

Learning and generalization in an isometric visuomotor task

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¹Department of Mechanical Engineering, Stanford University, Stanford, California; ²Department of Biomedical Engineering, Ben-Gurion University of the Negev, Beer Sheva, Israel; ³Department of Health Sciences and Technology, ETH Zurich, Zurich, Switzerland; ⁴Kennedy Krieger Institute, The Johns Hopkins University, Baltimore, Maryland; and ⁵Department of Neuroscience, The Johns Hopkins School of Medicine, Baltimore, Maryland

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Rotella MF, Nisky I, Koehler M, Rinderknecht MD, Bastian AJ, Okamura AM. Learning and generalization in an isometric visuomotor task. *J Neurophysiol* 113: 1873–1884, 2015. First published December 17, 2014; doi:10.1152/jn.00255.2014.—Adaptation is a prominent feature of the human motor system and has been studied extensively in reaching movements. This study characterizes adaptation and generalization during isometric reaching in which the arm remains stationary and the participant controls a virtual cursor via force applied by the hand. We measured how learning of a visual cursor rotation generalizes across workspace 1) to determine the coordinate system that predominates visual rotation learning, and 2) to ascertain whether mapping type, namely position or velocity control, influences transfer. Participants performed virtual reaches to one of two orthogonal training targets with the applied rotation. In a new workspace, participants reached to a single target, similar to the training target in either hand or joint space. Furthermore, a control experiment measured within-workspace generalization to an orthogonal target. Across position and velocity mappings, learning transferred predominantly in intrinsic (joint) space, although the transfer was incomplete. The velocity mapping resulted in significantly larger aftereffects and broader within-workspace generalization than the position mapping, potentially due to slower peak speeds, longer trial times, greater target overshoot, or other factors. Although we cannot rule out a mixed reference frame in our task, the predominance of intrinsic coding of cursor kinematics in the isometric environment opposes the extrinsic coding of arm kinematics in real reaching but matches the intrinsic coding of dynamics found in prior work. These findings have implications for the design of isometric control systems in human-machine interaction or in rehabilitation when coordinated multi-degree-of-freedom movement is difficult to achieve.

isometric reaching; force control; visuomotor rotation; kinematic adaptation; workspace generalization

TO PERFORM GOAL-ORIENTED REACHING, the motor system plans a movement and uses internal models to calculate the motor commands and predict the sensory outcomes (Kawato 1999; Wolpert and Flanagan 2009). In isometric reaching, force or torque produced by a static hand is mapped to the movement of a cursor. The actual dynamics of the arm are removed, and arm motion is replaced by the programmable dynamics of a virtual cursor on a screen. Isometric control is a compelling alternative to movement input for human-machine interaction because it uses a smaller workspace and is associated with an unlimited potential set of virtual dynamics. A particular application of interest is rehabilitation in which isometric control has been

used to evaluate motor impairment (Casadio et al. 2004; Dewald et al. 2001) and to treat movement deficits (Ellis et al. 2005). However, during isometric reaching, proprioceptive feedback of the arm is greatly reduced, and the required muscle activity differs from that used for movement (Sergio et al. 2005).

In real movement, discrepancies between the desired and actual state of the arm, estimated from visual and/or proprioceptive feedback, drive adaptation of an internal model (Sabes 2000; Shadmehr and Mussa-Ivaldi 1994). Adaptation of the motor system to changes in arm dynamics and kinematics has been extensively studied in real reaching. Typically, arm dynamics have been perturbed by applying a mechanical force field (Shadmehr and Mussa-Ivaldi 1994) or inertial mass (Sainburg et al. 1999) on the hand, whereas arm kinematics have been altered by rotating or scaling a visual cursor representing the hand (Krakauer et al. 2000; Pine et al. 1996). The coordinate frame in which the internal model encodes kinematic and/or dynamic information has been debated.

Commonly, the intrinsic coordinate frame relates to the muscles or joints, whereas the extrinsic frame corresponds to hand-, eye-, or task-centered space. Generalization, or the transfer of motor learning from a practiced to an unpracticed movement, has been used to distinguish between these coordinate frames. In a typical experimental paradigm, a perturbation is learned in one workspace (or arm configuration), and transfer of this learning to a new workspace, compatible in selected coordinates, is tested. Studies employing generalization and other methods have found evidence that arm dynamics are largely represented in the intrinsic frame (Gandolfo et al. 1996; Malfait et al. 2002; Orban de Xivry et al. 2011; Sainburg et al. 1999; Shadmehr and Moussavi 2000; Shadmehr and Mussa-Ivaldi 1994) such that the internal model maps the desired motion directly to the required muscle activations. In comparison, arm kinematics are largely coded in extrinsic coordinates (Flanagan and Rao 1995; Krakauer et al. 2000; Vetter et al. 1999; Wolpert et al. 1995).

Taken together, these studies suggest that dynamic and kinematic internal models are learned in different coordinate frames and thus adapt independently (Flanagan et al. 1999; Krakauer et al. 1999). However, more recent evidence suggests that the coordinate frame for each internal model may be mixed. For example, arm dynamics were learned in both intrinsic and extrinsic frames in autistic children (Haswell et al. 2009) and when visual feedback was aligned with the plane of the arm (Parmar et al. 2011). Arm dynamics were also coded in a combination of intrinsic, extrinsic, and object-based coord-

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dinates that was influenced by local learning effects in a study by Berniker et al. (2014). Moreover, visuomotor rotation learning was dependent on intrinsic arm posture (Baraduc and Wolpert 2002) and was coded in a multiplicative, intrinsic-extrinsic gain field when generalization was tested across many combinations of target direction and workspace (Brayanov et al. 2012).

Isometric adaptation to a visuomotor rotation has also been studied. Researchers have investigated the roles of visual feedback (Hinder et al. 2008a), synergistic muscle activity (de Rugy et al. 2009; de Rugy 2010; de Rugy and Carroll 2010; Gentner et al. 2013; Shemmell et al. 2005), and spatial/sensory cues (Hinder et al. 2008b; Woolley et al. 2007, 2008, 2011) in adaptation to a single cursor rotation or set of opposing rotations. However, there is a lack of consensus on the coordinate frame in which a visual perturbation is learned. If isometric learning is similar to movement, we would expect cursor kinematics also to be coded in extrinsic space. We previously found that similarity exists in the time course and extent of adaptation in isometric and movement conditions (Rotella et al. 2013), and Hinder et al. (2007) found that the retention and interference of isometric learning paralleled those in movement studies. Furthermore, target separation in visual (extrinsic) space was found to be a required factor for isometric dual adaptation (Woolley et al. 2011). However, muscle synergies, which may involve either extrinsic or intrinsic coordinates, have been found to have a major contribution in isometric learning. When participants adapt to a visuomotor rotation or a perturbed muscle-to-force mapping, it was found that modifying the activation of an existing muscle synergy (vs. recruiting new muscles) led to faster and more efficient adaptation (Berger et al. 2013; de Rugy et al. 2009) and broader generalization (de Rugy 2010). The fact that these adaptation effects did not transfer across joints led de Rugy et al. (2009) to suggest that muscle-based coordinates play a part in some portion of the adaptation. Together, the evidence related to isometric adaptation supports a mixed-coordinate reference frame in which both extrinsic and intrinsic representations contribute to the total adaptation process. Moreover, evidence of a mixed-coordinate representation has been found during interlimb transfer of visuomotor learning in a finger-based isometric task (Carroll et al. 2014).

In this work, we investigate the nature of isometric adaptation and generalization in a horizontal plane during a virtual reaching task. The primary objective was to determine the coordinate frame that is predominant in learning a visuomotor rotation in an isometric environment. Whereas previous work on isometric reaching has primarily implemented joint-based cursor control in which isometric torque produced at the elbow, forearm, or wrist controlled the movement of a cursor along intrinsic axes, we use Cartesian-space control. Our experiment sampled two workspaces in the reachable area of the arm and used between-workspace generalization to distinguish between intrinsic (joint space) and extrinsic (hand space) frames. The secondary goal was to determine whether the type of isometric mapping, either position or velocity control, significantly influences adaptation and the extent of generalization. To identify the contribution of the change in pose, we also added a control condition in which we tested generalization to an orthogonal target in a single workspace.

MATERIALS AND METHODS

Participants performed an isometric reaching task requiring the movement of a cursor on a screen to one of two circular targets at a 10-cm distance. Using only the right arm, reaches were made by applying force to the locked handle of a robotic manipulandum with both position and velocity control mappings. We investigated two workspaces of the arm (denominated left and right) that were separated by a 90° shoulder rotation. As depicted in Figs. 1 and 2, the left configuration (L) corresponded to the upper arm at ~90° relative to the frontal plane, and the elbow at ~90° relative to the upper arm. The right configuration (R) required the upper arm to be aligned with the frontal plane and the elbow at 90° flexion. We explored the transfer of visuomotor rotation learning under the two isometric control mappings and three combinations of workspace and target direction.

Participants

Forty-eight healthy, right-handed individuals (31 men and 17 women) participated in the study. Participants were 28 ± 6.9 (mean \pm SD) yr old over a range of 18–58 yr. The study was approved by the Stanford University Institutional Review Board, and all participants provided informed, written consent before participation.

Experimental Setup

The experimental setup is depicted in Fig. 1. A 2-degree-of-freedom planar manipulandum, described in a previous study (Rotella et al. 2013), was used as a force-input device for this study. The links of the robot were mechanically locked, fixing the handle in a static location. The participant's hand grasped a freely rotating rubber handle with an embedded ATI Mini45 force-torque sensor, allowing measurement of planar force at the hand in x - and y -directions. Force on each axis was sampled at 1 kHz, filtered using a second-order, discrete Butterworth filter with 6-Hz cutoff frequency, and mapped to

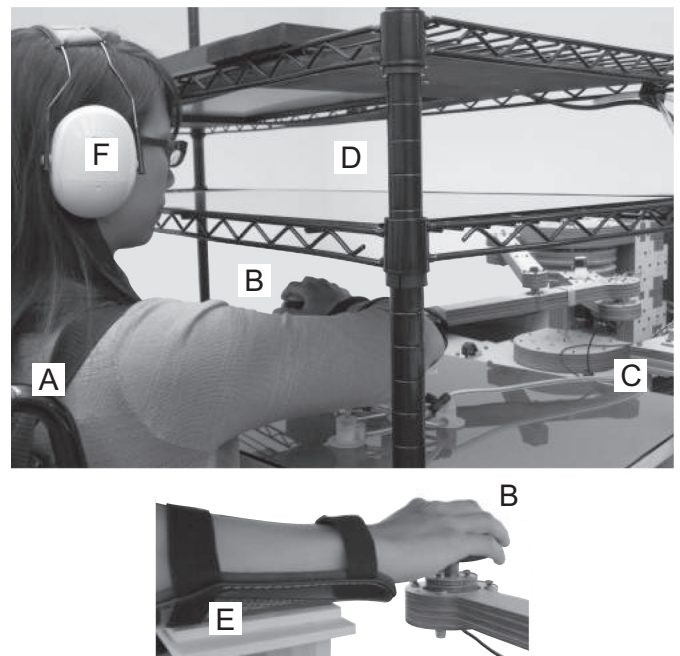


Fig. 1. Participants interact with the experiment workstation while seated in a mobile transport chair (A) with adjustable shoulder straps. Force applied by the participant on the handle (B) of the stationary manipulandum (C) is measured by a force-torque sensor and is used to control a cursor displayed via a mirror-projection system (D). The weight of the arm is supported (E), and participants don noise-isolating headphones to facilitate focus on the task (F). Here, the arm of the participant is in the left workspace.

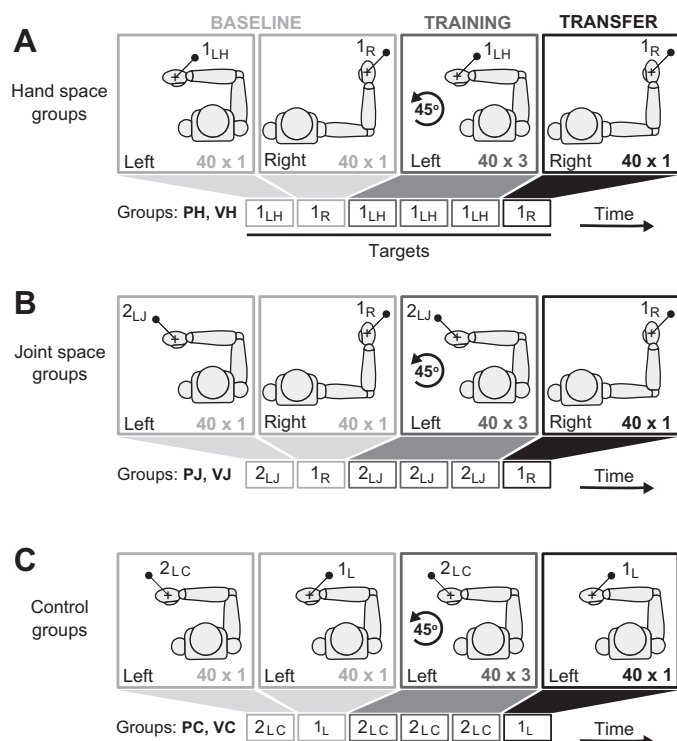


Fig. 2. Experiment design and participant groups. All participants performed 2 sets of 40 baseline trials, 3 sets of 40 training trials in which the displayed cursor was rotated 45° counterclockwise, and 1 set of 40 transfer trials in which the cursor rotation was removed. Participants made center-out reaches to *target 1* or *target 2* located at 45° and 135° from horizontal, respectively. Targets are further labeled by subscript L or R, indicating left or right workspace of the arm, and by subscript H, J, or C, indicating the target is similar to the transfer target in hand space, similar to the transfer target in joint space, or serves as an orthogonal control to the transfer target. P, position; V, velocity. A: hand-space groups (PH and VH) performed all reaches to *target 1*, including baseline trials in the left and right configurations, training trials in the left configuration, and transfer trials in the right configuration. B: joint-space groups (PJ and VJ) repeated the same sequence of arm configurations but performed the 1st baseline and training segments to *target 2*. C: the control groups (PC and VC) performed all trials with the arm in the left configuration, removing the effect of the posture change. Participants in this group made baseline reaches to *target 2* and *target 1*, trained to *target 2*, and tested to *target 1*, isolating the effects of generalization to an orthogonal target in a single workspace.

the movement of a cursor displayed on a screen. The force-sensing resolution was 0.125 N, and unfiltered forces of magnitude <0.2 N were neglected to prevent unwanted cursor behavior (resulting from drift and noise in the force sensor) at the start of movement.

Participants were seated in a lockable transport chair with shoulder straps that immobilized the torso. The seated height of the participant was adjusted using seat cushions. The arm of the participant was positioned in plane with the shoulder, and the forearm was fastened to a support with adjustable Velcro straps. Participants wore noise-isolating headphones to improve overall comfort and reduce distraction while performing the task.

A mirror-projection system provided a visual display to the participant. Graphics were projected from a 24-in. monitor onto a horizontal mirror positioned above the arm. The mirror height was approximately halfway between the arm and monitor, providing visual collocation of the arm and the cursor movement planes. The arm and hand remained occluded from the participant throughout the experiment.

Force calibration and control mappings. For both position- and velocity-based isometric cursor mappings, gains were selected to transform planar input force, $\vec{f}_{in} = (f_{x_{in}}, f_{y_{in}})^T$, to cursor movement. A

force calibration task was used for each participant to scale control gains based on individual ability. Force targets, displayed as wedges on the screen, visually guided participants to apply force in four directions (toward, away, left, right) within an acceptable 20- to 45-N range. Participants were instructed to apply a “force that would be comfortable to hold for 10 s,” targeting the midrange of their ability. In each direction, force was applied for 3 s, and a maximum force was calculated as the average of the highest 10 force measurements. The smallest maximal force for all 4 directions was taken as the calibration force, f_{cal} .

The calibration force was used as a scaling factor in each type of isometric mapping. For the position mapping, the input force was directly scaled to the position of the cursor, $\vec{x}_{cursor} = (x, y)^T$, via the position gain, k_p .

$$\vec{x}_{cursor} = k_p \vec{f}_{in}$$

The k_p gain was computed as $k_p = c_p / f_{cal}$, with the control constant $c_p = 0.24$ m. The value of c_p was selected based on our previous investigation (Rotella et al. 2013) with slight modification to improve cursor responsiveness and speed. Similarly for the velocity mapping, input force scaled to the velocity of the cursor, $\vec{x}_{cursor} = (\dot{x}, \dot{y})^T$, by gain k_v .

$$\vec{x}_{cursor} = k_v \vec{f}_{in}$$

The rate gain, k_v , was calculated as $k_v = c_v / f_{cal}$, with the control constant $c_v = 1.5$ m/s. The values of the control constants c_p and c_v were chosen empirically based on our previous investigation (Rotella et al. 2013), with slight modification to improve cursor responsiveness, and speed-responsive enough to avoid excessive fatigue but slow enough such that performance of the reach task is feasible.

Experimental Protocol

Six groups of participants ($n = 8$ per group, 48 total) were recruited for this experiment, and the groups were randomly assigned: half of the groups performed the experiment with the position mapping, whereas the other half used the velocity mapping. Within each mapping, three groups were tested: the hand-space and joint-space groups tested the effects of arm configuration and target direction on learning transfer, and a control group tested generalization to an orthogonal target within a single workspace. Groups are described by two letters, the first indicating the type of mapping (position, P; or velocity, V) and the second indicating the space (hand, H; joint, J; or control, C).

Participants made virtual reaches to 2 targets. *Target 1* was 45° counterclockwise (CCW) from the rightward-lateral 0° direction, and *target 2* was 135° CCW from 0°. These target directions are similar to those used by Malfait et al. (2002) and are close to orthogonal in both hand and joint space. Participant groups performed 40 baseline (BL) reaches to the training target, 40 BL reaches to the transfer target, 120 training (TRN) reaches with a 45° CCW cursor rotation, and 40 transfer (TFR) reaches with the rotation removed. Breaks were provided after every block of 40 trials, but no minimum break time was enforced. Rest periods were on the order of seconds to minutes with typically greater time elapsed when participants were physically repositioned to a new workspace. To change between L and R workspaces between blocks of trials, participants were physically repositioned relative to the stationary handle of the manipulandum.

The experimental protocol is summarized in Fig. 2, in which target labels indicate the corresponding workspace (L or R) and group (H, J, or C). For all groups, transfer reaches were made to *target 1* with the arm in the left or right workspace. Groups PH and VH performed the first BL and training blocks with the arm in the left workspace to *target 1_{LH}*. Subscript H indicates that the training target was similar to the transfer target in hand space (located at the same position on the

screen) and was close to orthogonal in joint space. The second BL and transfer blocks were made with the arm in the right workspace to *target 1_R*. Groups *PJ* and *VJ* performed the first BL and training blocks with the arm in the left workspace to *target 2_L*, and the second BL and transfer blocks in the right workspace to *target 1_R*. *Target 2_L* was similar to the transfer target, *1_R*, in joint space (positioned similarly relative to the hand) and was orthogonal in hand space.

The control group followed a similar procedure but maintained the left arm configuration throughout the experiment. The first BL and training blocks were made to *target 2_{LC}*. In the second BL and transfer blocks, the arm position was maintained, and participants reached to *target 1_L*. The training target, *2_{LC}*, was close to orthogonal to the test target in both hand space and joint space. Therefore, the control group was used to determine the extent of generalization to an orthogonal target in a single workspace for both position and velocity mappings. In the control group, breaks were provided every 40 trials; a minimum break time of 90 s was enforced only for breaks corresponding to workspace changes in the other groups.

For all reaches, participants were instructed to make quick and accurate center-out movements of the cursor (0.6-cm radius) from the center of the workspace (circle with 1-cm radius) to a circular target (1-cm radius) located 10 cm away. To acquire a target successfully, the cursor had to be inside the target circle and “stopped” (speed < 0.01 m/s) for 0.5 s. Participants were instructed to release the force on the handle after each trial, and the cursor automatically returned to center. The velocity components of the cursor were calculated using numerical differentiation and filtered using a second-order discrete filter, described by a linear difference equation and cutoff frequency of 8 Hz. At the end of each trial, participants received feedback on the maximum speed of the cursor, encouraging between-trial speed correction. Speed was visually displayed via a speedometer that presented the target peak speed range (0.4–0.6 m/s) in a green color. Trials in which the reaching attempt duration exceeded 5 s from when the cursor center left the center of the workspace were automatically ended, initiating the start of the next trial. This feature was designed to reduce participant frustration, and none of the trials was removed from the analysis based on completion time criteria.

Data Analysis

Cursor position and force data were recorded at 500 Hz. Position components (*x* and *y*) were independently filtered using a second-order, low-pass Butterworth filter with 6-Hz cutoff frequency applied in forward and reverse directions. Cursor speed was taken as the magnitude of the velocity components, found by numerically differentiating the filtered position. For each reaching trial, the onset of movement was defined by searching backward from the peak speed and identifying where the speed first dropped below 5% of the maximum. The corresponding unfiltered cursor position was taken as the path start. Trials in which a single, targeted reach was not made or the device became unlocked were invalid and removed from the analysis.

To assess adaptation, we measured the angular error (in degrees) between the first cursor position exceeding a 3.5-cm Euclidean distance from the onset position and the straight-line path from onset to target. Positive angular error indicated a CCW rotation of the path. The distance-from-start metric was chosen to address differences in the timing characteristics (maximum speed and movement duration) of position- and velocity-based trials, discussed in the following section. Across all participants, the point at which error was measured corresponded to the early part of the trajectory, before the expected effect of feedback. An analysis of the last 20 trials in the 1st BL segment for each participant revealed that the selected distance corresponded to an average of 137 ± 31 ms from onset for the position mapping and 182 ± 39 ms for the velocity mapping.

For all participants, the angular error was calculated for each of the 240 trials. The valid errors for each trial were subsequently averaged

across participants within each group, producing an average error curve per group. The corresponding standard error of the mean (SE) was calculated for each average error point. A double-exponential curve (sum of exponential terms plus constant) was fit to the average errors in the adaptation phase for each group, modeling fast and slow learning processes. A time constant, τ , was calculated to describe the overall learning rate per group, similar to Lang and Bastian (1999). However, here the time constant was calculated from a double- (vs. single-) exponential curve fit to the errors and was taken as the whole number of trials for the fitted error to drop below 63.2% of the difference between the initial and final model values. We also used the fast and slow learning rates of the double-exponential fit to quantify the time scale of adaptation.

To quantify learning and generalization effects further, we analyzed single trials including the first/last TRN trials (81 and 200) as well as the first/last TFR trials (201 and 240). For this single-trial analysis, we applied a correction to remove the BL bias for each participant. The bias for each BL was taken as the average of the last 20 BL errors. For each participant, the bias from the 1st BL was subtracted from the TRN trials, and the bias from the 2nd BL was subtracted from the TFR trials. To test for complete learning (error reduced to 0), a 1-sample, 2-tailed *t*-test was performed on the last BL-corrected TRN errors in each group. One-sample, two-tailed *t*-tests were also performed on first/last BL-corrected TFR errors in each group to test for a statistically significant aftereffect/complete washout of learning, respectively. The threshold for statistical significance for all tests was at $\alpha = 0.05$, and all statistical tests were performed using SPSS Statistics (version 20; IBM, Armonk, NY). All other analysis was performed using MATLAB (version R2010a; MathWorks, Natick, MA).

A 2-way ANOVA was conducted to test the effects of mapping type (position or velocity) and space (joint, hand, or control) on the transfer of visuomotor learning, represented by the 1st BL-corrected TFR errors. Given the small sample size ($n = 8$ for each of the 6 groups), the Wilk-Shapiro test was used to evaluate the normality of errors in each group, and Levene's test was used to assess the equality of error variances. For significant, multilevel independent factors, Tukey post hoc test determined significant comparisons.

To characterize differences in participant performance for position and velocity control further, we analyzed the trajectory kinematics of the last 20 reaches of the 1st BL segment, in which all participants were positioned in the left workspace. We measured temporal aspects of the trajectories, including peak cursor speed and total trial time, which was taken as the time between movement onset and trial end (target acquisition or time out). With respect to spatial characteristics, we additionally quantified the target overshoot by measuring the maximum distance of the cursor from the onset position. For each metric, the trial values were grouped by mapping and averaged, and means were compared in an independent-samples *t*-test.

RESULTS

We found that transfer of isometric visuomotor rotation learning took place in joint space independent of the type of mapping (position or velocity). Despite the similar learned coordinate frame across mappings, mapping type influenced the extent of learning transfer, as larger aftereffects were found using velocity control. The influence of mapping type on learning reflects differences in task performance under position and velocity control.

Participant Force Calibration and Trial Selection

The average calibration force for the 48 participants was 25.51 ± 4.54 N (mean \pm SD). Of the study participants, a single participant in the *PH* group achieved a much lower

calibration force of 11.49 N. Although the position mapping experienced by this participant may have differed from the other participants, there was no significant difference in the results when this participant was included or excluded from the analysis. Thus no participants were excluded from the study. Across all virtual reaching trials (240 per participant, total of 11,520 trials), we identified 73 trials (0.63%) as invalid and removed them from further analysis.

Time Course and Extent of Adaptation

When we visually rotated the cursor during virtual reaching, participants adapted to the perturbation to a similar extent and at a similar rate in all groups. The time course of angular error, averaged across the eight participants in each group, is shown in Fig. 3. In all BL segments, the average angular error typically remained within $\pm 10^\circ$. The bias errors in the first and second BL segments, averaged across all participants, were $1.28 \pm 3.59^\circ$ and $-0.35 \pm 3.45^\circ$ (mean \pm SD), respectively. At the onset of perturbation (*trial 81*), the average error peaked for all groups and reduced over the TRN phase. Participants completely adapted to the perturbation in all groups (Fig. 4),

given that the BL-corrected errors in the last training trial were not statistically significantly different from 0° ($t_7 = 2.045$ and $P = 0.080$ for *VJ* and $P \geq 0.114$ for all others). This result is typical of an adaptive process in which the motor system continually adjusts to reduce error and restore straight cursor paths. The rate of adaptation, described by τ , was rapid and similar across all groups; the double-exponential curve fit to the average errors reduced by 63.2% within three or four isometric reaches.

Despite these group similarities, we found a statistically significant difference in the amplitude of the first training error between the position and velocity mappings (Fig. 4). We expected the initial error at the onset of perturbation to be $\sim 45^\circ$, equivalent to the magnitude of the applied visual rotation. Instead, larger initial errors were found for the position mapping. The first, BL-corrected TRN error averaged across participants in the position groups ($52.15 \pm 8.17^\circ$, mean \pm SD) was 8.37° greater than the initial TRN error for participants in the velocity groups ($43.78 \pm 8.61^\circ$). A *t*-test confirmed that this difference was statistically significant ($t_{43} = 3.333$, $P = 0.002$).

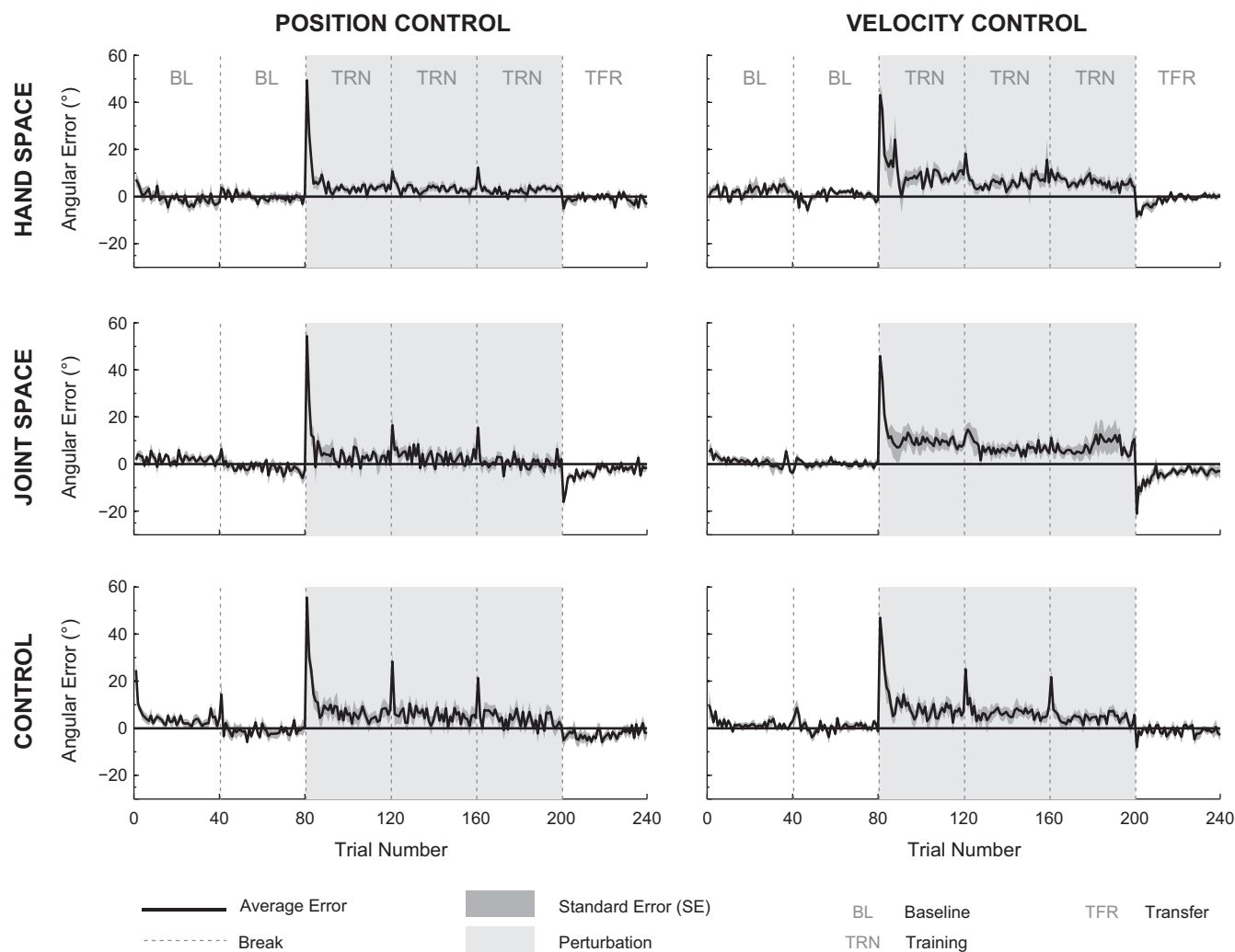


Fig. 3. Angular error averaged by participant quantifies the time course of adaptation in position and velocity control mappings. Errors (black) are plotted before baseline correction across baseline (BL), training (TRN), and transfer (TFR) segments, and the corresponding shading (dark gray) indicates the standard error (SE) about the mean ($n = 8$) per group. Error is small in the baseline, spikes at the onset of the 45° visual cursor perturbation (light gray shading), and decreases over 120 trials. Breaks are included every 40 trials (gray dashed lines). The 1st transfer error (*trial 201*) characterizes the magnitude of the aftereffect.

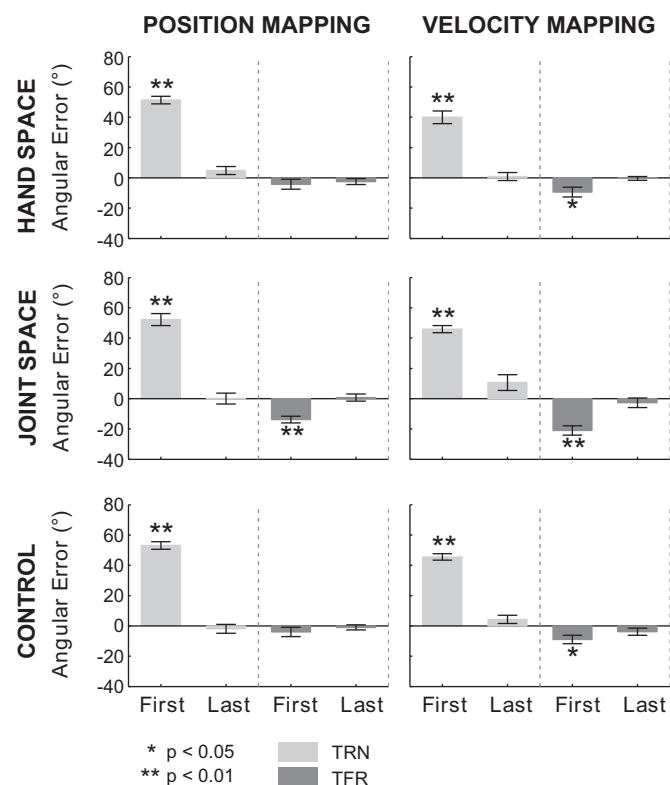


Fig. 4. First and last errors for TRN and TFR segments indicate the extent of rotation learning and unlearning with error bars indicating SE of the mean. In all groups, an angular error statistically significantly different from 0° ($P < 0.01$) was present in the 1st training trial in which the cursor rotation was introduced. Angular error subsequently reduced to 0 over 120 trials, indicating complete adaptation in all groups. The aftereffect, measured by the 1st transfer error, was extremely significant for *PJ* and *VJ* groups ($P < 0.01$) and significant for *VH* and *VC* groups ($P < 0.05$). All errors are corrected for baseline bias; for each participant, TRN and TFR errors were corrected using the average error of the last 20 trials of the 1st and 2nd baseline segments, respectively.

Furthermore, we observed some interesting occurrences in the time course of average errors over the TRN phase. Abrupt peaks in angular error throughout training often accompanied the first trial after a break (Fig. 3), indicating a forgetting of the learned rotation during the break. Additionally, errors in the first training period of the *VH* group and the last training period of the *VJ* group diverged from the smooth, decreasing learning curve we expected. These irregular segments may be the result of large errors of two atypical participants, indicated by large standard errors about these points. The removal of the data of these atypical participants from the overall analysis eliminated these irregularities but did not change the results of our statistical analysis of initial training and transfer errors. Therefore, we present the analysis of our entire participant population without removing the atypical participants.

Effects of Mapping and Space on Learning Transfer

Generally, transfer of learning was the greatest in joint-space groups (*VJ* and *PJ*), moderate in the other velocity groups (*VH* and *VC*), and absent in the other position groups (*PH* and *PC*). Typical cursor trajectories from the first TFR trial in each group graphically illustrate these results (Fig. 5). *VJ* and *PJ* trajectories demonstrated the most pronounced aftereffects,

apparent in the large cursor deviation from the straight path. *VH* and *VC* trajectories typically showed less deviation compared with the joint-space trajectories. In contrast, the trajectories for *PC* and *PH* groups were nearly a straight path to the target.

To quantify these effects, we analyzed the first, BL-corrected TFR error for all groups (Fig. 4). A significant transfer of learning was found in *PJ* and all velocity groups. Of these groups, *VJ* had the largest aftereffect of -21.02° , followed by *PJ* with an aftereffect of -13.85° . Compared with the corresponding first BL-corrected TRN error (which would indicate a 100% transfer), these values represented 45.8 and 26.6% transfer of learning for *VJ* and *PJ* groups, respectively. One-sample *t*-tests showed that the aftereffects in both joint-space groups were statistically significantly different from 0° with $P < 0.001$ for both *VJ* ($t_7 = -6.828$) and *PJ* ($t_7 = -6.214$). Whereas the aftereffects were also statistically significant for *VH* (-9.41° ; $t_7 = -2.927$, $P = 0.022$) and *VC* (-8.98° ; $t_7 = -3.193$, $P = 0.015$) groups, the percentage transfer of learning was $<24\%$ in each group. No statistically significant transfer was observed in the *PH* (-4.25° ; $t_7 = -1.282$, $P = 0.241$) and *PC* (-3.98° ; $t_7 = -1.276$, $P = 0.243$) groups. Although joint-space learning was dominant, all groups demonstrated incomplete generalization in the TFR phase. Aftereffects of learning in all groups completely washed out over 40 TFR trials. All BL-corrected errors in the last transfer trial (Fig. 4) were not statistically significantly different from 0° ($t_7 = -1.606$, $P = 0.152$ for *VC* and $P \geq 0.250$ for all other groups), indicating a return to BL performance and straight cursor trajectories.

When the effects of isometric mapping (position or velocity) and training space (hand, joint, or control) were analyzed together, we found that both factors statistically significantly influenced learning transfer, with the greatest transfer associated with the velocity mapping and joint space. Before implementing a two-way ANOVA, results of the Wilk-Shapiro test

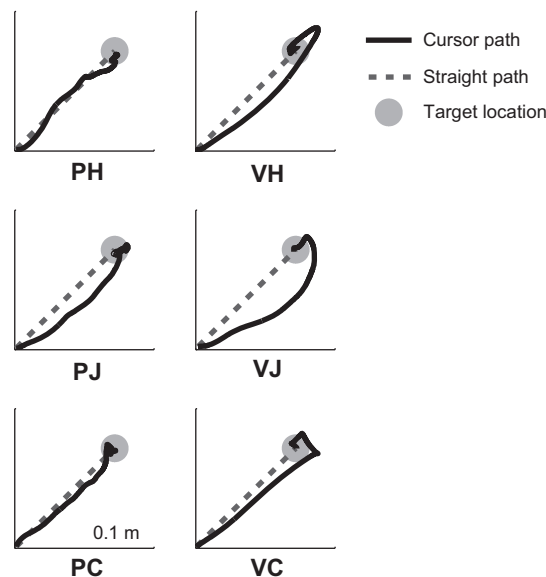


Fig. 5. Cursor paths for selected 1st transfer trials categorized by group. In position and velocity mappings, the angular deviation from the straight path is larger in joint-space groups (*PJ* and *VJ*) compared with hand-space (*PH* and *VH*) and control (*PC* and *VC*) groups. Generally, the errors associated with the velocity mapping were greater than those in the position mapping.

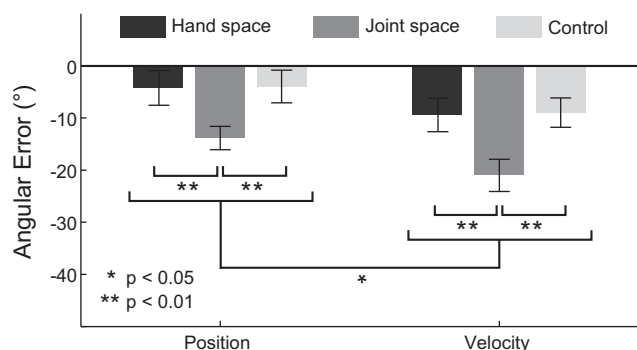


Fig. 6. Comparison of 1st transfer errors for all groups. Bars indicate the mean error, and error bars indicate the SE about the mean. Asterisks indicate statistical significance in 2-way ANOVA and post hoc tests for mapping and space factors; single asterisk comparisons are significant with $P < 0.05$, whereas double asterisks comparisons are significant with $P < 0.01$. In both position and velocity mappings, the joint-space group has a significantly greater aftereffect compared with the control and hand-space groups. Transfer errors in the velocity mapping are significantly larger than transfer errors in the position mapping. All errors are corrected for baseline bias, calculated as the average error in the last 20 trials of the 2nd baseline segment for each participant.

and Levene's test verified that the first BL-corrected TFR errors were normally distributed ($W_g = 0.844$, $P = 0.082$ for PH and $P \geq 0.149$ for all other groups) with equal variance ($F_{5,42} = 0.214$, $P = 0.955$). We found no statistically significant interaction between mapping and space factors ($F_{2,42} = 0.082$, $P = 0.922$) and, therefore, independently analyzed the effect of each. As shown in Fig. 6, there was a significant difference in learning transfer between position and velocity mappings ($F_{1,42} = 5.618$, $P = 0.022$) with a greater aftereffect for the velocity mapping ($-13.14 \pm 10.00^\circ$, mean \pm SD) compared with the position mapping ($-7.36 \pm 9.20^\circ$). Furthermore, the training space significantly influenced learning transfer ($F_{2,42} = 8.697$, $P = 0.001$). Tukey post hoc test indicated that the joint-space groups generated greater transfer compared with both the hand-space ($P = 0.003$) and control ($P = 0.002$) groups. The difference between the joint-space and control groups indicates that the observed aftereffects in PJ and VJ can be attributed to the change in workspace and are not a result of a broad generalization across orthogonal targets.

Comparison of Position and Velocity Mappings

Whereas evidence of a joint-space coordinate learning frame was found for both the position and velocity mappings, we observed differences in participant performance under the two types of cursor control with respect to the required input force and temporal/spatial cursor characteristics. Figure 7 highlights these differences and displays the force trajectories, speed trajectories, and path of an example reach under each mapping. In the position mapping, the required force magnitude resembled a ramp that plateaus, as a constant force was required to stabilize the cursor within the target. The corresponding cursor speed, found by differentiating the path components, was similar in shape to the bell-shaped velocity profiles associated with actual reaching movements (Flash and Hogan 1985). In the velocity mapping, the components of input force were directly mapped to cursor velocity such that the cursor speed resembled the force magnitude (scaled by gain k_v). Whereas the position mapping required generally lower forces main-

tained over a longer period, the velocity mapping required higher force over a short duration.

The sample trajectories illustrate additional observations of differences in cursor kinematics between the mappings, including higher peak speeds, shorter trial times, and less overshoot at the target in position control. The peak speed averaged across the selected BL reaches was greater for the position mapping (0.54 ± 0.13 m/s, mean \pm SD) compared with the velocity mapping (0.42 ± 0.11 m/s), and the difference was statistically significant ($t_{924} = 15.578$, $P < 0.001$). Likely, greater cursor speed contributed to a reduced average trial completion time in the position trials (1.46 ± 0.60 s). Velocity trials lasted 2.01 ± 0.84 s and were of statistically significantly longer duration than position trials in a t -test ($t_{868} = -11.619$, $P < 0.001$). During target acquisition, velocity trials also displayed significantly greater overshoot, given a maximum average distance of 11.89 ± 1.79 cm compared with 10.51 ± 0.58 cm in the position mapping ($t_{580} = -16.104$, $P < 0.001$). In the velocity mapping, on average, the cursor exceeded the 10-cm target distance by nearly 2 cm. This finding is not surprising given that overshoot was not penalized in our task and was allowed to achieve the primary goal of maintaining the target cursor speed. Although less overshoot was apparent in the position mapping, we observed that it required more effort to stabilize the cursor at the target location.

Although the adaptation rates, expressed in terms of τ , were similar between the position and velocity mappings, there was evidence that average learning rates may be slightly faster in position control. An analysis of the coefficients of the double-exponential curve fit to angular errors revealed a faster rate in the fast learning process; the corresponding rate coefficient averaged across position groups was -0.73 ± 0.11 , compared with -0.50 ± 0.06 for the velocity groups, with $t_4 = -3.220$, $P = 0.032$. Despite this difference, the rate of the slow learning

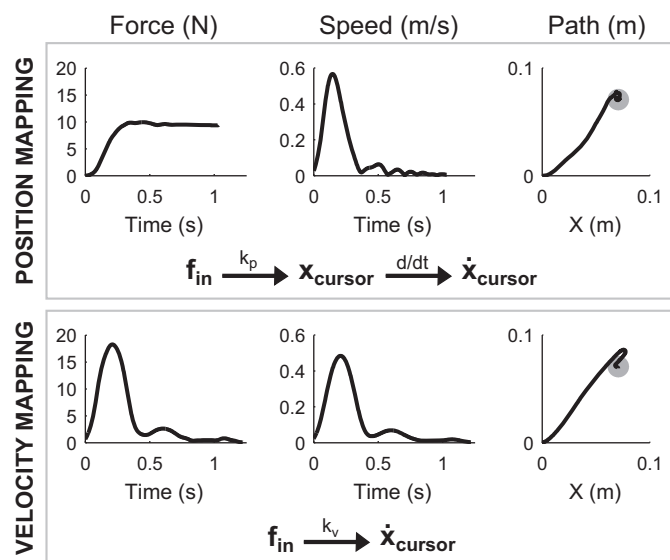


Fig. 7. Comparison of force and cursor trajectories and cursor paths between the 2 control mappings (position and velocity) during 2 representative target reaches. In the position mapping (top), input force, f_{in} , is multiplied by control gain, k_p , and maintained at a constant value to achieve the target. In the velocity mapping (bottom), f_{in} is scaled by gain k_v , to produce the cursor speed, \dot{x}_{cursor} . Both mappings result in a straight cursor path to the target. Typically, the velocity mapping resulted in slower peak speeds, greater overshoot in the cursor path, and longer trial completion times.

process was not significantly different between mappings ($t_4 = -1.117$, $P = 0.327$) with average rate coefficient -0.007 ± 0.004 for position and -0.004 ± 0.002 for velocity mappings.

DISCUSSION

The aims of the study were to determine 1) which coordinates, intrinsic (joint space) or extrinsic (hand space), are predominant in the internal representation of visuomotor rotation in isometric reaching, and 2) whether the type of isometric mapping (position or velocity control) influences the adaptation and generalization processes. By testing the transfer of learning of a 45° CCW visual perturbation to a new workspace, we found that joint coordinates are predominant in rotation learning in an isometric environment. Whereas mapping type minimally influenced adaptation, the velocity mapping yielded greater between-workspace transfer and generalized more widely compared with the position mapping.

Time Course and Extent of Adaptation

All groups completely adapted to the 45° CCW visual cursor rotation, with 63.2% of learning taking place early in the training phase (within 3–4 reaches). This rapid learning is primarily attributed to the required learning of only a single target direction. When 8 target directions were learned in our previous isometric study, a comparable amount of learning required over 20 reaches for both position and velocity mappings (Rotella et al. 2013), amounting to a similar number of trials per target to achieve 63.2% adaptation.¹ Generally, this result is consistent with the finding that, for real reaching, the rate of visuomotor adaptation to multiple targets is slower than adaptation to a single target and is comparable if calculated in terms of trials per target (Krakauer et al. 2000). It is plausible that in the isometric environment, like in movement, adaptation to the visual rotation generalizes narrowly across target direction, and exposure to error in multiple directions is necessary for complete generalization within a single workspace. With respect to the extent of learning, we demonstrated complete adaptation for all isometric groups. Similarly, near-complete adaptation (81%) was found after 60 dynamic reach reversals with a 30° CCW cursor rotation (Krakauer et al. 2000). Overall, the time course and extent of motor errors suggest similarity between visuomotor learning in isometric and dynamic reaching.

Effects Of Mapping and Space on Learning Transfer

The main finding of this study is that the internal representation of isometric cursor kinematics was coded predominantly in intrinsic (joint) coordinates in both position and velocity mappings. Although we cannot rule out a mixed-coordinate frame in both mappings, the predominance of the intrinsic coordinates was clearly demonstrated in the position mapping, in which significant learning transfer occurred only in *PJ*. The nonsignificant aftereffect observed for the *PC* group supports a narrow within-workspace generalization function for the posi-

tion mapping in which there is little generalization away from the learned reaching direction.

A wider within-workspace generalization function was present for the velocity mapping; the significant aftereffect in *VC* indicates that some learning in the TRN target direction transferred to the TFR target, positioned 90° away. We hypothesize that the broader generalization is the result of longer trial times and greater target overshoot associated with the velocity mapping, which may produce more submovements over a broader range of directions. Motor corrections have also been found to influence visuomotor generalization in actual reaching, especially for movement directions far from the training direction (Taylor et al. 2013). The within-workspace generalization of both mappings is consistent with the minimal transfer of rotation learning to an orthogonal target (approximately <25%) found in dynamic reaching (Krakauer et al. 2000; Pine et al. 1996).² Wider generalization for the velocity mapping may have contributed to the transfer of learning observed in *VH*, which was similar in magnitude to that in *VC*.

In the literature, there is evidence that intrinsic coordinates contribute to adaptation in isometric tasks involving a variety of control spaces and virtual dynamics. de Rugy et al. (2009) performed a similar center-out targeting task requiring adaptation to a 45° visual cursor rotation, although the arm was positioned out of plane. The finding that the behavior of muscle synergies at the wrist did not follow those at the elbow suggests that visuomotor adaption involved at least some neural processing in muscle-based coordinates. Our experiment did not distinguish between joint-space and muscle-space coordinate frames, found to be distinct for the shoulder and elbow (Flanders and Soechting 1990; Sergio and Kalaska 1997). [These coordinate frames are reported to be more similar to each other for the wrist (de Rugy et al. 2012a).] The agreement of a learned intrinsic frame is also interesting given the difference in the task coordinates between the two studies; we transformed extrinsic force commands to Cartesian-space cursor movement, whereas de Rugy et al. (2009) mapped torques to a joint-space display. Furthermore, Berger et al. (2013) showed that the recruitment of modulated, vs. new, muscle synergies increases the rate of adaptation even when the force-controlled cursor represents a critically damped mass with an adaptive mass-spring-damper filter. Together, this evidence suggests that isometric learning may occur at least partially in intrinsic coordinates, independent of the particular task and cursor mapping. The fact that patterns of joint torques generalized more widely than patterns of force in a 1-degree-of-freedom isometric object manipulation task (Mah and Mussa-Ivaldi 2003) further emphasizes that intrinsic coordinates may be important not only in simple force/torque cursor control, but also in the control of complex virtual dynamic systems.

The most interesting implication of the predominance of intrinsic transfer is that, despite similarities in the rate and extent of visuomotor learning in isometric and dynamic tasks, there may be fundamental differences in learning processes in the two environments. Our results, alongside evidence of neural activation and coordinate frame coding, suggest that

¹ However, there were differences in the analysis between the studies. Here, τ was calculated from a double-exponential curve fit to angular errors nearest to 3.5 cm from the start of movement, whereas in Rotella et al. (2013), τ was calculated from a two-state learning model fit to errors nearest to 150 ms from movement onset. With the selected control gains, the distance metric was more appropriate in capturing early angular errors in both mappings.

² We note that the transfer of learning in Krakauer et al. (2000) represents the amount of generalization to a test condition in which the rotation is present. In our study and in Pine et al. (1996), transfer is quantified by the magnitude of the aftereffect present when the rotation is removed.

learning a visuomotor rotation in an isometric environment may be more closely related to learning arm dynamics than arm kinematics. In real reaching, adaptation to a visual or force-field perturbation activates key motor regions including the primary motor cortex (M1), somatosensory cortex, and cerebellum (Diedrichsen et al. 2005; Donchin et al. 2012; Galea et al. 2011) in addition to error-specific motor areas. In the case of a visual rotation, learning is driven by visual error that represents the discrepancy between visual and proprioceptive representations of the hand (Krakauer et al. 1999). Adaptation is achieved by sensory recoordination in the premotor cortex (Krakauer et al. 2004), posterior parietal cortex (PPC; Diedrichsen et al. 2005; Ghilardi et al. 2000; Krakauer et al. 2004; Tanaka et al. 2009), and frontal-parietal/frontal-central areas (Contreras-Vidal and Kerick 2004), regions that are generally coded in extrinsic coordinates centered on the eye or hand (Buneo et al. 2002; Buneo and Andersen 2006; Kakei et al. 2001, 2003; Scott et al. 1997). Extrinsic neural coding is consistent with the extrinsic frame in which a visual rotation is learned.

In contrast, adaptation to a dynamic perturbation is mostly driven by intrinsic, proprioceptive errors (Krakauer et al. 1999) that change the activation rate and spatial tuning of neurons in M1 (Li et al. 2001), the cerebellum (Xiao et al. 2006), and, to a lesser degree, the premotor areas (Xiao et al. 2006). Although M1 has been found to contain both extrinsic and intrinsic neurons necessary for transforming visual trajectory information to intrinsic motor commands (Kakei et al. 2001) and an intermediate coordinate frame (Yanai et al. 2008), there may be a correlation between the large percentage of intrinsic M1 neurons (Scott and Kalaska 1997) and the intrinsic frame in which dynamics are learned. The intrinsic generalization in this experiment may indicate that M1 also plays an important role in isometric adaptation; evidence of M1 activation in isometric force control (Sergio et al. 2005), M1 involvement in early learning of an isometric visuomotor rotation (Riek et al. 2012), and M1 sensitivity to changes in static arm pose in force generation (Sergio and Kalaska 1997, 2003) corroborate this possibility. Directly testing the hypothesis of shared neural mechanisms in the learning of arm dynamics and isometric visual perturbations is beyond the scope of this work and is left for future investigations.

Although we designed our experiment based on the assumption of a single frame of reference for isometric visuomotor rotation learning, recent evidence suggests that the internal representations involved in adapting to visual perturbations (Baraduc and Wolpert 2002) and force fields (Haswell et al. 2009; Parmar et al. 2011) may occur in a mixed-coordinate frame. In a compelling reaching study, Brayanov et al. (2012) investigated the generalization of visuomotor learning across multiple combinations of movement direction and workspace and revealed an internal representation that was a multiplicative gain-field combination of extrinsic and intrinsic coordinates. Our results are in line with the gain-field model given that we sampled only one (vs. multiple) target directions in our transfer experiment. Mixed-coordinate frames are further supported by the mixed neural coding found in some motor control areas, including M1 (Kakei et al. 1999, 2001; Kalaska 2009; Wu and Hatsopoulos 2006) and PPC (Scott et al. 1997; Snyder et al. 1998). The presence of a mixed-coordinate gain field may explain the incomplete transfer that we observed in both *PJ* and

VJ groups and potentially the small extrinsic transfer in *VH*. As suggested by Brayanov et al. (2012), it is possible that an intermediate target direction, not solely associated with hand or joint space, may result in maximal or complete transfer. Testing this hypothesis would require a wider exploration of how isometric rotation learning generalizes across multiple target directions in a new workspace.

In addition to a mixed-coordinate representation, it is possible that a forgetting process may have contributed to the attenuated aftereffects. The average angular error curves for all groups contained sharp increases in error on postbreak trials. These are consistent with error peaks in saccade adaptation (Ethier et al. 2008) and have been attributed to a fast forgetting process. Assuming that an active forgetting process occurred in our task, the break preceding the TFR phase may also have contributed to incomplete learning transfer. A specific exploration of the effect of time between sessions on transfer aftereffects would be needed to support this idea further.

Comparison of Position and Velocity Mappings

When we analyzed participant performance using both position and velocity control mappings, we found that the position mapping generated faster peak cursor speeds and shorter trial times, whereas the velocity mapping produced more overshoot. These properties reflect both the nature of the mapping and the control gains, which were selected to achieve peak speeds between 0.4 and 0.6 m/s. In the position mapping, the significantly shorter trials may have been the result not only of faster peak speeds, but also the unidirectional, vs. bidirectional, pattern of force input. Kim et al. (1987) explored position and rate control in a displacement- and force-based joystick manipulandum and similarly found that position control was associated with shorter mean completion times. Position control required a single movement (or force) input vs. a more complex and time-intensive pair of opposing movements (or forces) in rate control.

The required input force further influenced cursor performance at the target. In position control, a constant force was needed to stabilize the cursor, and small corrective movements were often observed at the target. These corrections may be the result of signal-dependent noise in the motor system (Faisal et al. 2008). Specifically, greater variability and physiological noise has been associated with maintaining a large constant isometric force control (Jones et al. 2002). We suggest that noise had less of an effect on endpoint stabilization in the velocity mapping, requiring the force to be below 0.2 N to stop the cursor inside the target. Furthermore, the velocity mapping was associated with greater cursor overshoot to achieve the target speed range. The large overshoot could be eliminated in future studies by relaxing the constraint on the maximum cursor speed for the velocity-mapped trials or by making the maximum speed criteria more achievable via modification of the control gain. Mitigating the differences in reach amplitude between the mappings would help to isolate adaptive changes in the cursor trajectory from changes in final position, which are found to have separate adaptive mechanisms (Ghez et al. 2007; Scheidt and Ghez 2007).

Although the extent of adaptation was comparable in all groups, the subtleties of cursor kinematics across mappings may have contributed to differences in the initial training error and

adaptation rate. In the position mapping, the average error in the first training trial exceeded the anticipated 45° magnitude and was significantly larger than the corresponding error in the velocity mapping. This may be related to some general postbreak effect of a clockwise bias in initial movements that had an additive effect to the overall error (see Fig. 3 BL and TRN trials). The information that was collected in the current study does not provide us with an explanation about the origin of this bias or why this effect was exacerbated in the position mapping. Nevertheless, even though we do not understand the origin of this error overshoot, it may have contributed to faster learning. Since visual feedback of the cursor was provided in all trials, participants in the position groups visually perceived a larger initial error, which may have contributed to the slightly accelerated fast learning rate that was observed (Patton et al. 2013).

With respect to learning generalization, the type of mapping influenced both the within-workspace generalization and the transfer of learning to the new workspace. Again, we hypothesize that greater generalization for the velocity mapping may be the result of increased exposure to the perturbation. The relatively greater transfer implies that the velocity mapping more closely resembles actual movement and thus could represent a more effective isometric control strategy for rehabilitation in which we seek to maximize the transfer of learning to new environments and slow the washout process. The next step toward this end is to investigate a more sophisticated mapping that attributes realistic arm dynamics to the cursor, including inertial and damping effects. Berger et al. (2013) implemented such a mapping in which force at the hand controlled a cursor with mass-spring-damper dynamics. Their work investigated adaptation to virtual surgeries that perturbed the muscle-to-force mapping, requiring the modification of existing synergies (compatible surgery) or the recruitment of new synergies (incompatible surgery). Although participants adapted to both virtual surgeries, demonstrating an ability to learn the complex mapping, the rates of learning differed. Faster learning was associated with the compatible surgery, which required a rescaling of practiced muscle patterns (de Rugy et al. 2012b), whereas slower learning was found for incompatible surgeries, which required the recruitment of new synergies. Similar mass-spring-damper dynamics were implemented by Gentner et al. (2013) in a study that demonstrated the robustness of muscle synergies in isometric adaptation to a visuomotor rotation. Further investigation of cursor dynamics could involve modeling the cursor as a realistic arm using participant-specific parameters (Melendez-Calderon et al. 2011) and exploring the use of virtual avatars to enhance embodiment in isometric tasks.

Implications for Rehabilitation

When people suffer from stroke or other movement disorders, physical therapy may be used to restore lost arm strength and movement coordination. Although the delivery of frequent and highly intensive therapy is beneficial, treatment is limited by the time and physical resources of the therapist. Robots can improve treatment by allowing intensive therapy, precise kinematic measurements, and the ability to assist or resist movement. However, robotic devices may be large and complex, require the sensing and actuation of many degrees of freedom, and introduce additional safety concerns for the patient. Isometric training, in which a cursor or virtual avatar is controlled by input force, represents a potential rehabilitation solution in

which patients may learn virtual dynamics while interacting with a simple interface that is safe and cost-effective. An isometric rehabilitation strategy is further appealing because it requires only minimal strength and coordination capabilities, can be responsive to changes in patient ability and performance, and may be integrated in home and clinical settings with modest hardware and software requirements. One possible outcome of isometric training would be the transfer of motor learning to actual movement. The finding of the predominance of intrinsically coded internal representation in our isometric task suggests that isometric training involving joint-space coordinates and torque production may be more intuitive to learn than training involving Cartesian-space tasks. In future studies of isometric training, various mixed-coordinate mappings may be tested to find the optimal training approach.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

M.F.R., I.N., A.J.B., and A.M.O. conception and design of research; M.K. and M.D.R. development of software; M.F.R. and M.K. performed experiments; M.F.R., I.N., and M.D.R. analyzed data; M.F.R., I.N., A.J.B., and A.M.O. interpreted results of experiments; M.F.R. prepared figures; M.F.R. drafted manuscript; M.F.R., I.N., M.K., M.D.R., A.J.B., and A.M.O. edited and revised manuscript; M.F.R., I.N., M.K., M.D.R., A.J.B., and A.M.O. approved final version of manuscript.

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