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Transfer of Dynamic Learning Across Postures

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Ahmed AA, Wolpert DM. Transfer of dynamic learning across
postures. *J Neurophysiol* 102: 2816–2824, 2009. First published
August 26, 2009; doi:10.1152/jn.00532.2009. When learning a diffi-
cult motor task, we often decompose the task so that the control of
individual body segments is practiced in isolation. But on re-compo-
sition, the combined movements can result in novel and possibly
complex internal forces between the body segments that were not
experienced (or did not need to be compensated for) during isolated
practice. Here we investigate whether dynamics learned in isolation
by one part of the body can be used by other parts of the body to
immediately predict and compensate for novel forces between body
segments. Subjects reached to targets while holding the handle of a
robotic, force-generating manipulandum. One group of subjects was
initially exposed to the novel robot dynamics while seated and was
then tested in a standing position. A second group was tested in the
reverse order: standing then sitting. Both groups adapted their arm
dynamics to the novel environment, and this movement learning
transferred between seated and standing postures and vice versa. Both
groups also generated anticipatory postural adjustments when stand-
ing and exposed to the force field for several trials. In the group that
had learned the dynamics while seated, the appropriate postural
adjustments were observed on the very first reach on standing. These
results suggest that the CNS can immediately anticipate the effect of
learned movement dynamics on a novel whole-body posture. The
results support the existence of separate mappings for posture and
movement, which encode similar dynamics but can be adapted
independently.

INTRODUCTION

Skilled movement depends on our ability to apply suitable
control to compensate for external dynamics and predict the
consequences of that control. Our everyday movements gen-
erate forces on the environment as well as forces on our own
bodies. When these forces are predictable, voluntary move-
ment is usually preceded by anticipatory postural adjustments
(APAs). APAs involve activity in muscles not directly in-
volved in generating the movement per se but in maintaining
postural equilibrium. For example, prior to rapid arm move-
ments, the trunk muscles are activated to compensate for the
impending inertial forces and shift in center-of-mass position.
APAs have been frequently observed in self-generated limb
movements, object lifting, and load catch-and-release para-
digms (Aruin et al. 1998; Bouisset and Zattara 1987; Commis-
saris and Toussaint 1997). They are specific to the properties of
the preceding voluntary movement (Bouissett and Zattara
1987) and can be further modulated depending on perturbation
uncertainty, magnitude, direction, biomechanical constraints,
and even fear (Adkin et al. 2002; Bouisset and Zattara 1987;

Bouisset et al. 2000; Cordo and Nashner 1982; Horak et al.
1984; Marsden et al. 1977; Pedotti et al. 1989). It has been
hypothesized that APAs involve a feedforward process,
whereby a representation of the dynamics of the body and the
environment (internal model) is used to predict the conse-
quences of the movement and generate the appropriate postural
adjustment in an anticipatory manner. Similar anticipatory
adjustments are also observed in grip force control during
object manipulation in stationary postures and locomotion
(Flanagan and Wing 1997; Gysin et al. 2008) and are tightly
coupled to anticipatory control at the gross postural level
during stance (Forssberg et al. 1999; Wing et al. 1997). These
results suggest that a common encoding underlies the antici-
patory adjustments of posture and grip, but the extent to which
APAs can be adapted to novel movement dynamics and the
specificity of this adaptation to a given postural configuration
is not well understood.

Because APAs are usually associated with well-practiced
movements, it is thought that they are the result of a long-term
learning process. Indeed APAs in an unfamiliar movement
such as when bending backward are typically absent in un-
trained subjects but consistently evident in well-trained gym-
nasts (Pedotti et al. 1989). Similarly, APAs preceding lateral
leg raises are significantly different between gymnasts and
untrained subjects (Mouchnino et al. 1992). In addition, rapid
learning of APAs has been observed in object lifting tasks
(Commissaris and Toussaint 1997; Forssberg et al. 1999;
Toussaint et al. 1998; Wing et al. 1997), when weights are
added to the limbs (Bouisset et al. 2000; Horak et al. 1984; Lee
et al. 1989; Li et al. 2007) as well as when reaching in
microgravity environments (Kingma et al. 1999; Li 2007;
Patron et al. 2005). It has been consistently shown that APAs
are also highly flexible and can be modulated almost sponta-
neously by perturbation magnitude and direction and biome-
chanical support conditions (Commissaris and Toussaint 1997;
Cordo and Nashner 1982; Marsden 1977; Pigeon et al. 2003).

The familiarity of the movement and/or the load in these
previous studies of APAs precluded an investigation of the
adaptation of postural activity and its relationship to the ability
to control the movement itself. Any learning observed was
rapid. Subjects were usually given a few practice trials to
familiarize themselves with the task, and these initial learning
trials were frequently removed from the analysis (Aruin et al.
1998; Commissaris and Toussaint 1997; Toussaint et al. 1998).
It remains unclear whether APAs can be generated for novel
and complex dynamic loads that are learned in the absence of
the need for APA and, therefore, how postural learning relates
to the learning of arm movement control. Learning novel
dynamics can also provide insights into the underlying mech-

anism of adaptation by slowing down the rate of adaptation and revealing the process at a finer temporal resolution.

The purpose of the current study is to investigate the learning of novel movement and postural dynamics and its ability to transfer between seated and standing postures. We examined whether APAs have access to dynamics learned in the absence of the need for APAs. That is, after learning to make arm movements in the presence of dynamic perturbations in a seated position, will the postural system be able to generalize to standing and predict and immediately compensate for the destabilizing consequences of these dynamics? Such an ability would suggest that APAs can adjust for expected forces on the postural system even though no forces have yet been experienced. Alternatively the postural system may be required to experience the destabilizing forces to be able to generate APAs.

To investigate these questions, we used a well-established experimental paradigm for dynamic adaptation of reaching movements. Participants made reaching movements while grasping the handle of a robotic force-generating manipulandum, which generated a force perturbation proportional to the handle speed and perpendicular in direction. They learned this task while seated, thereby not requiring APAs. We then examined whether on standing APAs would need to be learned for the perturbation on the hand or whether the APA system could immediately utilize knowledge of the expected force to generate APAs. In addition we examined whether learning the dynamics while standing would transfer to performance while seated.

METHODS

Thirteen right-handed participants (7 male and 6 female) gave informed consent and made planar reaching movements in both a seated and standing posture. The experimental procedures were approved by the Local Ethics Committee. A testing session took ~45 min.

Apparatus

Experiments were carried out using a vBOT (Howard et al. 2009) The vBOT is a custom-built back-drivable, planar robotic manipulandum that exhibits low mass at its handle. Optical encoders allowed the position of the handle of the vBOT to be sampled at 500 Hz, and torque motors allowed translational forces to be updated at the same rate. A planar virtual reality projection system was used to overlay images of targets and cursors in the plane of the vBOT's movements, and subjects were prevented from viewing their arm directly. Participants grasped the handle of the vBOT and moved a cursor (1 cm radius) representing the handle position, from a start circle (2 cm radius, positioned on the mid-sagittal pane ~30 cm from the participant's chest) to a single target (2 cm radius) located 15 cm to the right in the horizontal plane. Targets were within reach of the subjects and did not require trunk movement. Task-relevant visual feedback was presented within the plane of movement via a semi-silvered mirror, reflecting the display of an LCD monitor suspended horizontally above (Fig. 1A). This allowed visual feedback of the targets and feedback of hand position to be overlaid into the plane of the movement. When standing, participants stood with feet slightly apart on a six-axis force-torque sensor (ATI Technologies, Apex, NC), which recorded three-dimensional forces (F_x, F_y, F_z) and moments (M_x, M_y, M_z) about its center (Fig. 1B). Subjects were told not to lean on the vBOT. However, as the robot is free to move in the horizontal direction with low friction, any forces downward have minimal stability effects.

When seated, subjects sat in a robust medical treatment chair that had a full back support going to above head height. In addition their legs did not touch the ground, preventing them from using any leg postural adjustment while seated. Also the forces from the vBOT (see following text) were backward, pushing subjects into the chair. Therefore postural adjustments were not required to maintain posture (or stability) while seated.

Experimental protocol

Participants sat or stood with their trunk in the upright position. On a single trial, participants experienced one of three possible types of force environments: 1) null trials, where no forces were generated by
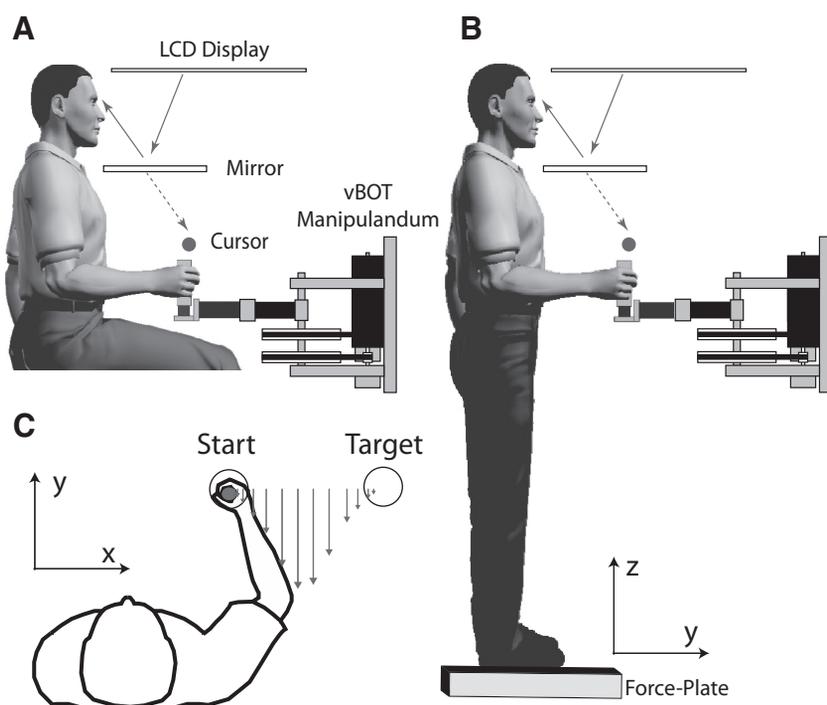

FIG. 1. The experimental setup: participants held the handle of the vBOT and made planar reaching movements to targets presented within the plane of movement while in a seated posture (A) or a standing posture (B). When in a standing posture, a forceplate beneath their feet measured ground reaction forces. C: visual feedback and robot-generated forces (arrows equally spaced in time).

the robot, *2*) force trials, where a viscous curl field was generated by the robot: the force on the hand was proportional to its velocity, and perpendicular (clockwise) to its direction (Fig. 1*C*)

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = k \begin{bmatrix} 0 & 1 \\ -1 & 0 \end{bmatrix} \begin{bmatrix} V_x \\ V_y \end{bmatrix}, \quad \text{where} \quad k = 0.2 \text{ Ns/cm}$$

and *3*) catch trials, where a simulated force channel restricted handle motion to a straight path between the target and start position. Such trials are known to have a minimal effect on any learning or unlearning (Scheidt et al. 2000). Participants received an error message if movements out to the target and back to the start circle were longer than 1.6 s in duration. On force and catch trials, forces remained present on the return movement.

Participants were randomly assigned to either the stand ($n = 7$) or sit ($n = 6$) group, named for the postural configuration in which the first force trial was experienced (Fig. 2). The stand group initially performed 350 trials in the standing position. The first 50 were null trials used to measure baseline performance (baseline). The following 300 trials were force trials (learning). The number of trials was chosen based on previous studies of force-field learning. They then switched to a seated posture and performed 100 force trials (transfer), followed by 100 null trials to extinguish the adaptation (washout). To quantify the transfer of the washout, participants then returned to the original standing configuration for another 100 null trials (transfer2). In the sit group, the order of postural configurations was reversed: 350 sitting trials; 200 standing; 100 sitting. Participants in the sit group performed an additional baseline (50 null trials) in a standing configuration prior to the seated baseline trials at the start of the experiment (Fig. 2). For each subject, foot and chair placement were marked to ensure consistency between phases.

Included in the preceding trials were random catch trials (1 in 5), 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 measuring any small deviations into the wall. When subjects transferred to a new posture, the first trial was always a catch trial.

Data acquisition and analysis

Robot handle position, velocity, acceleration and force were recorded at 500 Hz. Force plate forces (F) and moments (M) were also recorded at 500 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 center of pressure (CP) was determined as $[CP_x \; CP_y] = [M_y \; M_x]/F_z$, where x and y denote mediolateral and antero-posterior axes, respectively. CP was normalized with respect to each subject's foot length, and 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 between the start and target circles (Fig. 1*C*). To quantify the feedforward component of the learned force, we measured the signed peak force generated into the walls on catch trials.

Learning and transfer of movement dynamics was evaluated by comparing performance at nine stages of the experiment (Fig. 2; shaded areas): late baseline (last 5 trials in baseline phase); early learning (1st trial in learning phase); late learning (last 5 trials in learning phase); early transfer (1st trial in transfer phase); late transfer (last 5 force trials in transfer phase); early washout (1st trial); late washout (last 5 trials); early transfer2 (1st trial); and late transfer2 (last 5 trials).

Postural variables

Anticipatory postural control was quantified as the mean CP velocity in the direction of the perturbation in a 150-ms time window starting 100 ms prior to movement initiation and ending 50 ms after movement initiation. Horak and Nashner (1986) observed reactive response latencies varying from 73 to 110 ms in the tibialis anterior in response to unexpected backward sway perturbations. 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 movement.

Movement of the CP in the direction of the impending force perturbation, prior to movement initiation, is considered evidence of an anticipatory postural adjustment. In the present experiment, the robot forces primarily act in the y direction because the subject reached to target along the x axis, and the curl field acted at an angle of 90° in a clockwise direction. Thus we monitored the velocity of the CP along the y axis. APAs specific to the perturbation, without the confounding effect of the reaching movement, can be clearly isolated because they have orthogonal lines of action. As subjects reached from left to right, we would expect also to see x axis APAs. However, the requirements in this direction do not change in any of the conditions whether the force field is on or not, and as there are no perturbations in this direction, these will simply be prelearned APAs that are not relevant to the hypothesis we are testing. An analyses of the x-axis APAs showed they were indeed present and stable throughout the experiment and therefore we report only y-axis APA (CP) data.

A secondary measure of postural activity is the reactive control observed on each trial. This was quantified as the maximum absolute CP velocity recorded 50 ms after movement onset until the end of the
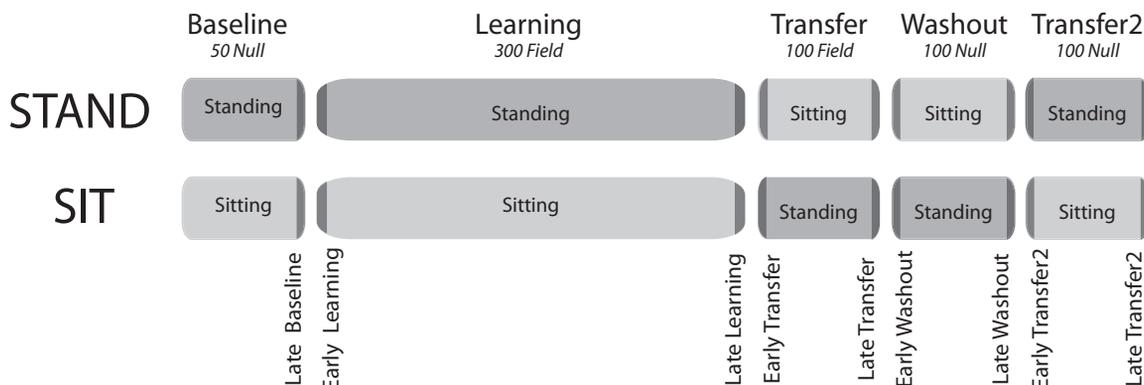

FIG. 2. Protocol: both experimental groups (stand, sit) experience baseline, learning, transfer, washout, and transfer2 phases. The stand group is first exposed to the force field in a standing posture and the sit group is first exposed in a sitting posture. Statistical comparison of movement variables examined the initial (early) and final (late) trials in each phase (shaded regions).

movement along the axis of the perturbation. Higher values indicate increased reactive postural corrections and ineffective anticipatory control. But this measure is also confounded by the presence of the robot forces on force and catch trials that may be transmitted to the force platform. Postural variables were only recorded when the participant was in a standing configuration.

For posture, we compared the following stages in the stand group (Fig. 2; shaded areas in standing configuration): late baseline, early learning, late learning, and early transfer2, late transfer2. The corresponding stages in the sit group are: late baseline, early transfer, late transfer, and early washout, late washout. For postural variables, baseline measurements are taken from the standing baseline phase in both the sit and stand groups.

Data were analyzed with repeated-measures ANOVAs. To determine transfer of learning and transfer of washout, two planned comparisons were made ($\alpha = 0.05$). To quantify learning in each phase, pair-wise comparisons were also carried out between early and late learning, early and late transfer, early and late washout, early and late transfer2, and late baseline and late transfer2. To determine group differences in movement error, we used a repeated-measures ANOVA with group as a between-subjects factor. In the stand group, the rate of learning of movement and postural variables during the learning phase was compared using a repeated-measures ANOVA.

RESULTS

Overview

Reaching performance, quantified as movement error and peak catch force produced, transferred from sitting to standing (sit group) and from standing to sitting (stand group). Anticipatory postural adjustments specific to the arm perturbation gradually developed in the stand group and more slowly than the adaptation of movement control. APAs were immediately evident in the sit group when they transferred to a standing position even though they had not previously experienced the perturbation in a standing posture.

Subjects found the task straightforward. Average movement durations were similar between groups; 1.42 s [0.06] and 1.51 s [0.10] for the stand and sit groups, respectively ($P > 0.05$, t-test).

Stand group results

Figure 3A (*left*) shows three key trials from a typical subject in the stand group. In the baseline phase (*I,* baseline trial) both the CP velocity (—) and force generated by the robot (- - -) were essentially flat. On the first trial in which the robot forces were turned on (*II,* 1st learning trial). the CP velocity lagged behind the robot force by around 200 ms as would be expected for a reactive response. By the end of learning (*III,* final learning trial), the CP velocity was in advance of the robot forces (and arm movement onset) by around 50 ms, demonstrating an anticipatory postural adjustment.

Turning to the group data, when initially exposed to the force field, subjects generated large movement errors (Fig. 4A), which were reduced significantly by the end of the learning phase ($P < 0.001$). The magnitude of peak force measured on catch trials (Fig. 4B) during this period increased significantly ($P = 0.028$), suggesting that subjects were not simply using a co-contraction strategy. As expected, when first exposed to the perturbation, anticipatory postural activity (Fig. 4C) could not be distinguished from the preceding baseline trials ($P = 0.945$). But over the course of learning, subjects adapted their APAs
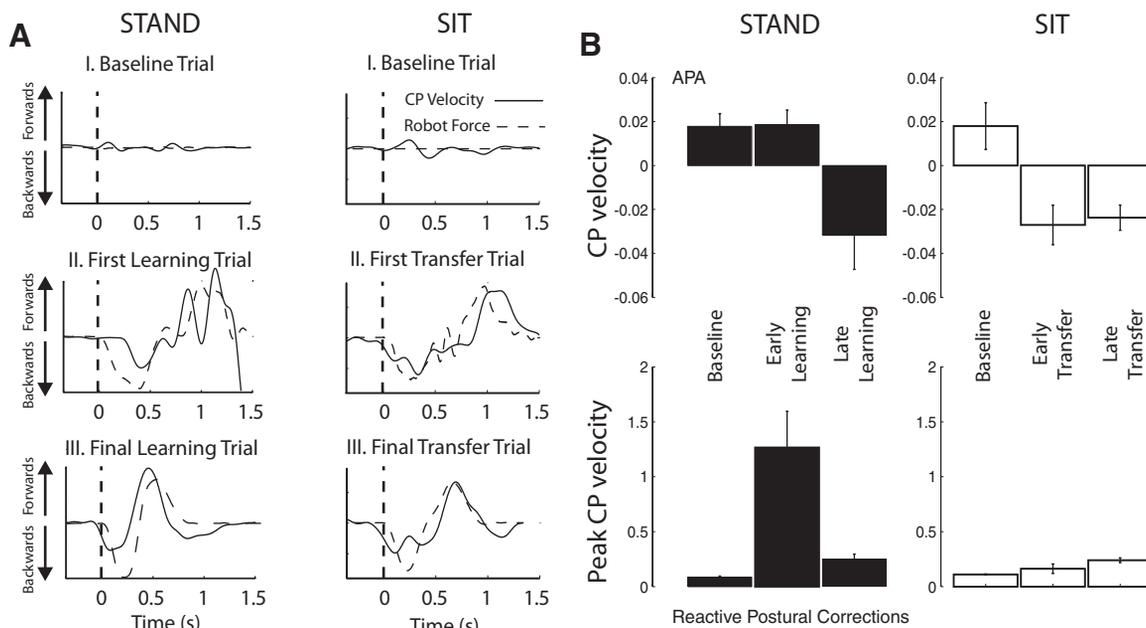

FIG. 3. *A*: representative data: development of anticipatory postural adjustments in a representative subject from each group. Center of pressure (CP, —) velocity and robot-generated forces (- - -) in the *y* axis are shown and scaled to allow for comparison on a single graph. The initiation of arm movement (time = 0 s) is denoted with the vertical dashed line. Stand group (*left*): *I,* final trial in baseline phase; *II,* 1st trial in learning phase and 1st exposure to forces; *III,* final trial in learning phase shows anticipatory CP movement prior to the initiation of hand movement and robot forces. Sit group (*right*): *I,* final trial in standing baseline phase. *II,* 1st trial in transfer phase and 1st exposure to forces in a standing position. Appropriate anticipatory CP movement is evident prior to hand movement. *III,* final trial in transfer phase shows CP movement similar to 1st standing exposure trial. *B*: generalization of postural learning: comparison of postural variables in stand (*left*) and sit (*right*). Data points are shown for the 3 stages of interest, all measured when participants were in a standing posture. Stand stages: baseline, early learning, and late learning. Sit stages: baseline, early transfer, and late transfer. The average across subjects is shown. Error bars indicate one standard error. *Top*: anticipatory CP activity measured prior to movement initiation. *Bottom*: reactive CP activity measured after movement initiation.
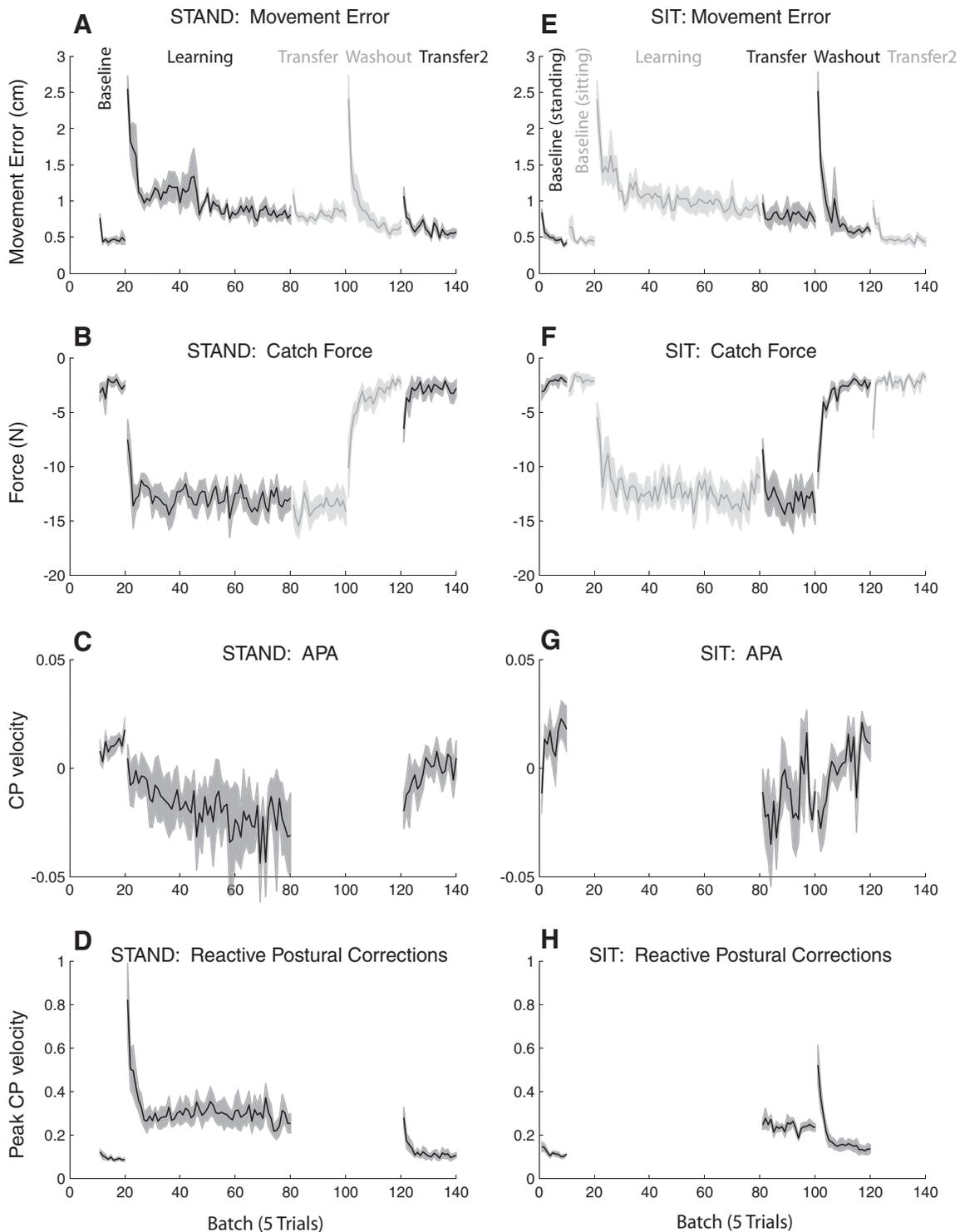
FIG. 4. *Left*: stand results. *Right*: sit results. Dark and light shading indicate when participants are in a standing or a seated posture, respectively. The sit group has both a standing and a seated baseline phase. *A* and *E*: average movement error per batch of 5 trials. Shaded areas represent ± 1 SE. *B* and *F*: feedforward forces along the *y* axis generated on catch trials. *C* and *G*: anticipatory CP velocity; average per batch (s^{-1}). *D* and *H*: reactive CP velocity; average per batch (s^{-1}).

compared with the first exposure trial ($P = 0.039$). Concomitant with the APA changes, the initial trials resulted in large reactive postural corrections (Figs. 3*B, left,* and 4*D*) that were reduced over the learning phase ($P = 0.013$) but remained higher than baseline ($P = 0.004$).

To quantify the rate of learning of each of the performance measures, an exponential function was fit to individual subject

data in the learning phase to determine each subject's time constants. Figure 5 shows three typical subjects' data for the APA learning (CP velocity, $\circ$) and catch force development ($\triangle$) together with the exponential fits. Also shown in Fig. 5 is the group average of the fits to each subject's data. Differences between these learning rates for different conditions were determined with a repeated-measures ANOVA on the time
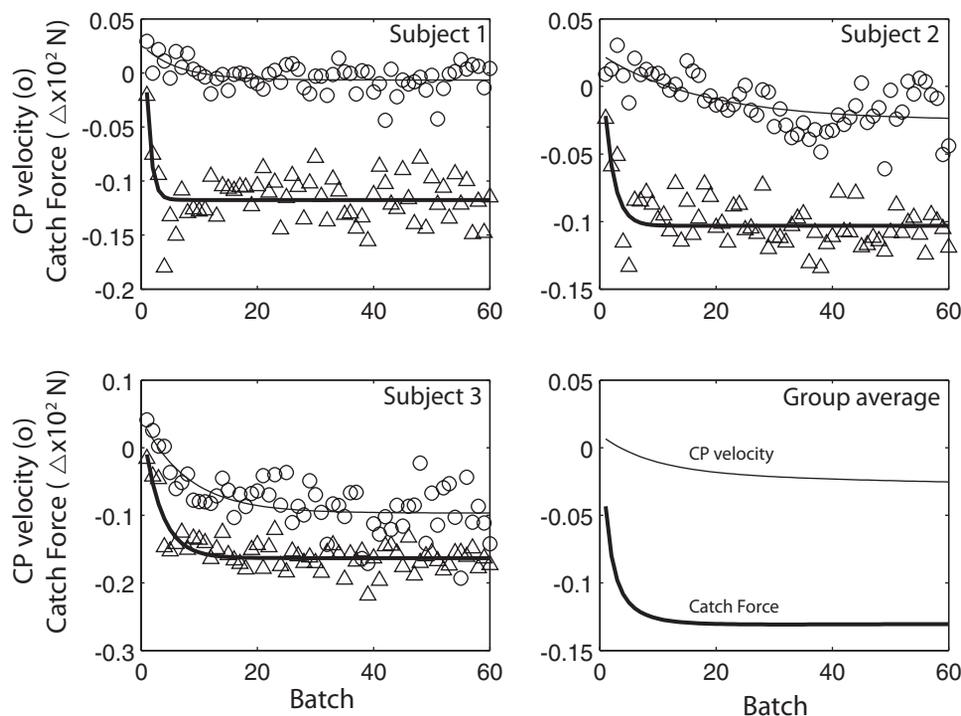
FIG. 5. Learning rates for APA and feedforward arm movement compensation. Shown are 3 typical subjects' data for the APA learning (○, CP velocity averaged over each batch) and catch force development (△) together with the exponential fits. Also shown is the group average of the fits to each subject's data.

constants. APA learning was slower than both the reduction of movement error, and the development of appropriate feedforward forces [15.56 ± 3.95 (mean ± SD), 1.66 ± 0.63, 7.88 ± 2.29, respectively; $P < 0.05/2$, Bonferroni correction]. But reactive postural adjustments were reduced more rapidly than the APAs, similar to the movement error and catch force development (1.89 ± 0.36; $P > 0.05$).

On transferring to sitting, the movement error did not change significantly ($P = 0.244$). Similarly, the initial catch trial in the new posture did not change significantly from the last learning trials ($P = 0.691$). On the sudden removal of the field, large movement errors (aftereffects) were observed with errors as large as those observed on initial exposure to the field ($P = 0.71$). After 100 washout trials, movement error was once again lowered ($P = 0.001$). Having washed out learning in the sitting posture, we examined washout on transfer to the original standing posture. Movement error increased on standing ($P = 0.005$) but was less than initial washout error ($P = 0.001$). This was confirmed by an analysis of the first catch trial in the standing posture, which had an abrupt increase in force ($P = 0.011$) compared with baseline and to the previous null trial ($P = 0.011$). Further evidence of only partial transfer is the continued washout evident in the significant decrease in the force ($P = 0.005$). Over the course of the final 100 washout trials, the movement error decreased further ($P = 0.016$).

APAs observed on standing but in the absence of the force field could not be distinguished from those at the end of learning in the standing configuration ($P = 0.479$) and were greater than the baseline ($P = 0.045$). De-adaptation progressed and by the end of the washout period, APAs were reduced ($P = 0.035$).

After washing out learning in the seated position, significant reactive postural corrections were observed when the group returned to their original standing posture ($P = 0.007$, wrt baseline), and were reduced after 100 trials ($P = 0.019$).

Sit group results

Figure 3*A* (*right*) shows three key trials from a typical subject in the sit group. In the baseline phase (*I,* baseline trial) both the CP velocity (—) and force generated by the robot (- - -) were close to flat (this is a standing trial before sitting). On the first transfer trial in which subjects stood for the first time with the robot forces turned on (*II,* 1st transfer trial), the CP velocity was in advance of the robot forces (and arm movement onset) by around 50 ms, demonstrating an anticipatory postural adjustment. By the final transfer trial (*III,* final transfer trial), the CP velocity was still in advance of the robot forces (and arm movement onset) by around 50 ms.

Turning to the group data, when initially exposed to the force field, subjects generated large movement errors (Fig. 4*E*), which were reduced significantly by the end of the learning phase ($P = 0.002$). The forces measured on catch trials during this period (Fig. 4*F*) increased significantly ($P < 0.001$), suggesting again that subjects were not simply using a co-contraction strategy. On transferring to the standing posture, the movement error increased 0.27 ± 0.119 (SD) cm, but this increase was not statistically significant ($P = 0.062$) and small compared with the mean difference between the first and last learning trials (1.73 ± 0.246 cm). Moreover, the forces generated in the initial catch trial in the new posture did not change significantly from the last learning trials ($P = 0.188$).

Examinations of the first trial on transfer to the standing posture showed that, in stark contrast to the stand group, APAs specific to the impending perturbation (Figs. 3, *A* and *B, right*, and 4*G*) were immediately present. CP velocity increased in the direction of the perturbation prior to movement initiation, compared with the velocities observed at baseline ($P = 0.027$). After 100 trials, CP velocity remained similar to the initial exposure trial ($P = 0.780$). A comparison of the magnitude of the APA (Fig. 3*B*) showed that they were greater in the sit than the stand group on the first standing trial (*t*-test, $P < 0.05$), also

indicating that seated learning facilitates APA adaptation when standing. The sit group did not show such large reactive corrections in the first perturbed stand trial (Fig. 3*B*). Corrections were much smaller than the stand group (*t*-test, $P < 0.05$). Moreover, no learning, or reduction in the magnitude of these corrections was observed through the course of learning ($P > 0.05$).

Large movement errors (aftereffects) were observed on the sudden removal of the field with errors as large as those observed on initial exposure to the field ($P = 0.310$). After 100 washout trials, movement error was once again lowered ($P = 0.001$). On the first washout trial, APAs were identical to the previous batch of exposure trials ($P = 0.410$) and greater than baseline ($P = 0.012$), further indicating anticipatory control. By the end of the washout period, APAs were reduced and returned to baseline levels ($P = 0.492$). Having washed out learning in the standing posture, we examined washout on transfer to the seated posture. Movement error increased on sitting ($P = 0.015$) but was less than initial washout error ($P = 0.002$). This was confirmed by an analysis of the first catch trial in the new posture which had an abrupt increase in force ($P = 0.003$) compared with baseline and to the previous null trial ($P = 0.002$). Further evidence of only partial transfer is the continued washout evident in the significant decrease in the force ($P = 0.002$). Over the course of the final 100 washout trials, the error decreased further ($P = 0.004$).

Movement error was also compared between groups to determine whether participants were able to reduce their error to a lesser extent in either posture. Movement errors on initial exposure, after learning, and on initial washout were statistically indistinguishable between groups (2-way ANOVA, $P > 0.05$, Fig. 6).

Similar to the movement error, reactive postural adjustments peaked on the first washout trial ($P = 0.008$, wrt baseline) and returned to baseline levels by the end of the washout period ($P = 0.167$).

DISCUSSION

Here we have presented evidence that anticipatory postural adjustments can be adapted for novel reaching dynamics even though the postural system had not directly experienced the novel dynamics. APAs have frequently been observed in well-practiced, self-generated body-movements, object lifts, and load catch/release paradigms. In this study, we document the gradual development of anticipatory postural activity in the case of a novel dynamic perturbation. In the stand group, anticipatory control of the center of pressure was initially absent but was clearly evident after 300 trials. Evidence of adaptation was also seen in the sit group during their standing trials. When the robot forces were abruptly turned off, subjects initially continued to exhibit anticipatory CP shifts (aftereffects).

The observed APAs appropriately reflected the anticipatory control of arm trajectory dynamics. This suggests that a common dynamic encoding underlies both posture and movement control. However, a comparison of movement and postural adaptation in the stand group revealed that anticipatory postural adaptation occurs at a slower rate than learning of the reaching dynamics for arm control as evidenced in the catch force. This supports the existence of two mappings, one for
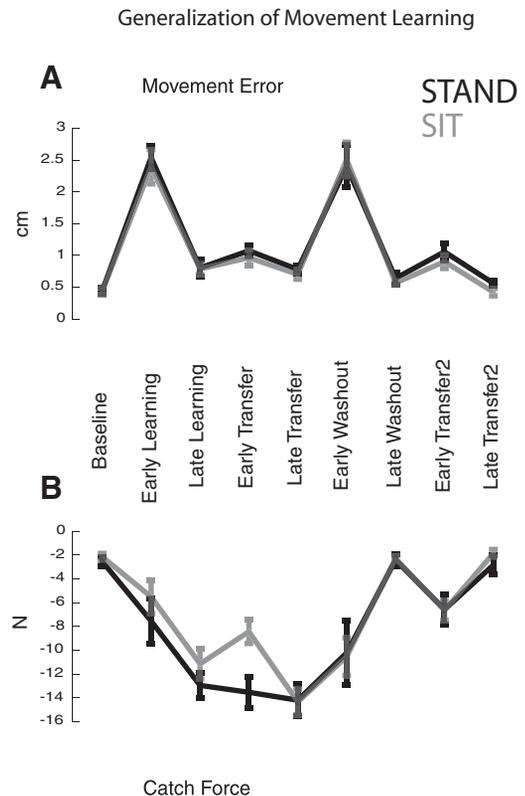

FIG. 6. Generalization of movement learning: black and gray lines represent the stand and sit group, respectively. The average across subjects from both groups at the 9 stages of interest are overlaid. Error bars indicate 1 SE. *A*: movement error. *B*: feedforward forces generated along the *y* axis on catch trials.

maintenance of posture and one for movement, that encode similar dynamics but are adapted independently.

Support for distinct mappings is also provided by the sit group, which shows that after learning a sensorimotor map for arm control in one supporting posture, the postural system can immediately generate perturbation-specific anticipatory activity needed in a novel posture. A single controller that maps desired arm and postural movement onto the required command signals would have led to similar learning rates and no generalization. But this is not supported by the independent learning rates or by the transfer of learning observed. This implies that the CNS employs a modular approach to dynamics learning where two separate mappings: one of the novel arm dynamics and one of the body posture are used to predict and compensate for dynamics in multiple postures. Evidence for distinct representations for posture and movement at the neuronal level has been shown previously (Kurtzer et al. 2005). Such a modular approach, although more computationally demanding, would allow for more flexible control and generalization of dynamics learning.

Similar to previous studies, the generalization observed is better described with two mappings (Massion 1992; Patron et al. 2005). However, these mappings can take various forms, and previous studies have made no distinction. One solution would be to use two inverse controllers, one mapping desired arm trajectory and arm motor commands and another mapping desired postural orientation to postural commands. In the case of arm trajectory inverse models, learning has not generalized to novel postures (Baraduc and Wolpert 2002; Gandolfo et al.

1996). This would suggest that the adapted postural inverse controller would be specific to the trained posture and theoretically would not generalize to a new posture. Our results do not support this hypothesis. We have shown that learning is independent of the supporting postural configuration and can generalize between supporting postures with increasing degrees of freedom.

We believe these findings are parsimoniously explained with two mappings: an inverse mapping for arm control (in accordance with previous studies) and a forward mapping for postural control. A forward internal representation of the dynamics of the environment, coupled with a forward model of the postural dynamics, would allow the CNS to predict movement consequences on an upright posture and generate the appropriate compensatory control.

A hypothesis involving both a forward and an inverse internal model is also supported by the different learning rates, which imply that control of the arm trajectory precedes predictive control of the supporting posture. This appears to contradict previous findings where prediction preceded control of object dynamics (Flanagan et al. 2003), but the present results may be related to the reactive control observed at the postural level. Although perturbation-specific anticipatory control of posture lagged arm control, subjects were still able to minimize the reactive control needed as quickly as they learned to control the arm. They may have achieved this through a nonspecific anticipatory control strategy that relied on muscle co-activation to stiffen the lower limbs and reject the perturbation. Having achieved stabilization, although in a suboptimal manner, subjects could learn to predict the perturbations and generate a specific strategy at a rate of their choosing.

An intriguing result was the incomplete transfer of washout between postural configurations. Feedforward adaptation of arm movement and postural control transferred between postures, but complete unlearning in one posture led to a re-emergence of the adaptation in the original posture. This was true whether transitioning from standing to sitting or vice versa. Evidence of this reappearance was observed in all learning measures: movement error, catch forces, and both APAs and reactive postural adjustments (stand group). Incomplete transfer of washout implies there is an asymmetry between the transfer of learning and unlearning of a novel dynamics across contexts. An underlying assumption in the literature on generalization of motor learning is that the processes of learning and unlearning are symmetric: learning that transfers will also transfer on unlearning (Nozaki et al. 2006). Our findings imply that the underlying mechanisms may only be partially overlapping. Nozaki et al. also observed incomplete washout on switching between a bi- and a unimanual configuration, but transfer of learning was also incomplete. One possible explanation is that generalization of learning across contexts occurs at different timescales. Perhaps less transfer would have been observed had we tested for transfer of learning earlier. And if the washout period had been longer, this would have also washed out learning, although invisible, in other postures.

The APAs seen in our task can be conceptualized as performing one of two tasks (or a combination), that is, stabilizing the body or counteracting the forces applied by the robotic interface. The present analysis does not distinguish between the two tasks. In either case, our results show that the CNS can anticipate the effects of learned movement dynamics on a novel whole-body posture. Our analysis also cannot rule out the possibility that, although unnecessary, seated APAs were present. Subjects were fully supported by the chair when seated, and therefore APAs were not required when seated to compensate for the robot forces in the backward direction. However, whether they were present or not, our results support our conclusion that the CNS can anticipate the effects of learned movement dynamics on a novel whole-body posture.

Conclusions

Subjects' arm movements were exposed to a novel dynamic environment, which resulted in an adaptation of the sensorimotor map for arm movement as well as the map for postural control. Additionally, the flexibility of APAs observed in well-practiced movements is also observed in movements involving recently learned dynamics. The CNS can immediately anticipate the effect of novel dynamics on different body postures. This novel paradigm lends itself to the simultaneous investigation of the nature of the dynamic representations underlying posture and movement control in a variety of unfamiliar, yet well-controlled environments. A greater understanding of their adaptability and flexibility will provide essential insights to guide the development of future rehabilitation techniques and interventions.

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