rothwell JC**, **Marsden CD.** Anticipatory postural reflexes in Parkinson's disease and other akinetic-rigid syndromes and in cerebellar ataxia. *Brain* 103: 393–412, 1980. doi:10.1093/brain/103.2.393.

7. **Bouisset S**, **Richardson J**, **Zattara M.** Are amplitude and duration of anticipatory postural adjustments identically scaled to focal movement parameters in humans? *Neurosci Lett* 278: 153–156, 2000. doi:10.1016/s0304-3940(99)00912-x.

8. **Bouisset S**, **Zattara M.** Biomechanical study of the programming of anticipatory postural adjustments associated with voluntary movement. *J Biomech* 20: 735–742, 1987. doi:10.1016/0021-9290(87)90052-2.

9. **Stapley PJ**, **Pozzo T**, **Cheron G**, **Grishin A.** Does the coordination between posture and movement during human whole-body reaching ensure center of mass stabilization? *Exp Brain Res* 129: 134–146, 1999. doi:10.1007/s002210050944.

10. **Stapley P**, **Pozzo T**, **Grishin A.** The role of anticipatory postural adjustments during whole body forward reaching movements. *Neuroreport* 9: 395–401, 1998. doi:10.1097/00001756-199802160-00007.

11. **Ahmed AA**, **Wolpert DM.** Transfer of dynamic learning across postures. *J Neurophysiol* 102: 2816–2824, 2009. doi:10.1152/jn.00532.2009.

12. **Manista GC**, **Ahmed AA.** Stability limits modulate whole-body motor learning. *J Neurophysiol* 107: 1952–1961, 2012. doi:10.1152/jn.00983.2010.

13. **Pienciak-Siewert A**, **Barletta AJ**, **Ahmed AA.** Transfer of postural adaptation depends on context of prior exposure. *J Neurophysiol* 111: 1466–1478, 2014. doi:10.1152/jn.00235.2013.

14. **Pienciak-Siewert A**, **Horan DP**, **Ahmed AA.** Role of muscle coactivation in adaptation of standing posture during arm reaching. *J Neurophysiol* 123: 529–547, 2020. doi:10.1152/jn.00939.2017.

15. **Pienciak-Siewert A**, **Horan DP**, **Ahmed AA.** Trial-to-trial adaptation in control of arm reaching and standing posture. *J Neurophysiol* 116: 2936–2949, 2016. doi:10.1152/jn.00537.2016.

16. **Criscimagna-Hemminger SE**, **Donchin O**, **Gazzaniga MS**, **Shadmehr R.** Learned dynamics of reaching movements generalize from dominant to nondominant arm. *J Neurophysiol* 89: 168–176, 2003. doi:10.1152/jn.00622.2002.

17. **Malfait N**, **Ostry DJ.** Is interlimb transfer of force-field adaptation a cognitive response to the sudden introduction of load? *J Neurosci* 24: 8084–8089, 2004. doi:10.1523/JNEUROSCI.1742-04.2004.

18. **Oldfield R.** The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9: 97–113, 1971. doi:10.1016/0028-3932(71)90067-4.

19. **Kluzik J**, **Diedrichsen J**, **Shadmehr R**, **Bastian AJ.** Reach adaptation: what determines whether we learn an internal model of the tool or adapt the model of our arm? *J Neurophysiol* 100: 1455–1464, 2008. doi:10.1152/jn.90334.2008.

20. **Scheidt RA**, **Reinkensmeyer DJ**, **Conditt MA**, **Rymer WZ**, **Mussa-Ivaldi FA.** Persistence of motor adaptation during constrained, multi-joint, arm movements. *J Neurophysiol* 84: 853–862, 2000. doi:10.1152/jn.2000.84.2.853.

21. **Holbein-Jenny MA**, **McDermott K**, **Shaw C**, **Demchak J.** Validity of functional stability limits as a measure of balance in adults aged 23-73 years. *Ergonomics* 50: 631–646, 2007. doi:10.1080/00140130601154814.

22. **King MB**, **Judge JO**, **Wolfson L.** Functional base of support decreases with age. *J Gerontol* 49: M258–M263, 1994. doi:10.1093/geronj/49.6.m258.

23. **Lee TH**, **Lee YH.** An investigation of stability limits while holding a load. *Ergonomics* 46: 446–454, 2003. doi:10.1080/0014013021000039583.

24. **Winter DA**, **Prince F**, **Frank JS**, **Powell C**, **Zabjek KF.** Unified theory regarding A/P and M/L balance in quiet stance. *J Neurophysiol* 75: 2334–2343, 1996. doi:10.1152/jn.1996.75.6.2334.

25. **Joiner WM**, **Brayanov JB**, **Smith MA.** The training schedule affects the stability, not the magnitude, of the interlimb transfer of learned dynamics. *J Neurophysiol* 110: 984–998, 2013. doi:10.1152/jn.01072.2012.

26. **Aruin AS**, **Latash ML.** The role of motor action in anticipatory postural adjustments studied with self-induced and externally triggered perturbations. *Exp Brain Res* 106: 291–300, 1995. doi:10.1007/BF00241125.

27. **Patron J**, **Stapley P**, **Pozzo T.** Human whole-body reaching in normal gravity and microgravity reveals a strong temporal coordination between postural and focal task components. *Exp Brain Res* 165: 84–96, 2005. doi:10.1007/s00221-005-2283-0.

28. **Berniker M**, **Kording K.** Estimating the sources of motor errors for adaptation and generalization. *Nat Neurosci* 11: 1454–1461, 2008. doi:10.1038/nn.2229.

29. **Torres-Oviedo G**, **Bastian AJ.** Natural error patterns enable transfer of motor learning to novel contexts. *J Neurophysiol* 107: 346–356, 2012. doi:10.1152/jn.00570.2011.

30. **Werner S**, **Strüder HK**, **Donchin O.** Intermanual transfer of visuomotor adaptation is related to awareness. *PLOS One* 14: e0220748, 2019. doi:10.1371/journal.pone.0220748.

31. **Taylor JA**, **Wojaczynski GJ**, **Ivry RB.** Trial-by-trial analysis of intermanual transfer during visuomotor adaptation. *J Neurophysiol* 106: 3157–3172, 2011. doi:10.1152/jn.01008.2010.

32. **Gage WH**, **Sleik RJ**, **Polych MA**, **McKenzie NC**, **Brown LA.** The allocation of attention during locomotion is altered by anxiety. *Exp Brain Res* 150: 385–394, 2003. doi:10.1007/s00221-003-1468-7.

33. **Lajoie Y**, **Teasdale N**, **Bard C**, **Fleury M.** Attentional demands for static and dynamic equilibrium. *Exp Brain Res* 97: 139–144, 1993. doi:10.1007/BF00228824.

34. **Lajoie Y**, **Teasdale N**, **Bard C**, **Fleury M.** Upright standing and gait: are there changes in attentional requirements related to normal aging? *Exp Aging Res* 22: 185–198, 1996. doi:10.1080/03610739608254006.

35. **Remaud A**, **Boyas S**, **Caron GA**, **Bilodeau M.** Attentional demands associated with postural control depend on task difficulty and visual condition. *J Mot Behav* 44: 329–340, 2012. doi:10.1080/00222895.2012.708680.

36. **Fujita H**, **Kasubuchi K**, **Wakata S**, **Hiyamizu M**, **Morioka S.** Role of the frontal cortex in standing postural sway tasks while dual-tasking: a functional near-infrared spectroscopy study examining working memory capacity. *BioMed Res Int* 2016: 7053867, 2016. doi:10.1155/2016/7053867.

37. **Little CE**, **Woollacott M.** EEG measures reveal dual-task interference in postural performance in young adults. *Exp Brain Res* 233: 27–37, 2015. doi:10.1007/s00221-014-4111-x.

38. **Brown LA**, **Shumway-Cook A**, **Woollacott MH.** Attentional demands and postural recovery: the effects of aging. *J Gerontol A Biol Sci Med Sci* 54: M165–M171, 1999. doi:10.1093/gerona/54.4.M165.

39. **Maki BE**, **Zecevic A**, **Bateni H**, **Kirshenbaum N**, **McIlroy WE.** Cognitive demands of executing postural reactions: does aging impede attention switching? *Neuroreport* 12: 3583–3587, 2001. doi:10.1097/00001756-200111160-00042.

40. **Norrie RG**, **Maki BE**, **Staines WR**, **McIlroy WE.** The time course of attention shifts following perturbation of upright stance. *Exp Brain Res* 146: 315–321, 2002. doi:10.1007/s00221-002-1172-z.

41. **O'Brien MK**, **Ahmed AA.** Threat affects risk preferences in movement decision making. *Front Behav Neurosci* 9: 150, 2015. doi:10.3389/fnbeh.2015.00150.

42. **Kagerer FA**, **Contreras-Vidal JL**, **Stelmach GE.** Adaptation to gradual as compared with sudden visuo-motor distortions. *Exp Brain Res* 115: 557–561, 1997.

43. **Michel C**, **Pisella L**, **Prablanc C**, **Rode G**, **Rossetti Y.** Enhancing visuomotor adaptation by reducing error signals: single-step (aware) versus multiple-step (unaware) exposure to wedge prisms. *J Cogn Neurosci* 19: 341–350, 2007. doi:10.1162/jocn.2007.19.2.341.

44. **Fine MS**, **Thoroughman KA.** Trial-by-trial transformation of error into sensorimotor adaptation changes with environmental dynamics. *J Neurophysiol* 98: 1392–1404, 2007. doi:10.1152/jn.00196.2007.

45. **Herzfeld DJ**, **Vaswani PA**, **Marko MK**, **Shadmehr R.** A memory of errors in sensorimotor learning. *Science* 345: 1349–1353, 2014. doi:10.1126/science.1253138.

46. **Marko MK**, **Haith AM**, **Harran MD**, **Shadmehr R.** Sensitivity to prediction error in reach adaptation. *J Neurophysiol* 108: 1752–1763, 2012. doi:10.1152/jn.00177.2012.

47. **Scheidt RA**, **Dingwell JB**, **Mussa-Ivaldi FA.** Learning to move amid uncertainty. *J Neurophysiol* 86: 971–985, 2001. doi:10.1152/jn.2001.86.2.971.

48. **Trent MC**, **Ahmed AA.** Learning from the value of your mistakes: evidence for a risk-sensitive process in movement adaptation. *Front Comput Neurosci* 7: 118, 2013. doi:10.3389/fncom.2013.00118.

49. **Wei KL**, **Körding K.** Uncertainty of feedback and state estimation determines the speed of motor adaptation. *Front Comput Neurosci* 4: 11, 2010. doi:10.3389/fncom.2010.00011.

50. **Stevenson IH**, **Fernandes HL**, **Vilares I**, **Wei KL**, **Körding KP.** Bayesian integration and non-linear feedback control in a full-body motor task. *PLOS Comput Biol* 5: e1000629, 2009. doi:10.1371/journal.pcbi.1000629.

51. **Binda SM**, **Culham EG**, **Brouwer B.** Balance, muscle strength, and fear of falling in older adults. *Exp Aging Res* 29: 205–219, 2003. doi:10.1080/03610730303711.

52. **Campbell AJ**, **Borrie MJ**, **Spears GF.** Risk factors for falls in a community-based prospective-study of people 70 years and older. *J Gerontol* 44: M112–M117, 1989. doi:10.1093/geronj/44.5.M112.

53. **Fujimoto M**, **Hsu WL**, **Woollacott MH**, **Chou LS.** Ankle dorsiflexor strength relates to the ability to restore balance during a backward support surface translation. *Gait Posture* 38: 812–817, 2013. doi:10.1016/j.gaitpost.2013.03.026.

54. **Maki BE**, **Holliday PJ**, **Topper AK.** A prospective-study of postural balance and risk of falling in an ambulatory and independent elderly population. *J Gerontol* 49: M72–M84, 1994. doi:10.1093/geronj/49.2.m72.

55. **Melzer I**, **Benjuya N**, **Kaplanski J.** Postural stability in the elderly: a comparison between fallers and non-fallers. *Age Ageing* 33: 602–607, 2004. doi:10.1093/ageing/afh218.

56. **Overstall PW**, **Exton-Smith AN**, **Imms FJ**, **Johnson AL.** Falls in elderly related to postural imbalance. *Br Med J* 1: 261–264, 1977. doi:10.1136/bmj.1.6056.261.

57. **Chen TR**, **Chou LS.** Altered center of mass control during sit-to-walk in elderly adults with and without history of falling. *Gait Posture* 38: 696–701, 2013. doi:10.1016/j.gaitpost.2013.03.007.

58. **Hurt CP**, **Grabiner MD.** Age-related differences in the maintenance of frontal plane dynamic stability while stepping to targets. *J Biomech* 48: 592–597, 2015. doi:10.1016/j.jbiomech.2015.01.003.

59. **Rogers MW**, **Kukulka CG**, **Brunt D**, **Cain TD**, **Hanke TA.** The influence of stimulus cue on the initiation of stepping in young and older adults. *Arch Phys Med Rehabil* 82: 619–624, 2001. doi:10.1053/apmr.2001.20833.

60. **Graham DF**, **Carty CP**, **Lloyd DG**, **Barrett RS.** Biomechanical predictors of maximal balance recovery performance amongst community-dwelling older adults. *Exp Gerontol* 66: 39–46, 2015. doi:10.1016/j.exger.2015.04.006.

61. **Honarvar MH**, **Nakashima M.** A new measure for upright stability. *J Biomech* 47: 560–567, 2014. doi:10.1016/j.jbiomech.2013.09.028.

62. **Kuo AD**, **Zajac FE.** A biomechanical analysis of muscle strength as a limiting factor in standing posture. *J Biomech* 26, Suppl 1: 137–150, 1993. doi:10.1016/0021-9290(93)90085-s.

63. **Robinovitch SN**, **Heller B**, **Lui A**, **Cortez J.** Effect of strength and speed of torque development on balance recovery with the ankle strategy. *J Neurophysiol* 88: 613–620, 2002. doi:10.1152/jn.2002.88.2.613.

64. **Maylor EA**, **Wing AM.** Age differences in postural stability are increased by additional cognitive demands. *J Gerontol B Psychol Sci Soc Sci* 51: P143–P154, 1996. doi:10.1093/geronb/51b.3.p143.

65. **Woollacott M**, **Shumway-Cook A.** Attention and the control of posture and gait: a review of an emerging area of research. *Gait Posture* 16: 1–14, 2002. doi:10.1016/s0966-6362(01)00156-4.

66. **Reisman DS**, **Wityk R**, **Silver K**, **Bastian AJ.** Split-belt treadmill adaptation transfers to overground walking in persons poststroke. *Neurorehabil Neural Repair* 23: 735–744, 2009. doi:10.1177/1545968309332880.