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Stability limits modulate whole-body motor learning

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Manista GC, Ahmed AA. Stability limits modulate whole-body motor learning. *J Neurophysiol* 107: 1952–1961, 2012. First published January 11, 2012; doi:10.1152/jn.00983.2010.—Our daily movements exert forces upon the environment and also upon our own bodies. To control for these forces, movements performed while standing are usually preceded by anticipatory postural adjustments (APAs). This strategy is effective at compensating for an expected perturbation, as it reduces the need to compensate for the perturbation in a reactive manner. However, it can also be risky if one anticipates the incorrect perturbation, which could result in movements outside stability limits and a loss of balance. Here, we examine whether the margin for error defined by these stability limits affects the amount of anticipation. Specifically, will one rely more on anticipation when the margin for error is lower? Will the degree of anticipation scale with the margin for error? We took advantage of the asymmetric stability limits (and margins for error) present in the sagittal plane during upright stance and investigated the effect of perturbation direction on the magnitude of APAs. We also compared anticipatory postural control with the anticipatory control observed at the arm. Standing subjects made reaching movements to multiple targets while grasping the handle of a robot arm. They experienced forward or backward perturbing forces depending on the target direction. Subjects learned to anticipate the forces and generated APAs. Although subjects had the biomechanical capacity to adapt similarly in the forward and backward directions, APAs were reduced significantly in the backward direction, which had smaller stability limits and a smaller margin for error. Interestingly, anticipatory control produced at the arm, where stability limits are not as relevant, was not affected by perturbation direction. These results suggest that stability limits modulate anticipatory control, and reduced stability limits lead to a reduction in anticipatory postural control.

anticipatory postural adjustment; biomechanics; neuromechanics; reaching movement; internal model

HUMANS HAVE AN IMPRESSIVE ability to learn to move in novel, dynamic environments. This ability has been elegantly quantified in a number of seated arm-reaching experiments, where adaptation is observed in environments with uncertain and unstable dynamics (Franklin et al. 2003; Scheidt et al. 2001; Shadmehr and Mussa-Ivaldi 1994), but little is known about our ability to learn novel dynamics when there is a risk of instability. Whereas such environments are not typically experienced during seated arm-reaching tasks, they are a hallmark of our movements during upright standing. During upright standing, all movements must take place within stability limits, generally defined by our base of support. For movement perturbations within these limits, balance is recoverable. Beyond these limits, we lose control and risk an injurious fall.

A prudent strategy is to ensure that all movements are well within stability limits. This strategy has been observed when

subjects are exposed to postural perturbations and forced to take a compensatory step (Hasson et al. 2009; Schulz et al. 2006). People choose to step before their stability limits are exceeded. They also step earlier and at smaller perturbation levels when perturbed in the backward compared with the forward direction (Schulz et al. 2006). This has been attributed to smaller stability limits in the backward compared with the forward direction (Holbein-Jenny et al. 2007; King et al. 1994). King et al. (1994) showed that the functional base of support size, i.e., maximal center of pressure (CP) excursion capacity, was smaller in the posterior direction, relative to CP location during quiet standing.

Such an asymmetric, reactive response to the direction of a postural perturbation poses an intriguing question. Are anticipatory postural adjustments (APAs) similarly affected by perturbation direction? Voluntary movements generate forces upon the environment but upon the body as well. These forces must be controlled to maintain postural equilibrium and achieve the desired movement. When these forces are predictable, movements are preceded by APAs, which can act either to stabilize the whole-body center of mass or accelerate the center of mass in the direction of movement (Bouisset et al. 2000; Bouisset and Zattara 1987; Stapley et al. 1998, 1999). APAs have been shown to be modulated by movement magnitude, direction, stability, and even confidence (Adkin et al. 2002; Aruin et al. 1998; Aruin and Latash 1995; Bouisset et al. 2000; Commissaris and Toussaint 1997; Cordo and Nashner 1982; Horak et al. 1984; Toussaint et al. 1998). However, no studies explicitly compared the effect of direction on APA magnitude, because perturbation magnitude was not tightly controlled across movement directions. And whereas reduced stability during stance on a narrow beam leads to reduced APAs, it is not clear whether this is a direct result of reduced biomechanical capacity (Aruin et al. 1998). Furthermore, only well-practiced movements, such as raising the arm or lifting a weight, were investigated. In the present study, our goal was to quantify adaptation to a movement with novel dynamics, since familiarity can mask some of the basic mechanisms underlying motor adaptation. We also carefully controlled perturbation magnitude and ensured that adaptation was not biomechanically constrained.

Adaptation to novel dynamics has been investigated extensively in seated, arm-reaching movements (Gandolfo et al. 1996; Shadmehr and Mussa-Ivaldi 1994). When reaching in multiple directions and exposed to novel, dynamic perturbations, adaptation is gradually developed in each direction. However, when reaching in an unstable, dynamic environment, subjects use an alternative strategy and increase joint stiffness to counteract the perturbations (Franklin et al. 2003, 2008). This suggests that with a greater risk of instability in the posterior direction, the postural controller may rely less on

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APAs. It may instead increase joint stiffness or use a reactive response to counter the perturbations. Indeed, in a study where subjects lifted boxes of unknown weights, the postural controller relied more on reactive responses rather than anticipating an uncertain load and risk instability (Toussaint et al. 1998). However, the effect of stability limits on adaptation was not investigated. Here, we investigated whether APAs are observed in response to novel, multidirectional perturbations, where stability limits vary with direction.

The overarching research question is whether APAs will adapt in a direction-dependent manner in response to novel, multidirectional perturbations. More specifically, this study will investigate whether anticipatory adaptation to a perturbation in the posterior direction is reduced compared with adaptation to a perturbation in the anterior direction. Posterior stability limits are smaller, which we expect to lead to reduced APAs compared with the anterior direction because of the reduced margin for error. In other words, we expect APAs to scale with the margin for error. For the same perturbation magnitude, anticipatory adaptation will be larger when the margin for error is larger. This study tested the hypotheses that 1) the postural control system can adapt in an anticipatory, direction-specific manner to novel, dynamic perturbations and 2) APAs in the posterior direction will be reduced compared with adjustments in the anterior direction.

We built upon a well-studied experimental paradigm involving dynamic perturbations to arm-reaching movements. Subjects stood, rather than sat, and made reaching movements

while grasping the handle of a robotic manipulandum (Fig. 1A) (Ahmed and Wolpert 2009). They reached in five directions outward from the body (Fig. 1B). APAs aimed at controlling for the novel perturbation dynamics were quantified as the average CP velocity in the direction of the perturbation during a 150-ms window surrounding movement onset of the hand. This provides a measure of the net external moment generated about the ankle to control for the perturbation in an anticipatory manner. Movement directions included a rightward and a leftward reach, during which, the arm was perturbed in the forward and backward direction, respectively. As the perturbation magnitude was the same in all directions, theoretically, the magnitude of the APA should be the same in all movement directions. On the contrary, we expected that APAs would be reduced in the leftward-reaching movement compared with the rightward-reaching movement because of the smaller stability limits and margin for error in the backward direction. A potential confound in the interpretation of the results was that the leftward movement involved reaching across the body, whereas the rightward movement did not. To control for the effect of asymmetric movement biomechanics on adaptation, another group of subjects was tested. In this group, the direction of the perturbation was reversed (Fig. 1C). A rightward reach was perturbed in the posterior direction, whereas a leftward reach was perturbed in the anterior direction. Here, we expected that adaptation to the rightward reach would be reduced compared with the leftward reach. Together, these results allowed us to determine whether adaptation, reflected in

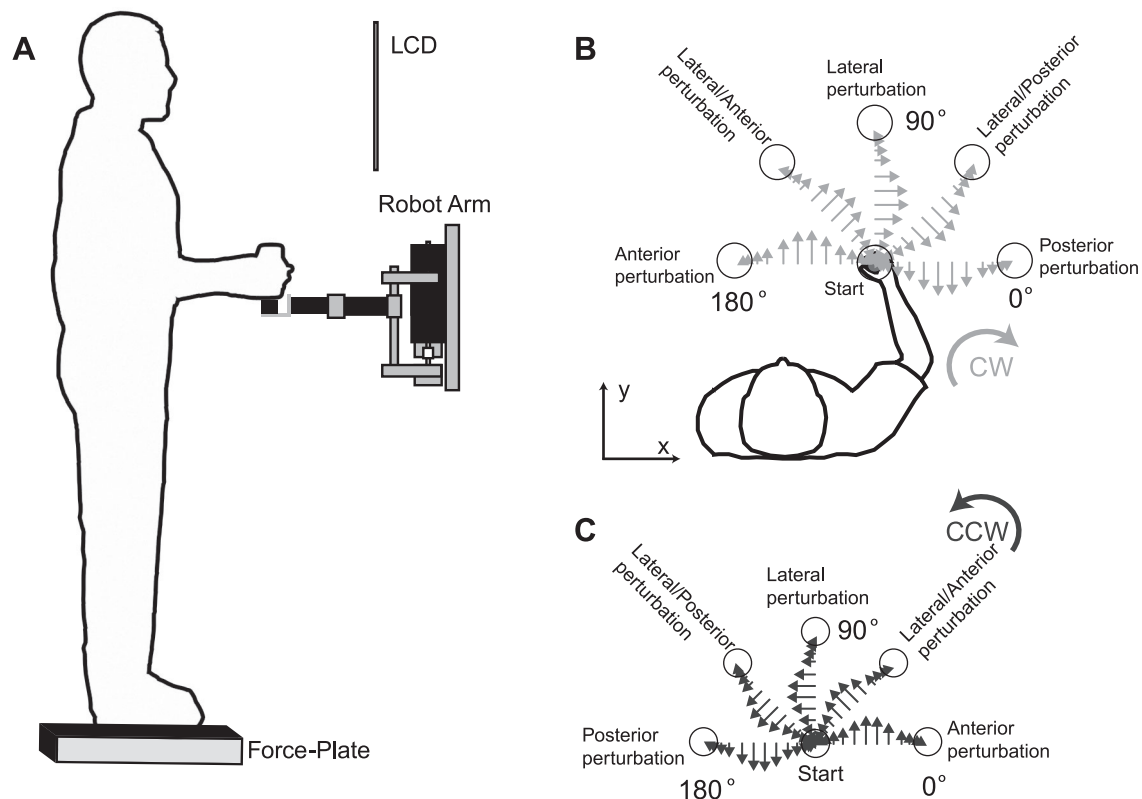


Fig. 1. Experimental set-up. A: barefoot subjects stood on a 6-axis forceplate while grasping the handle of a force-generating robotic arm and reaching in the horizontal plane. Handle movement was displayed as a cursor on a liquid crystal display (LCD) monitor suspended in front of the subject. The right arm was supported in the vertical direction using a plastic cradle attached to the robotic arm (not shown). B: start, target circles, and direction-dependent forces are shown for the clockwise (CW) group. Forces are proportional and act perpendicular to movement velocity. Also shown (text) is the resulting direction of the perturbation for each target direction. C: start, target circles, and direction-dependent forces are shown for the counter-CW (CCW) group. Note that a 0° reach results in an anterior perturbation, in contrast to a 0° reach in the CW group.

the strength of the observed APAs, is affected by the direction of the perturbation and consequently, stability limits.

METHODS

Subjects. Twelve young-adult participants {six male/six female; age [mean (SD)]: 23.4 yrs (2.6 yrs); height: 1.7 m (7.5 cm); mass: 69.2 kg (10.3 kg)} made planar-reaching movements while standing. All subjects provided informed consent, as approved by the University of Colorado's Institutional Review Board. All subjects were right-handed, as assessed by the Edinburgh Handedness Inventory. Each testing session took ~45 min.

Apparatus. Standing subjects made planar-reaching movements with their right hand while grasping the handle of a robotic arm (Shoulder-Elbow Robot 2, Interactive Motion Technologies, Watertown, MA; Fig. 1A). They were required to move a cursor (representing the handle position) from a start circle to one of five target circles, which appeared on the perimeter of a semicircle (15 cm radius), centered on the start circle. Targets were within arm's reach of the subjects and did not require trunk movement. Cursor, start, and target circles were presented on a liquid crystal display monitor, suspended vertically in front of the subject at eye level. Subjects stood with feet slightly apart on a six-axis forceplate (AMTI LG-6-4-1, Advanced Mechanical Technology, Watertown, MA), which recorded three-dimensional forces (F_x , F_y , F_z) and moments (M_x , M_y , M_z) about its center. The handle of the robotic arm was adjusted to subject height, such that the handle was level with the subject's sternum. Subjects were asked to keep their left arm at their side and not to rest their weight upon the handle.

Experimental protocol. Participants were randomly assigned to either the clockwise (CW; $k = 0.2$ Ns/cm; $n = 6$) or counter-CW (CCW; $k = -0.2$ Ns/cm) group, named for the direction of the curl field experienced in the force trials (Fig. 1, B and C). Figure 2 provides an outline of the trial sequence. Each group initially performed 150 null trials, where no forces were generated by the robot, to measure baseline performance (Baseline). The following 500 trials were force trials (Learning). The experimental session concluded with 100 null trials to extinguish the adaptation (Washout). Trial numbers were determined from pilot data and a previous study investigating postural adaptation (Ahmed and Wolpert 2009). Trials were grouped in batches of five. Every batch included one reach to each target direction, presented in random order. A rest period was provided after every 200 trials. Participants received an error message if movements out to the target were longer than 900 ms in duration. On all trials, once they had settled in the target, the robot gently moved the handle back to the start circle. Subjects were asked to adopt a comfortable stance width. Foot placement was marked to ensure consistency throughout the experiment.

On force trials, reaching movements were exposed to a viscous curl field: the force upon the hand was proportional to its velocity and perpendicular to its direction (Fig. 1, B and C)

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

where $|k| = 20$ Ns/m.

Included in the above trials were random catch trials (one in five), where the robot simulated a force channel, i.e., stiff walls along both sides of the line between the start and target circles. Handle movement was constrained to move along this path, while simultaneously recording any small deviations into the wall.

Data acquisition and analysis. Robot handle position, velocity, acceleration, and force were recorded at 200 Hz. Ground reaction forces and moments were also recorded at 200 Hz and low-pass filtered at 10 Hz, both forward and backward to remove any phase-shift artifact. As a measure of postural control, the location of the CP was determined as $(CP_x, CP_y) = (-M_y - F_x r_z, M_x - F_y r_z)/F_z$, where the x and y subscripts denote mediolateral and anteroposterior axes, respectively. The distance from the top of the forceplate to its origin is represented by r_z . CP velocity was calculated using a five-point differentiation algorithm.

Movement variables. Movement error was quantified as the maximum perpendicular deviation of the hand from a straight line, drawn from the start to the target circles. To quantify the feedforward component of the learned force, we measured the absolute force generated at the instant of peak velocity toward the target into the walls of the simulated force channels on catch trials (catch force). Such trials are known to have a minimal effect on any learning or unlearning (Scheidt et al. 2001).

Postural variables. APAs were quantified as the mean CP velocity in the direction of the perturbation (i.e., perpendicular to the target direction) in a 150-ms time window, starting 100 ms prior to movement initiation and ending 50 ms after movement initiation. This was taken as a measure of anticipatory control aimed at controlling for the novel perturbation dynamics. Reactive response latencies, varying from 73 to 110 ms in the tibialis anterior, have been observed in response to unexpected backward sway perturbations (Horak and Nashner 1986). This was after repeated exposure, which is known to reduce the latency of automatic postural responses. Therefore, we took 50 ms after movement onset as a conservative estimate of anticipatory adaptation, which also allowed us to quantify any anticipatory CP modulation that occurred simultaneously with the arm movement but before reactive control was possible. Movement of the CP in the direction of the impending force perturbation, before reactive control was possible, was considered evidence of an APA. APAs specific to the perturbation, without the confounding effect of the reaching movement, can be clearly isolated, since they have orthogonal lines of action. A secondary measure of postural activity is the reactive postural adjustment (RPA) observed on each trial. This was quantified as the maximum absolute CP velocity recorded 50 ms after movement onset until the end of the movement, along the axis of the perturbation. Greater values indicate increased RPAs and ineffective APAs.

Learning movement dynamics was evaluated by comparing performance at five stages of the experiment (Fig. 2): Late Baseline (last two batches in Baseline phase); Early Learning (first trial in Learning phase); Late Learning (last two batches in Learning phase); Early Washout (first trial); Late Washout (last two batches).

First, we examined whether subjects learned to anticipate the multidirectional perturbations (*Hypothesis 1*). Data were grouped across directions and analyzed with repeated measures ANOVAs,

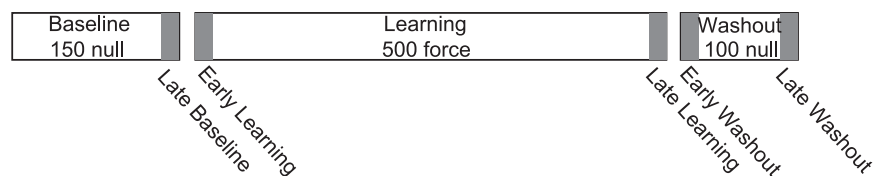


Fig. 2. Experimental protocol. The protocol was identical for both CW and CCW groups. After 150 null trials (Baseline), subjects' reaching movements were exposed to forces for 500 trials (Learning). The session concluded with 100 null trials (Washout). Key time points for evaluation and comparison of learning are at Late Baseline, Early Learning, Late Learning, Early Washout, and Late Washout.

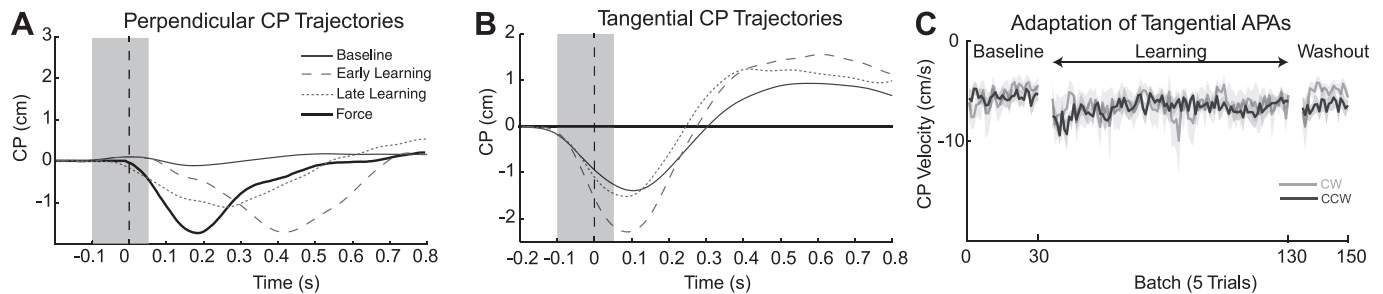


Fig. 3. Center of pressure (CP) trajectories. **A**: perpendicular CP trajectories. Single-subject trajectories are shown from the Baseline, Early Learning, and Late Learning phases for a subject experiencing a CCW perturbation. Negative values indicate a CCW perpendicular movement. The thick, black line represents the average perpendicular robot force generated during the Learning phase. The vertical, dashed line indicates movement onset of the handle. The gray, shaded region indicates the time window from which the anticipatory postural adjustment (APA) was calculated. **B**: tangential CP trajectories. Negative values indicate movement away from the target. Trajectories were similar in all phases of the experiment. The thick, black line (at 0) represents the lack of any tangential robot forces generated throughout the experiment. **C**: adaptation of tangential APAs. Solid lines are group means. Shaded areas represent \pm SE. Gaps along the x-axis have been inserted for clarity to indicate transitions among phases: Baseline–Learning–Washout.

with stage as a within-subject factor ($\alpha = 0.05$). To quantify learning/unlearning in each phase, planned comparisons were carried out between Early and Late Learning and Early and Late Washout ($\alpha = 0.05/2$) for all movement and postural variables.

To examine the effect of stability limits (*Hypothesis 2*), all movement and posture variables were grouped by perturbation direction. A perturbation in the forward direction had the largest stability limits and was considered the most stable (rightward reach for the CCW group, leftward reach for the CW group; Fig. 1, *B* and *C*). Stability limits were assumed to decrease as the target progressed around the semicircle, until the limits reached a minimum when the perturbation

acted in the posterior direction (leftward reach for the CCW group; rightward reach for the CW group). The data were then analyzed with repeated measures ANOVAs, with perturbation direction as a within-subjects factor and group as a between-subjects factor. Our primary analysis focused on direction-dependent effects on changes in APA magnitude between Late Baseline and Late Learning. As a secondary analysis, we also examined the effect of perturbation direction on changes in movement error, catch force, and RPAs. For each variable, planned comparisons were carried out between learning in the posterior direction (smallest stability limits) and learning in the anterior direction (largest stability limits; $\alpha = 0.05$).

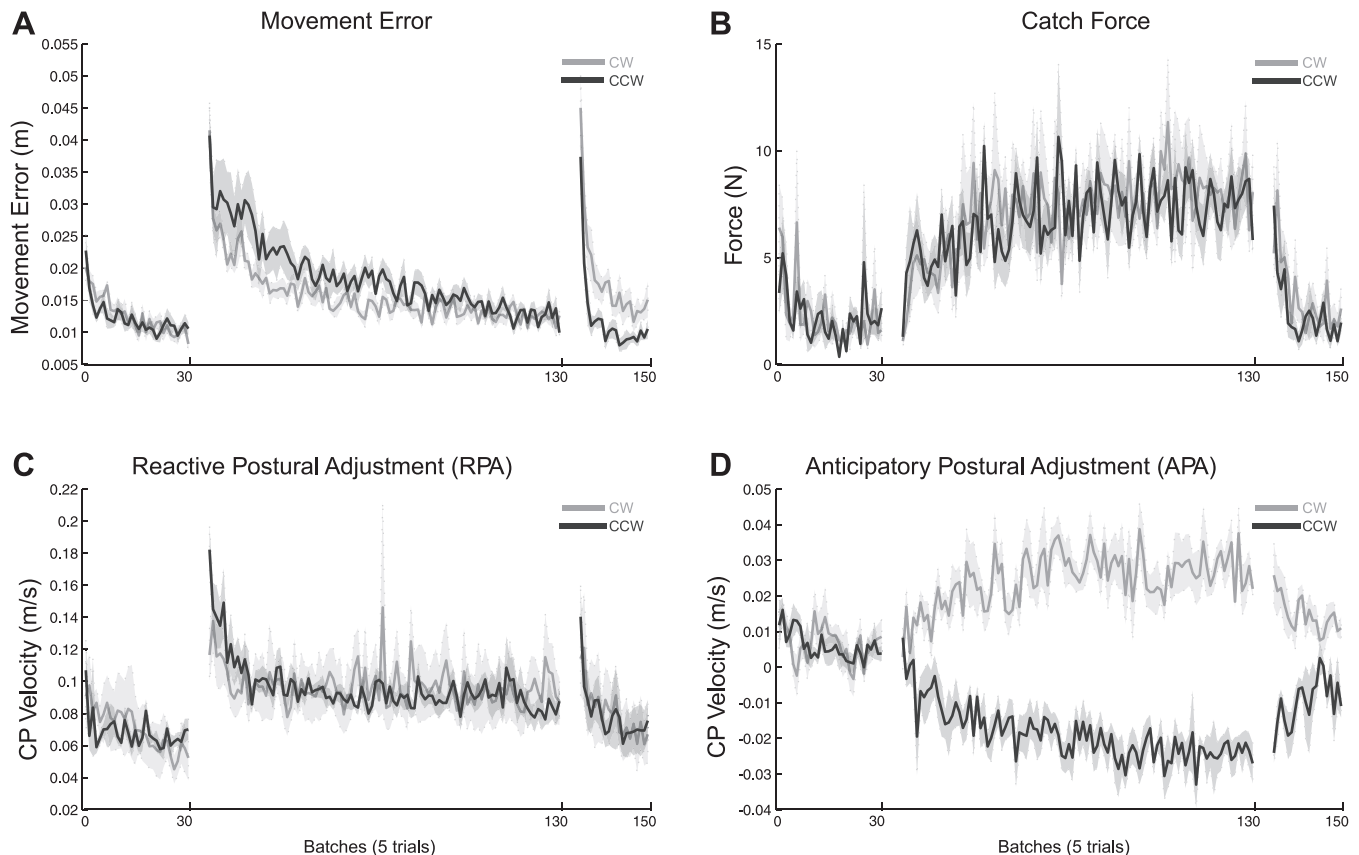


Fig. 4. Learning averaged over all directions per batch (5 trials). **A**: peak absolute perpendicular movement error. **B**: absolute perpendicular force generated on catch trials at instant of peak velocity (Catch Force). **C**: peak, absolute perpendicular CP velocity observed after movement onset [reactive postural adjustment (RPA)]. **D**: mean perpendicular CP velocity (APA). Positive values indicate a CW perpendicular velocity; negative values indicate a CCW perpendicular velocity. Solid lines are group means. Shaded areas represent \pm SE. Gaps along the x-axis have been inserted for clarity to indicate transitions among phases: Baseline–Learning–Washout.

RESULTS

Overview. When exposed to novel perturbations in multiple directions, both groups exhibited significant learning in all four movement and posture variables, supporting our first hypothesis (all $P < 0.003$). Upon closer inspection of adaptation, it was clear that the magnitude of the APAs in both groups was also affected significantly by perturbation direction ($P < 0.001$). Specifically, APAs were reduced when the perturbation was in the posterior direction compared with the anterior direction ($P = 0.011$).

For all measures, except one, no significant group effects were observed (CW vs. CCW). Group effects were only observed in the APAs. This is because of the reversed direction of adaptation between groups and the fact that the APA measure is represented by a signed velocity. The remaining variables are all absolute measures. Thus for the sake of clarity, the results for the two groups are presented together.

General characteristics of CP trajectories. Trajectories across multiple movement directions were each decomposed into two orthogonal components: tangential and perpendicular to the target direction. Positive tangential movement indicates movement toward the target, and negative indicates movement away from the target. Positive perpendicular movement corresponds to movement orthogonal to the target in the CCW direction, and negative corresponds to movement in the CW direction.

The novel forces applied to the handle acted perpendicular to the movement direction. Therefore, to quantify adaptation, we examined the component of the CP trajectory perpendicular to the target direction (and hand movement). During the Baseline phase, minimal movement was observed in the component of the CP trajectory perpendicular to hand movement (Fig. 3A). When initially exposed to the forces during the Early Learning phase, the perpendicular CP component reacted to the force perturbation (Fig. 3A). The data presented in Fig. 3 are from CCW perturbation trials that correspond to a perturbation in the negative direction. Also shown in Fig. 3A is the average force

perturbation applied to the hand during the Learning phase. To react to a CCW (negative) force perturbation, the CP moves in the same CCW direction. By the end of the Learning phase, the perpendicular CP component begins to move in an anticipatory manner in the negative direction before handle movement and force onset (Fig. 3A).

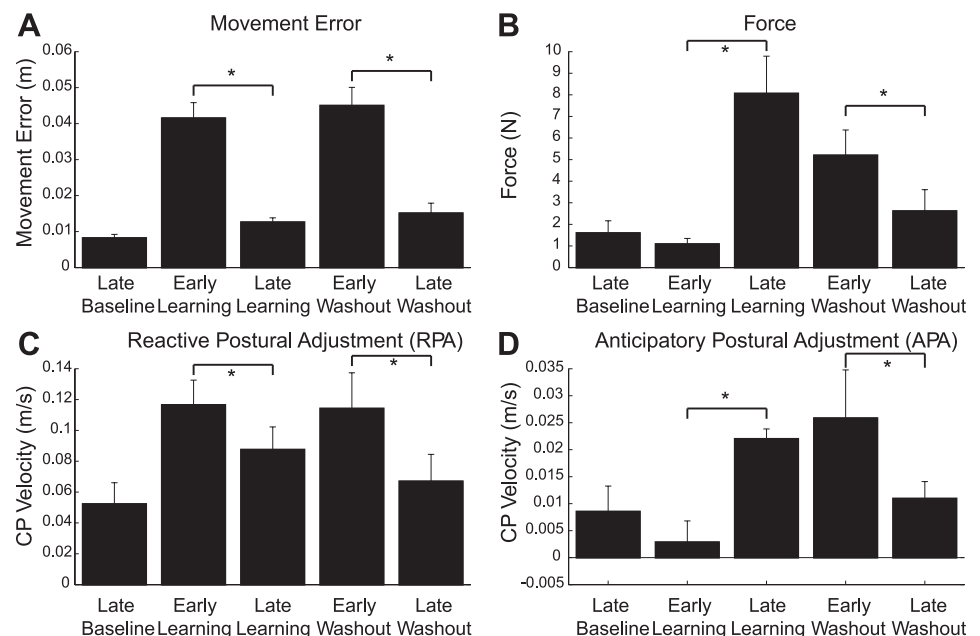
APAs in the direction tangential to the movement of the hand were observed consistently on all trials. Specifically, we observed movement of the CP away from the target prior to movement of the arm (Fig. 3B). This is expected, as the APA, acting in the direction of movement, is involved in the focal movement and likely accelerates the center of mass toward the target. There are no forces acting in the tangential direction at any point in the experiment (Fig. 3B). The magnitude of the tangential APA did not change upon exposure to or removal of the handle forces ($P > 0.3$; Fig. 3C).

Since the applied force acted perpendicular to the movement direction, and CP trajectories were most strongly affected in the perpendicular direction, we have focused our analysis of APA adaptation on the perpendicular component of the CP trajectory. All subsequent adaptation results are based on CP movement perpendicular to the target direction.

Learning in all directions. When first exposed to the novel perturbation, subjects' movement trajectories deviated from their Baseline movement trajectories and resulted in large movement errors (Figs. 4 and 5). By the end of Learning (500 trials), movement errors were reduced significantly compared with Early Learning (planned comparison; $P < 0.001$). From the forces measured on catch trials, it was clear that catch trial forces in Late Baseline were similar to those measured in Early Learning. By Late Learning, forces had increased and were significantly different than those observed in Early Learning ($P < 0.001$). This suggests that subjects had reduced their movement error by anticipating the impending perturbation and generating an anticipatory force to control for it.

Changes in postural variables mirrored the changes observed in the movement variables. The initial perturbation resulted in

Fig. 5. Learning averaged over all directions at key time points. Movement and posture variables from Fig. 3 for the CW group averaged at key time points. A: movement error; B: catch force; C: RPAs; D: APAs. Bars represent \pm SE ($*P < 0.05$).



large RPAs. By the end of the Learning phase, these were reduced significantly (planned comparison; $P < 0.001$). Concomitant with these changes, APAs had developed and were significantly greater than those measured in Late Baseline ($P < 0.003$).

Large movement errors and RPAs were again observed upon removal of the perturbing forces, whereas catch trial forces and APAs remained similar to the previous perturbation trials. Together, these results further support the hypothesis that subjects had indeed adapted in an anticipatory manner. By the end of Washout, all movement and postural variables had been reduced significantly compared with Early Washout (all $P < 0.003$; Figs. 4 and 5).

Learning grouped by target direction. Learning remains present in movement error when data were grouped and analyzed separately by target direction. For all target directions, movement error was reduced from Early Learning to Late Learning and Early Washout to Late Washout ($P < 0.001$; Fig. 6). Similar trends were observed in the APA (Fig. 7) and RPA data.

Effect of perturbation direction on magnitude of adaptation. To examine the effect of perturbation direction, we grouped trials in the Learning phase by the direction of the perturbation experienced. Then, for each direction, we calculated the magnitude of the change in APAs between Late Learning and Late Baseline. Learning was observed in both groups for all perturbation directions. However, the magnitude of the changes in both groups was dependent on the direction of the perturbation

($P < 0.001$). Specifically, smaller APAs were observed when the perturbation was applied in the posterior compared with the anterior direction ($P = 0.011$; Fig. 8).

We also examined the effect of perturbation direction on changes in movement error between Late Baseline and Late Learning. Movement error in the anterior and posterior directions was similar ($P = 0.793$; Fig. 8). As another measure of learning at the arm, we investigated whether the anticipatory forces generated on catch trials changed as a function of perturbation direction. For each subject and each direction, the average catch force in the last 25% of Learning trials (25 batches) was calculated. No significant differences between anterior and posterior perturbations were observed ($P = 0.5$; Fig. 8).

A correlated measure of reduced APAs is increased RPAs to compensate for the perturbing forces. However, when we compared RPAs in Late Baseline and Late Learning for each direction (Fig. 8), no effect of perturbation direction was observed ($P = 0.370$).

We examined the relationship between stability limits and APAs further by estimating the size of the stability limits in each perturbation direction and comparing them with the magnitude of the observed changes in APA magnitude. Stability limits were estimated by taking previously published data about maximal CP excursions. In an earlier study, young subjects were asked to lean forward and backward maximally, and the corresponding CP excursion with respect to CP loca-

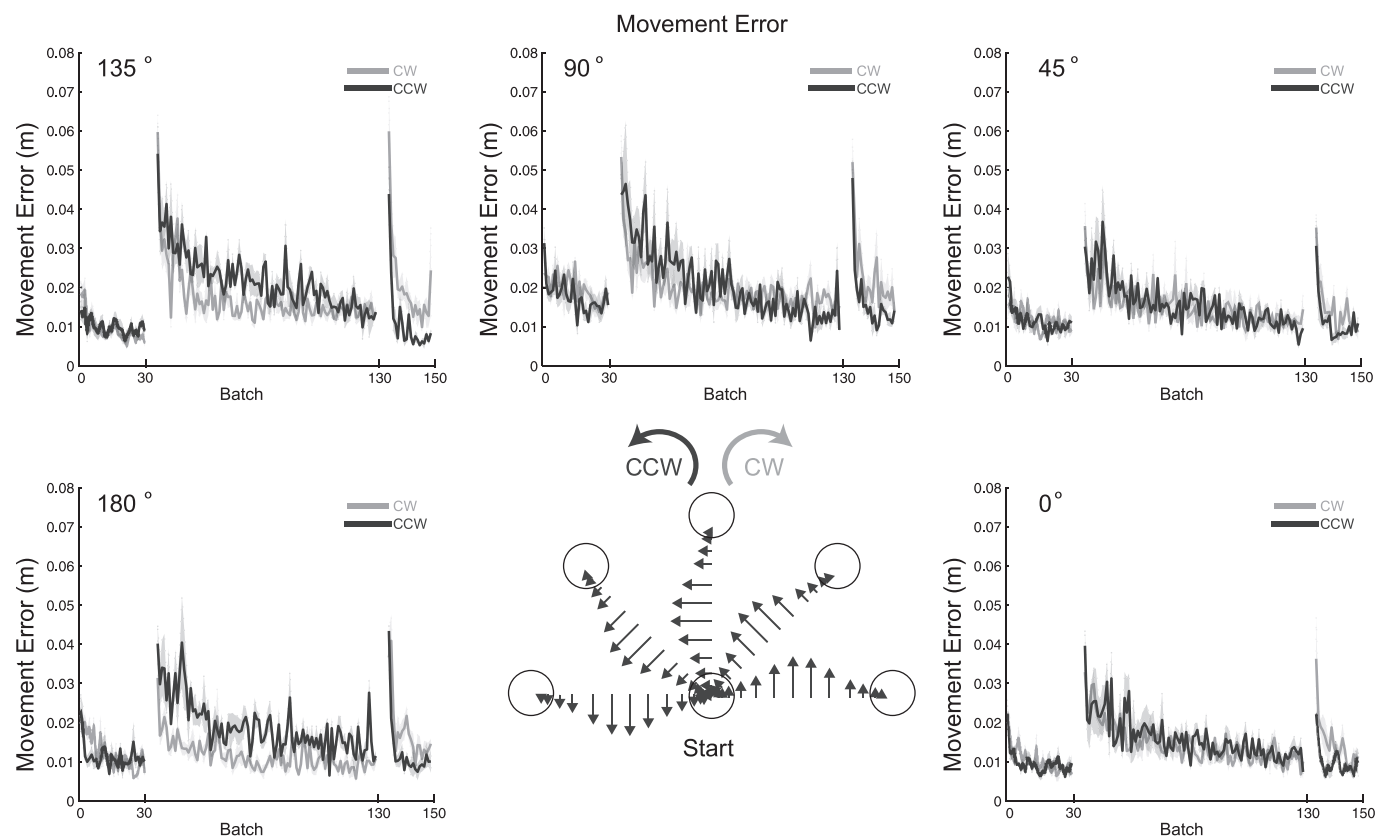


Fig. 6. Direction-specific learning (Movement Error). Movement error is grouped and plotted by target direction. Starting from *bottom right* and moving CCW: 0°, 45°, 90°, 135°, and 180°. Note that perturbation direction for each target direction is reversed between the CW and CCW groups. Each data point represents the error on the trial in the given direction within the specified batch. Solid lines are group means. Shaded areas represent \pm SE. Gaps along the x-axis have been inserted for clarity to indicate transitions among phases: Baseline–Learning–Washout. *Bottom middle*: diagram of target directions. Force vectors are shown only for the CCW group for clarity.

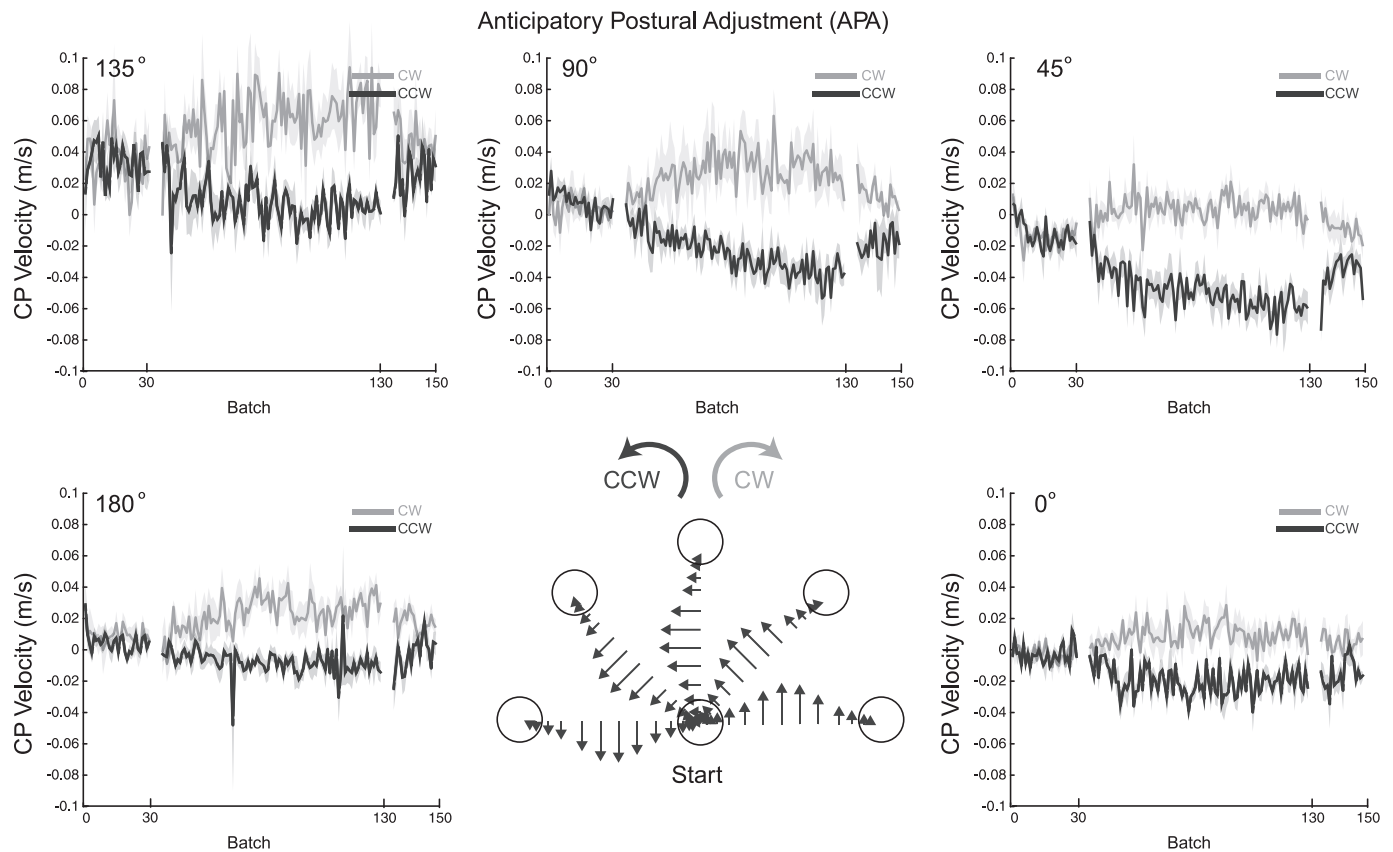


Fig. 7. Direction-specific learning (APA). APAs are grouped and plotted by target direction. Starting from *bottom right* and moving CCW: 0°, 45°, 90°, 135°, and 180°. Perturbation direction for each target direction was reversed between the CW and CCW groups. Hence, APAs were positive for the CW group, indicating a CW perpendicular velocity, as would be expected for adaptation to a CW perpendicular force perturbation (and vice versa for the CCW group). Solid lines are group means. Shaded areas represent \pm SE. Gaps along the x-axis have been inserted for clarity to indicate transitions among phases: Baseline–Learning–Washout. *Bottom middle*: diagram of target directions. Force vectors are shown only for the CCW group for clarity.

tion during quiet stance was measured (King et al. 1994). Maximal CP excursions, which represent stability limits, were found to be, on average, 10 cm and 5 cm in the anterior and posterior directions, respectively. As a measure of stability-limit size along the mediolateral axis, we used the average value calculated in a previous study of 74.1% and multiplied it by the average stance width observed in the current study (28.34 cm) (Holbein-Jenny et al. 2007). With the use of these values as estimates of average stability-limit size in the antero-posterior and medio-lateral directions, we calculated the size of the resultant stability limits in each perturbation direction (Fig. 9, A and B). As expected, we found a similar trend between estimated stability-limit size and APA adaptation in perturbation direction (Fig. 9, B and C). For example, perturbations directed partially—posteriorly and laterally—resulted in smaller APAs than perturbations directed purely anteriorly and those directed both laterally and anteriorly (Fig. 9C). This is an agreement with the smaller stability limits in the lateral/posterior direction, compared with the anterior and lateral/anterior directions (Fig. 9B).

Stability limits were measured in three of the subjects tested in the present study. Prior to performing the reaching task, three subjects performed a maximum CP excursion task. They controlled a cursor on a screen in front of them using their CP. They were required to make center-out reaching movements with their CP in eight target directions, equally spaced along the perimeter of a circle. All move-

ments began from the center of the circle. In these three subjects, we also observed smaller stability limits in the backward compared with the forward direction. The stability limits calculated based on experimental data are shown in Fig. 9B. They show the same trend observed in the stability limits based on data from previous literature. Importantly, both sets of data show that stability limits are smaller in the posterior compared with the anterior direction.

Alternative measures of APAs. There are alternative methods used in the literature to quantify APAs other than the CP velocity-based method used above. To investigate the sensitivity of our results to our APA measure, we repeated our analyses using three alternative measures of postural adaptation. The total perpendicular displacement of the CP during the 150-ms time interval surrounding movement onset was investigated. This measure is related to average perpendicular CP velocity and provided nearly identical results to the analysis using CP velocity. Another measure was the change in the angle of the CP vector during the same 150-ms time interval. This measure incorporated both the tangential and perpendicular components of the CP trajectory with respect to target direction. During the Baseline phase, the CP vector was directed in the negative tangential direction, indicative of a negligible perpendicular component. During the Learning phase, the vector gradually rotated as the magnitude of the perpendicular movement of the CP increased, and the magni-

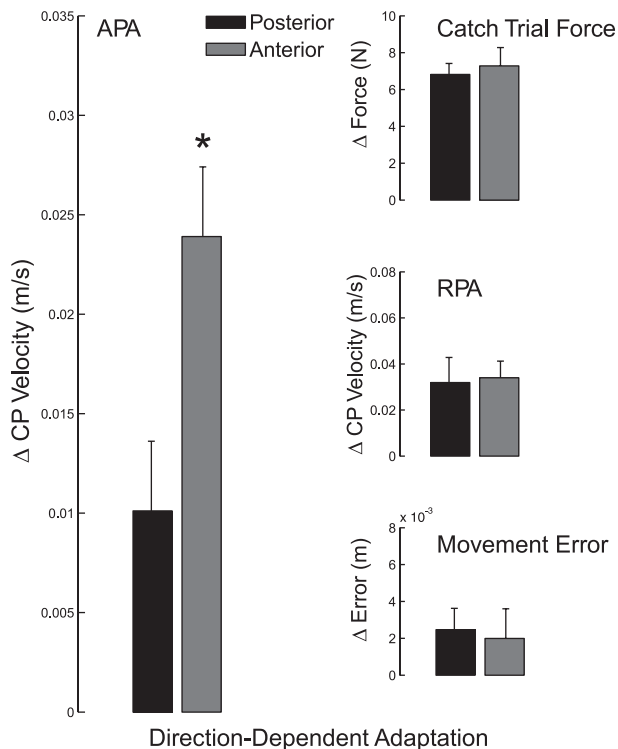


Fig. 8. Effect of perturbation direction. Changes (Δ) in performance between Late Baseline and Late Learning for anterior and posterior perturbations. Data shown are the average over both groups CW and CCW. Bars represent \pm SE. *Left*: APAs. APAs were significantly greater in the anterior direction ($*P = 0.011$). *Top right*: catch trial force; no difference between posterior and anterior perturbations. *Middle right*: RPAs; no effect of perturbation direction was observed. *Bottom right*: movement error; no significant differences between posterior and anterior perturbations.

tude of the tangential component remained the same. Both measures—CP displacement in the perpendicular direction and the direction of the CP vector—provided similar results as the perpendicular CP velocity measure.

DISCUSSION

Our results show that the postural control system can learn to anticipate novel, multidirectional, dynamic perturbations. The modulation of postural control in a feedforward manner to reaching in multiple directions has been observed previously in pointing movements made while standing (Leonard et al. 2009). Here, these results are extended to a task involving a novel, dynamic perturbation. An intriguing finding is that the extent of adaptation was dependent on the direction of the perturbation. Subjects adapted significantly less to posterior perturbations with smaller stability limits, compared with anterior perturbations where stability limits were larger.

We propose that although the perturbations are of equal magnitude, the subjective cost of a backward perturbation is larger, because it leads to a smaller safety margin and consequently, probability of instability. Our findings suggest that this increase in subjective cost leads to reduced APAs. In recent years, optimal control theory has emerged as a powerful framework for investigating the principles underlying human movement control (Todorov and Jordan 2002). A fundamental component of the theory is that movement is controlled in a manner that minimizes some subjective cost. Our findings are in line with this. Furthermore, the analysis of APA adaptation during upright standing is a novel experimental paradigm—rich with opportunities to investigate movement adaptation in conditions where instability and its associated costs are naturally present.

An alternative explanation is that there may be an increased threat associated with a fall in the backward direction, compared with the forward direction, where vision can help one more accurately place a compensatory step. The presence of postural threat has been shown to alter postural control even when the biomechanics of the task remain identical (Adkin et al. 2000, 2002). Both explanations imply that we attribute a greater cost to a backward perturbation compared with a forward perturbation of equal magnitude. Thus in the presence

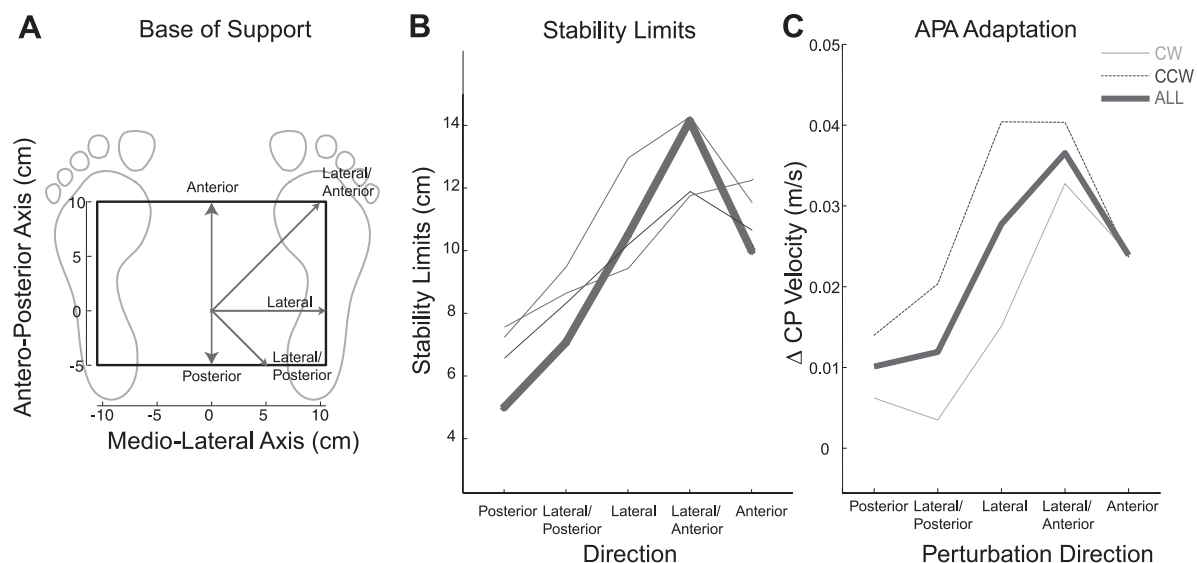


Fig. 9. Stability limits and adaptation. *A*: base of support and estimated stability limits with respect to CP location during quiet stance, based on published data and subject stance width. Arrows denote stability limits in the directions of the perturbations delivered in the present study to the CW group. Base of support is shown in gray as a reference. *B*: magnitude of stability limits from *A* is plotted vs. perturbation direction (thick line). Also shown are experimentally determined stability limits from 3 subjects (thin lines). *C*: changes in APAs between Late Baseline and Late Learning are plotted vs. perturbation direction. The thick line represents the average over both CW and CCW groups. Thin lines represent group means. APAs increased significantly with perturbation direction and increasing stability.

of asymmetric stability limits or postural threat in the anterior/posterior direction, movements are controlled and adapted in an asymmetric manner.

It is important to note that the reduced adaptation to posterior perturbations was not accompanied by reduced anticipatory control of forces at the arm. The fact that reduced adaptation was not observed at the arm suggests that the effect of instability was isolated and local to only the postural controller, rather than the arm controller. This distinction between the control of movement and posture is not surprising and is supported by a number of previous studies (Ahmed and Wolpert 2009; Kurtzer et al. 2005).

This is not the first study to examine the effect of stability limits on APAs, as APAs have been quantified in the context of familiar loading and unloading movements, where stability is manipulated by reducing the mechanical base of support by leaning forward or using a narrow beam (Aruin et al. 1998). In these studies, anticipatory control is reduced with instability. However, it was not determined whether anticipatory control was reduced because the required control exceeded the imposed stability limits or because of a person's desire to maintain a safety margin, even though the required movement was within the imposed stability limits. In the present study, the perturbations were mild and recoverable within the given stability limits. No compensatory steps were observed, even upon initial exposure to the robot forces or initial removal. Inspection of the CP trajectories revealed that all subjects exhibited greater CP excursions in the initial Learning and Washout trials than in the final Learning trials. The results show that subjects avoided approaching stability limits and reduced anticipatory CP movement, although compensating for the perturbation would not have involved compromising those stability limits. This suggests that subjects chose to maintain a safety margin between their movements and these stability limits.

A previous study has shown that motor learning can affect the choice to approach stability limits (Jessop et al. 2006). In a whole-body leaning study, it was observed that subjects were initially hesitant and avoided approaching their stability limits and reduced the extent of their lean. However, with time and practice, both healthy control subjects and Parkinson's patients leaned forward more, and more closely approached their stability limits. These results support our findings that the choice to approach stability limits is indeed a choice and is not determined biomechanically. Furthermore, these results show that with practice, one can learn to move closer to his or her stability limits. It will be interesting to examine whether in the present experimental paradigm, extended practice would also lead to movements closer to stability limits in all directions.

There are a number of limitations to this study. First, we do not quantify associated postural adjustments, which occur throughout the entire movement and can also be feedforward in nature (Leonard et al. 2009, 2011). The existence of APAs does not necessarily preclude the adaptation of associated postural adjustments occurring later in the movement. Future studies should investigate the postural adjustments, both preceding a movement and throughout its duration. Second, we cannot determine the functional role of the APAs, given the current data set. The adaptation in APAs may serve to either accelerate or stabilize the center of mass. However, our hy-

potheses and conclusions are not dependent on this differentiation. Nonetheless, it would be informative to use a combined modeling and experimental approach to understand the functional role of the APAs in this task. Third, the unilateral component of the task most certainly affected the postural control strategy. The counter-balanced design that exposed subjects to perturbations in opposite directions likely minimized any confounding effects on our interpretation of the data. However, it would be helpful to understand exactly how the unilateral movement affected whole-body postural control. Fourth, the robot handle could provide additional postural support to the subjects, although subjects were asked not to lean on the handle. Forces measured by a force transducer in the handle revealed that at most, subjects were resting on the hand with ~ 19 N, which corresponds to $\sim 3\%$ of body weight. Forces did not change significantly between Late Baseline and Late Learning, indicating that the observed APA adaptation was not a result of increased reliance on the handle for support; the average difference between vertical forces measured at the handle between these two phases was 0.49 N. The handle was also free to move in the horizontal plane and thus did not likely provide a significant amount of support. This is also confirmed by the fact that postural adaptation was observed despite the additional support.

Together, these results reveal a previously unknown relationship between the size of stability limits and motor learning. This is not apparent from investigations of motor learning, which commonly use dynamic environments that are entirely stable or entirely unstable. By exploiting an environment that is stable within certain limits and has asymmetric limits, we have shown that proximity to stability limits may be an important factor in motor learning. These results compel us to develop experiments and models that examine the role of stability limits and other factors that can affect the consequences of movement errors and their relationship to motor learning and control.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

Author contributions: A.A.A. conception and design of research; G.C.M. and A.A.A. performed experiments; G.C.M. and A.A.A. analyzed data; G.C.M. and A.A.A. interpreted results of experiments; A.A.A. prepared figures; A.A.A. drafted manuscript; A.A.A. edited and revised manuscript; G.C.M. and A.A.A. approved final version of manuscript.

REFERENCES

- Adkin AL, Frank JS, Carpenter MG, Peysar GW. Fear of falling modifies anticipatory postural control. *Exp Brain Res* 143: 160–170, 2002.
- Adkin AL, Frank JS, Carpenter MG, Peysar GW. Postural control is scaled to level of postural threat. *Gait Posture* 12: 87–93, 2000.

- Ahmed AA, Wolpert DM.** Transfer of dynamic learning across postures. *J Neurophysiol* 102: 2816–2824, 2009.
- Aruin AS, Forrest WR, Latash ML.** Anticipatory postural adjustments in conditions of postural instability. *Electroencephalogr Clin Neurophysiol* 109: 350–359, 1998.
- Aruin AS, Latash ML.** Directional specificity of postural muscles in feed-forward postural reactions during fast voluntary arm movements. *Exp Brain Res* 103: 323–332, 1995.
- 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.
- Bouisset S, Zattara M.** Biomechanical study of the programming of anticipatory postural adjustments associated with voluntary movement. *J Biomech* 20: 735–742, 1987.
- Commissaris D, Toussaint H.** Anticipatory postural adjustments in a bimanual, whole body lifting task with an object of known weight. *Hum Movement Sci* 16: 407–431, 1997.
- Cordo PJ, Nashner LM.** Properties of postural adjustments associated with rapid arm movements. *J Neurophysiol* 47: 287–302, 1982.
- Franklin DW, Burdet E, Tee KP, Osu R, Chew CM, Milner TE, Kawato M.** CNS learns stable, accurate, and efficient movements using a simple algorithm. *J Neurosci* 28: 11165–11173, 2008.
- Franklin DW, Osu R, Burdet E, Kawato M, Milner TE.** Adaptation to stable and unstable dynamics achieved by combined impedance control and inverse dynamics model. *J Neurophysiol* 90: 3270–3282, 2003.
- Gandolfo F, Mussa-Ivaldi FA, Bizzi E.** Motor learning by field approximation. *Proc Natl Acad Sci USA* 93: 3843–3846, 1996.
- Hasson CJ, Caldwell GE, van Emmerik REA.** Scaling of plantarflexor muscle activity and postural time-to-contact in response to upper-body perturbations in young and older adults. *Exp Brain Res* 196: 413–427, 2009.
- 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.
- Horak FB, Esselman P, Anderson ME, Lynch MK.** The effects of movement velocity, mass displaced, and task certainty on associated postural adjustments made by normal and hemiplegic individuals. *J Neurol Neurosurg Psychiatry* 47: 1020–1028, 1984.
- Horak FB, Nashner LM.** Central programming of postural movements: adaptation to altered support-surface configurations. *J Neurophysiol* 55: 1369–1381, 1986.
- Jessop RT, Horowicz C, Dibble LE.** Motor learning and Parkinson disease: refinement of movement velocity and endpoint excursion in a limits of stability balance task. *Neurorehabil Neural Repair* 20: 459–467, 2006.
- King MB, Judge JO, Wolfson L.** Functional base of support decreases with age. *J Gerontol* 49: M258–M263, 1994.
- Kurtzer I, Herter TM, Scott SH.** Random change in cortical load representation suggests distinct control of posture and movement. *Nat Neurosci* 8: 498–504, 2005.
- Leonard JA, Brown RH, Stapley PJ.** Reaching to multiple targets when standing: the spatial organization of feedforward postural adjustments. *J Neurophysiol* 101: 2120–2133, 2009.
- Leonard JA, Gritsenko V, Ouckama R, Stapley PJ.** Postural adjustments for online corrections of arm movements in standing humans. *J Neurophysiol* 105: 2375–2388, 2011.
- Scheidt RA, Dingwell JB, Mussa-Ivaldi FA.** Learning to move amid uncertainty. *J Neurophysiol* 86: 971–985, 2001.
- Schulz BW, Ashton-Miller JA, Alexander NB.** Can initial and additional compensatory steps be predicted in young, older, and balance-impaired older females in response to anterior and posterior waist pulls while standing? *J Biomech* 39: 1444–1453, 2006.
- Shadmehr R, Mussa-Ivaldi FA.** Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14: 3208–3224, 1994.
- Stapley P, Pozzo T, Grishin A.** The role of anticipatory postural adjustments during whole body forward reaching movements. *Neuroreport* 9: 395–401, 1998.
- 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.
- Todorov E, Jordan MI.** Optimal feedback control as a theory of motor coordination. *Nat Neurosci* 5: 1226–1235, 2002.
- Toussaint HM, Michies YM, Faber MN, Commissaris DA, van Dieën JH.** Scaling anticipatory postural adjustments dependent on confidence of load estimation in a bi-manual whole-body lifting task. *Exp Brain Res* 120: 85–94, 1998.