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Different Learned Coordinate Frames for Planning Trajectories and Final Positions in Reaching

Claude Ghez,^{1,*} Robert Scheidt,^{2,3,4,*} and Hank Heijink¹

¹Department of Neuroscience, Columbia University Medical Center, New York, New York; ²Department of Biomedical Engineering, Marquette University, Milwaukee, Wisconsin; ³Department of Physical Medicine and Rehabilitation, Feinberg School of Medicine, Northwestern University Medical School, Chicago, Illinois; and ⁴Sensory Motor Performance Program, Rehabilitation Institute of Chicago, Chicago, Illinois

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Ghez C, Scheidt R, Heijink H. Different learned coordinate frames for planning trajectories and final positions in reaching. *J Neurophysiol* 98: 3614–3626, 2007. First published September 5, 2007; doi:10.1152/jn.00652.2007. We previously reported that the kinematics of reaching movements reflect the superimposition of two separate control mechanisms specifying the hand's spatial trajectory and its final equilibrium position. We now asked whether the brain maintains separate representations of the spatial goals for planning hand trajectory and final position. One group of subjects learned a 30° visuomotor rotation about the hand's starting point while performing a movement reversal task ("slicing") in which they reversed direction at one target and terminated movement at another. This task required accuracy in acquiring a target mid-movement. A second group adapted while moving to—and stabilizing at—a single target ("reaching"). This task required accuracy in specifying an intended final position. We examined how learning in the two tasks generalized both to movements made from untrained initial positions and to movements directed toward untrained targets. Shifting initial hand position had differential effects on the location of reversals and final positions: Trajectory directions remained unchanged and reversal locations were displaced in slicing whereas final positions of both reaches and slices were relatively unchanged. Generalization across directions in slicing was consistent with a hand-centered representation of desired reversal point as demonstrated previously for this task whereas the distributions of final positions were consistent with an eye-centered representation as found previously in studies of pointing in three-dimensional space. Our findings indicate that the intended trajectory and final position are represented in different coordinate frames, reconciling previous conflicting claims of hand-centered (vectorial) and eye-centered representations in reach planning.

INTRODUCTION

In a previous report (Scheidt and Ghez 2007), we showed that adaptation to visuomotor rotations did not transfer substantially between two reaching tasks requiring spatial accuracy either mid-movement or at the end of movement. In the trajectory reversal task (slicing), subjects were to move out-and-back, transiently acquiring a visual target as the hand reversed direction. In the positioning task (reaching), they were to move their hand to the target and maintain it at the desired location. We found minimal transfer of visuomotor learning between trajectory reversals and stabilized positions regardless of whether subjects adapted to the imposed rotation while

reaching or while slicing. We did, however, observe adaptation-related changes in hand trajectories during learning and transfer, including increased hand path curvature in reaching but not slicing, as well as conspicuous hypermetria of slices performed after reach training. These observations were not consistent with the selection of separate control strategies in the two tasks based on contextual cues (e.g., target configuration or verbal instruction). Rather, these results were reproduced computationally by a heuristic model in which independent control mechanisms adaptively adjust the hand's trajectory and its final equilibrium position. We therefore proposed that the kinematic features of normal reaching movements also result from the superimposition of two sequential control actions by the brain: the first dominates as the hand is launched along an intended trajectory, accounting for the complexities of nonlinear limb dynamics in the feedforward plan. The second dominates later to terminate movement and stabilize the hand at the intended location as originally suggested in equilibrium models (Asatryan and Feldman 1965; Polit and Bizzi 1978). Slicing movements were proposed to include two successive trajectory phases in opposite directions followed by a final positioning phase about the starting position.

The use of separate adaptive control mechanisms within a single reach raises the possibility that the brain might maintain separate spatial representations of the target location in different coordinate frames: one for planning the hand's trajectory and the other for planning its final position. This study examined this possibility by asking how learning of a visuomotor adaptation acquired while moving within a limited region of the workspace generalizes to test movements performed in untrained regions. By identifying the axes along which accuracy is preserved or degraded in such test movements, we reasoned that it would be possible to determine whether the brain represents the spatial goal for intended hand trajectories and final positions in the same or different coordinate frames. Previous studies of horizontal slicing movements have shown that adaptation to 30° visuomotor rotations acquired while performing out-and-back movements between two targets generalizes well to movements of different extent, but poorly to movements in different directions (Krakauer et al. 2000; Pine et al. 1996). Furthermore, when the hand is covertly displaced from where it was during slice practice, subjects moved out and back along a path parallel to the practiced one, thus

* C. Ghez and R. Scheidt contributed equally to this study.

Address for reprint requests and other correspondence: C. Ghez, Ctr. for Neurobiology and Behavior, Columbia Univ. Medical School, 1051 Riverside Dr., New York, NY 10032 (E-mail: cpgl@columbia.edu).

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preserving movement direction even though the target was no longer acquired (Krakauer et al. 2000). Based on this evidence, we anticipated that the brain would again be found to represent the intended target for slicing in vectorial form, that is, with movement direction and extent specified relative to the initial position of the hand (Ghez et al. 1994, 1999; Rossetti et al. 1995; Vindras et al. 1998).

Several considerations suggest that, in planning the final positions of simple reaching movements, the target might instead be represented in a different egocentric reference frame. Because stabilizing the hand at the end of movement likely engages segmental reflex pathways involving muscle spindle proprioceptors (Shapiro et al. 2004), and because proprioceptive estimates of hand position are thought to be estimated relative to the shoulder (Flanders and Soechting 1990; van Beers et al. 1998), this might favor learning and generalization of adapted final positions in a coordinate frame centered at the shoulder. Alternatively, planning might be based on the expected location of the final position represented in a coordinate frame centered about the eye or head (an origin derived from binocular visual information), as has been suggested by studies of spatial generalization in three-dimensional (3D) positioning tasks (van den Dobbelen et al. 2003, 2004; McIntyre et al. 1997, 1998; Vetter et al. 1999). Because our reaching task requires subjects to actively regulate final position using proprioceptive feedback before they receive visual feedback (Scheidt and Ghez 2007), we propose that final hand positions achieved during both reaching and slicing are determined principally by the location of a planned equilibrium configuration. We therefore predicted that, unlike slice reversals, final position would be relatively insensitive to shifts in initial hand position (while a compensatory change in movement direction should occur).

Here we trained two groups of subjects to adapt to a 30° visuomotor rotation of cursor feedback about the hand's initial position as they performed either slicing or reaching. In the reaching task, subjects had to move their hand from an unseen origin to a single (90°, Fig. 1) target where they had to stop and stabilize the hand. In the slicing task, they were to reverse direction at that same target location and return the hand past the origin to stop and stabilize at a second target (270°). After training, we examined the kinematics of movements made without concurrent visual feedback: 1) in the untrained task, 2) when the initial position of the hand was covertly shifted to a new location, and 3) when the targets were rotated 45° clockwise (CW) from the trained direction. We sought to determine whether shifting the hand's initial position would induce differential effects on the reversals of slice trajectories and on the final endpoints of reaches and slices. We also wished to determine whether learning generalizes differently in moving to the untrained 45° target in the two tasks. Because we found both to be true, we assessed the origin of the coordinate frame modified during training in the positioning task. For each location in the workspace, we computed the likelihood that subjects had learned the imposed visuomotor transformation as a rotation about that location. We included in this analysis all final positions observed after rotation training in the positioning task as well as the final positions of test slices made after reach training. Portions of this work have been presented in abstract form (Ghez et al. 2004; Scheidt and Ghez 2006a,b).

METHODS

Two groups of six neurologically normal subjects (age, 24–62 yr; 7 men and 5 women) provided written, informed consent to participate in these experiments. Study procedures and consent forms were institutionally approved in accordance with the Declaration of Helsinki. Experiments were carried out at the Rehabilitation Institute of Chicago, and the setup and apparatus were the same as those described previously (Scheidt and Ghez 2007): seated subjects moved the instrumented handle of a horizontal planar, two-joint robot with their dominant hand between targets projected onto an opaque screen immediately above the plane of movement (Fig. 1). The subject's arm was supported against gravity (between 75 and 90° abduction angle) using a light-weight, chair-mounted arm support. A drape covering the shoulder and upper arm prevented subjects from seeing their hand and arm. Upper arm and forearm segment lengths were measured in each subject as was the shoulder center of rotation relative to the origin of the robot's workspace. Targets and starting positions were oriented such that movements directly forward (90°) and backward (270°) were directed along the mid-clavicular line on the subject's dominant side.

Tasks

Experimental sessions consisted of blocks of trials in which subjects were to perform either a positioning task (reaching) or a trajectory reversal task (slicing), depending on the configuration of the visual target used to cue the movement. Between trials of both types, subjects were to relax their arm as a robot moved the unseen hand to the designated starting position for the next trial. This initial position was to be shifted 4 cm to the right in some test trials. Whereas subjects returned the hand to its starting point during the slicing in our previous study (Scheidt and Ghez 2007), pilot studies revealed that 4-cm displacements imposed after such movements were very noticeable to subjects but not when shifts were introduced during passive returns from the reach target. To equate the salience of such shifts across tasks, subjects were instructed to extend the return phase of slicing motions beyond the origin to terminate movement at a second target

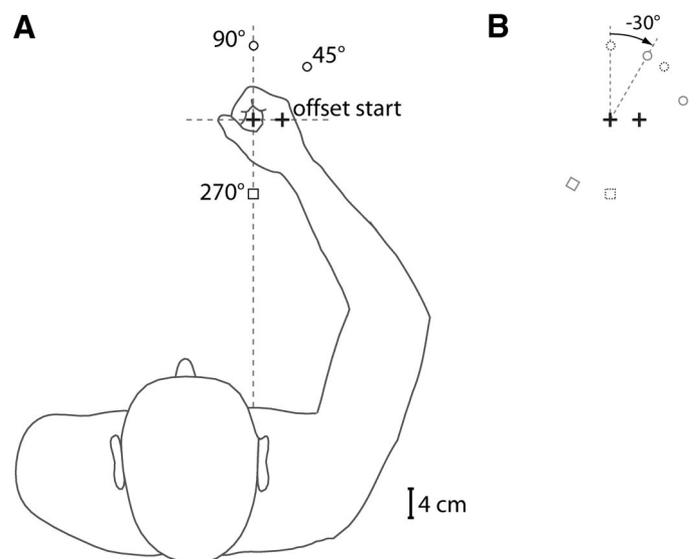


FIG. 1. Setup. *A*: locations of targets (empty black circles and square) and initial positions (+) projected on the workspace immediately above the subject's hand. During baseline training, subjects in the slice training group practiced reversing direction at the 90° target and terminating movement at the square (270° target), whereas subjects in reach training group practiced reaching and terminating movement at the 90° target. *B*: required hand locations at reversals and final positions for complete adaptation to imposed 30° counterclockwise (CCW) rotation of the visual cursor.

located 180° away from the reversal target relative to the hand's starting position (Fig. 1).

After being positioned by the robot at the next trial's starting position, subjects were instructed to maintain their hand steady for 1.0 s wherever it had been released. To require active control of hand position, we applied small force perturbations to the handle whenever hand speed was near zero (<0.1 m/s). These perturbations consisted of unpredictable forces (sum of 2.1- and 3.5-Hz sinusoids in the x - and y -directions; 3.5 N peak-to-peak) (Fig. 1F from Scheidt and Ghez 2007). These forces were unbiased across directions and were phased in and out smoothly over a period of 250 ms before the onset and after the termination of movement. Our intent was to induce subjects to co-contract antagonist muscles at the elbow and shoulder joints, and by increasing elbow and shoulder joint impedance during positional stabilization, to facilitate identification of the limb's equilibrium configuration. We provided a compensatory display of the initial hand position to help subjects maintain their hand at a precisely defined location after it was released by the robot. This consisted of a decomposition of the hand's deviation from the desired position as a pair of 3-mm cursors moving along x - and y -axes (each 6 cm in length) and was visible only before movement. These axes were projected 30 cm to the left and 20 cm forward from the vertical position of the hand and of the cursor (i.e., far from the region of the workspace used to display the target and feedback during practice). Thus we did not provide an explicit starting position that subjects could use to aim movements. Subjects were instructed to achieve a peak hand speed of 0.5 m/s across both trials and tasks and were provided with a bar graph display of the peak velocity after each trial to assist them in doing so.

SLICING TASK. Slicing movements were cued by the simultaneous appearance of two targets connected by a straight line: a 2-cm-diameter circle (the reversal target) with its center located 10 cm away from the body relative to the hand's usual starting location and a 2×2 -cm square (the return target) with its center 10 cm toward the subject relative to the starting position. Subjects were to move their hand to the circle (where they were to reverse direction without pausing) and return it to the square (where they were to maintain it stabilized for 1.5 s against the unpredictable robotic perturbation). A cursor representing hand location appeared concurrently with the target and was blanked after the stabilization period. It remained blanked as the robot brought the handle to the starting position for the next movement and while subjects maintained that initial position.

REACHING TASK. Reaching movements were cued by the appearance of a target circle (the reach target) at the same location as the reversal target used for slices. In this task, the cursor was not displayed during movement. Instead, subjects were to move the handle to the target and maintain stability against the perturbation without visual feedback for 1.5 s. The cursor was displayed for 1.0 s during which subjects were to slowly align the cursor and target (the cursor was blanked if hand speed exceeded 0.1 cm/s). The hand was then returned to the starting position by the robot without cursor feedback in preparation for the next trial.

DISTRACTOR TASK. Throughout the entire experimental session, subjects were also required to perform a secondary distractor task. This task required subjects to read aloud a series of random numbers projected on the left side of the workspace beneath the axes used to indicate errors in initial positioning. This was done to minimize awareness of imposed rotations and displacements in initial hand position and to minimize the use of explicit strategies to correct movement errors. These precautions were largely successful as only 1 of the 12 subjects was aware of a change in movement path or final position during the slowly imposed rotations.

Experimental design

After familiarization with the slicing and reaching movements and their respective cues, subjects in each group performed three consecutive blocks of trials. In an initial baseline block (150 trials), they practiced either slicing (the slice trained group) or reaching (the reach trained group) using visual feedback as described above. Four types of test trials, all performed without visual feedback, were presented pseudorandomly at a frequency of one in five trials. Test trials assessed the effect of practice on 1) the trained task cued by the trained target, 2) the trained task cued by the trained target with the hand's initial position shifted 4 cm to the right, 3) the trained task performed to an unpracticed target located 45° CW from the trained target, and 4) the unpracticed task. In the training block (110 trials), subjects adapted to a 30° CCW rotation of the cursor, applied in successive increments of 0.27° per trial. In the third or test block (150 trials), cursor feedback remained rotated by 30°, but here again, one of each of the four types of test trials was interspersed pseudorandomly once every five trials. These test trials assessed visuomotor learning in the trained conditions, the transfer of learning to the untrained task, and how this learning generalized to the untrained initial position and the untrained target. The final positions of test slices (directed to the 270° target) in reach adaptation provided an additional locus for assessing generalization of adaptation of final position.

Data analysis

Instantaneous hand position was recorded at 150 samples/s using 17-bit rotational encoders mounted on the robot's motors. Hand paths had a spatial resolution better than 0.2 mm and were low-pass filtered using a second-order, zero-lag Butterworth filter with 20-Hz cut-off frequency before computing hand velocities. Velocities were filtered similarly before computing hand accelerations. We identified several kinematic features for each movement using an automated algorithm within the MATLAB programming environment (The Mathworks, Natick, MA). Each was verified visually and was manually adjusted if necessary; in most instances, the algorithm erred when subjects failed to make movements of the instructed type or if movements were otherwise erratic. Such trials were excluded from further analysis and accounted for 8.7% of all test trials.

Analysis was focused mainly on movements made during test trials without visual feedback in both the baseline and test blocks. We also analyzed postadaptation slicing movements made with visual feedback for the trials immediately preceding test slices to the trained target. The hand's starting point was defined as its x - y location 100 ms before movement onset. Movement onset was identified as the moment when the hand velocity first exceeded 0.1 m/s at the beginning of a trial. The peak acceleration point consisted of the x - y location and peak hand acceleration taken when the hand acceleration reached its maximum positive value in the outward phase of the movement. The peak velocity point consisted of the x - y location and peak hand speed taken when the hand reached its maximum velocity in the outward phase of the movement. For slices, we defined the reversal point as the x - y location taken when the hand reached its maximum radial displacement from the home target in the outward phase of the movement. For movements of both types, the final position point consisted of the average x - y location over the last 50 data points during terminal stabilization.

We derived a number of secondary measures to assess transfer of visuomotor adaptation across tasks and generalization of this learning within the workspace. Angular deviation was calculated as the interior angle between the desired movement vector in extrinsic space and a second vector that was defined at two points in time. For slicing movements, this second vector pointed from the hand's starting position to its location at the time of peak velocity (initial direction) or to its location at reversal (peak distance from the origin). For

reaching, the second vector also pointed from the hand's starting location to either its location at the time of peak velocity or to the final position achieved during stabilization before visual feedback ("endpoint"). Thus if a subject had fully adapted to the imposed 30° rotation, the angular deviation measured at reversals of slices and endpoints of reaches should equal -30°. We also used these angular deviation measures to compute a proxy of movement curvature: the absolute magnitude of the angular difference in direction at peak distance for slices or endpoint of reaches and the spatial location reached at peak velocity: $|\Delta\theta|$ (Gordon et al. 1995). Finally, we estimated movement accuracy and precision for individual subjects by computing the centroids and areas of the 95% confidence ellipses for the distribution of endpoints within each test condition. We also evaluated the overall effects of training on endpoint variability in each test case by pooling data across all subjects before computing the grand population confidence ellipses.

Data processing and statistical testing was carried out within the Minitab (Minitab, State College, PA) and the Matlab (The Mathworks) computing environments. Data values are reported as mean \pm SD. Error bars in figures also represent \pm SD. Mixed model, repeated-measures ANOVAs and subsequent post hoc Tukey *t*-tests were used to compare performance measures across training conditions (slicing vs. reaching), experimental blocks (baseline vs. rotation), and targets (trained, shifted origin, 45 and 90°). Effects were considered statistically significant at the $P = 0.05$ level.

Identifying the coordinate frame learned during reaching

Our initial analysis of the adapted final positions of test reaches to the untrained 45° target and of test slices terminating near the 270° target yielded results that differed from those reported in previous studies of generalization with horizontal movements (Krakauer et al. 2000; Wang and Sainburg 2005). In particular, the findings were not consistent with the hypothesis that subjects remapped the desired target location (and thus the intended movement direction) as a coordinate rotation around the hand's initial position. We therefore asked whether the postadaptation distributions of final positions about the three test target locations (90, 45, and 270°) could be described as a simple transformation of the respective distributions obtained at baseline: a rotation θ about a common origin, $p_o = \{x_o, y_o\}$. Finding that such origins are confined to a single discrete region in peripersonal space would support the hypothesis that visuomotor adaptation acquired while moving to a single target results from a remapping of intended final positions in a coordinate frame centered on a point within that region. The finding of multiple discontinuous regions would contradict this hypothesis.

For each point on a tight horizontal plane grid covering the entire peripersonal workspace (100 \times 100 cm, sampled every 1 cm), we computed the likelihood that that point could serve as the origin for a common learned rotation (DeGroot and Schervish 2001). This was done using an optimization procedure in Matlab, which minimized the negative log likelihood across the three sets of distributions for different values of θ . (Note that minimizing the negative likelihood is equivalent to maximizing likelihood; the log of this value was used because of the exponential nature of the likelihood function.) The values thus obtained were plotted to yield a map of relative likelihoods that allowed a comparison of different loci as possible origins for a common learned rotation (see APPENDIX for further details).

RESULTS

Generalization during baseline practice

Subjects attained similar levels of accuracy during baseline training whether they had practiced slicing or reaching (Fig. 2A, black traces; compare mean endpoint locations), and out-

ward phases of both slicing and reaching movements had smooth bell-shaped profiles (Fig. 2B).

When transferring from trained slicing to the untrained reaching task, movements of both types had similar extents (11.3 ± 1.2 cm for slicing vs. 11.4 ± 1.0 cm for reaching; $P = 0.8$; Fig. 2C, left). After reach training, however, test slices were significantly hypermetric (13.7 ± 1.4 cm for slices vs. 11.0 ± 1.3 cm for reaches; $P < 0.001$; Fig. 2C, right) as we have reported previously (Scheidt and Ghez 2007). Peak velocities were also higher for untrained slices than for trained reaches (slice: 0.60 ± 0.17 m/s; reach: 0.47 ± 0.12 m/s; $P < 0.001$) as were hand displacements at peak velocity (slices: 13.7 ± 1.4 cm, reaches: 11.0 ± 1.3 cm; $P < 0.001$; Fig. 2C). In contrast, peak accelerations did not differ significantly for trained and untrained tasks (slice: 10.2 ± 0.5 m/s²; reach: 10.3 ± 0.5 m/s², $P = 0.97$; Fig. 2C). This supports the hypothesis (Scheidt and Ghez 2007) that subjects implement the same initial feedforward torques to accelerate the hand in the two tasks and that the trajectory controller is not informed of the impedance changes to be generated by the positional controller later in movement. As discussed in the preceding paper, the differences between the deceleratory phase of the outgoing stroke of slices and reaches can be explained as an interaction between an initial trajectory plan and a positional plan instantiated shortly thereafter. The latter regulates limb posture about a desired final equilibrium configuration (as a set point) and is presumed to use proprioceptive feedback.

When the hand was shifted 4 cm to the right before slicing, hand paths remained straight, whereas reversals were displaced 3.4 ± 0.4 cm to the right (Fig. 3A, left). Horizontal displacement of the endpoint was significantly less when the hand was shifted before reaching (1.6 ± 0.4 cm; slice vs. reach: $P < 0.0005$; Fig. 3B). Consequently, displacing the hand's initial position had a differential effect on movement direction in the two tasks: whereas displacement did not change the outward direction of slices, reaches were deviated CCW (reaches: $13 \pm 0.9^\circ$, slices: $0.582 \pm 1.06^\circ$; Fig. 3C) to terminate closer to the target than did slices ($P < 0.001$). In contrast, the hand's final positions were significantly less displaced in the return phase of slicing movements (2.09 ± 1.07 cm) than were the reversals of these same movements (Fig. 3A, left; reversal vs. final: $P = 0.031$).

Both slicing and reaching movements developed significant curvature when aimed for the unpracticed target at 45°; $|\Delta\theta|$ was significantly greater for the untrained 45° movements than for trained 90° movements ($P = 0.01$ and $P = 0.02$ for slicing and reaching, respectively). In both cases, this is likely to reflect unanticipated dynamic effects associated with the inertial properties of the manipulandum. Indeed it has been shown that learning of such dynamic properties does not generalize well across movement directions in hand-centered Cartesian space (Gandolfo et al. 1996; Sainburg et al. 1999; Thoroughman and Shadmehr 2000).

Generalization of rotation learning

Subjects compensated for the CCW rotation of the cursor by adjusting the directions of their hand movements CW (adaptive, directional deviations; Fig. 4A). Directional deviations at slice reversals and reach endpoints did not differ significantly for the two training groups in the test block (26.1 ± 2.9 and

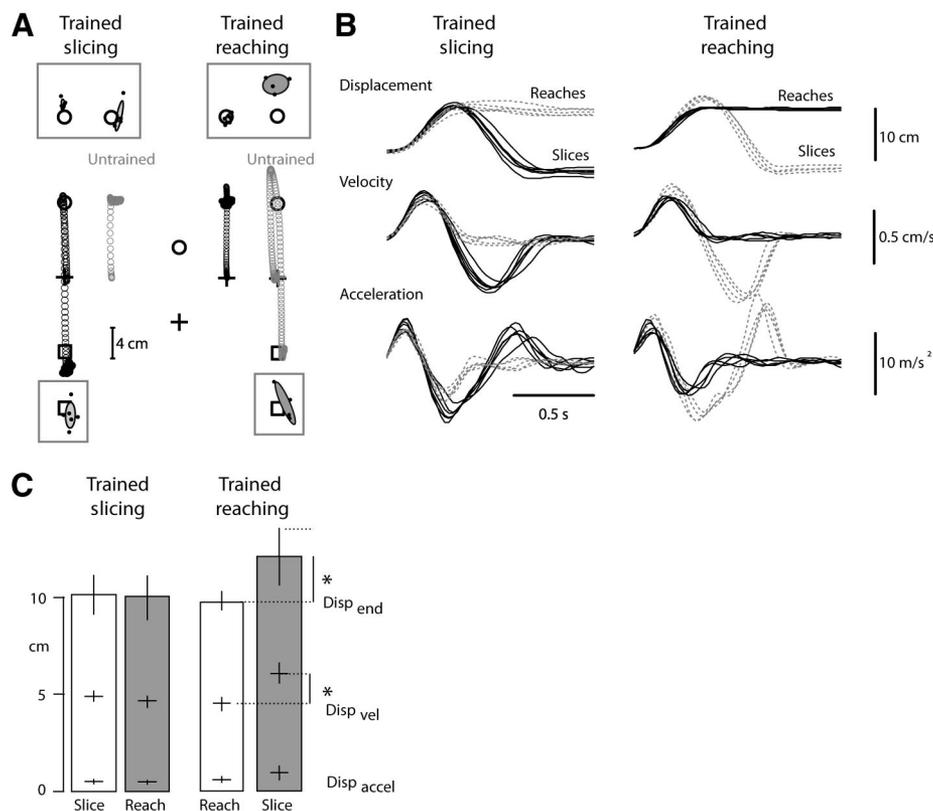


FIG. 2. Baseline performance: hand kinematics of practiced and unpracticed reaches and slicing movements. Hand kinematics from test movements made without cursor feedback. *A*: hand paths of slicing and reaching movements made by representative subjects trained either in slicing (*left*) or reaching (*right*) during baseline block. *Insets*: centroids of distributions and fitted 95% confidence ellipses for slice reversals and reach endpoints for all subjects (above paths) and for the slice endpoints (below paths). Note that all paths are straight and that centroids of trained slices and both trained and untrained reaches are clustered around the appropriate targets. In contrast, untrained slices are hypermetric. *B*: displacement, velocity, and acceleration records of trained (black) and untrained (gray) movements of single subjects trained in slicing (*left*) and reaching (*right*). Note increased peak displacements and velocities of untrained slices in subjects trained in reaching (*right*). *C*: mean peak values (\pm SD) for displacements achieved at peak extent (Disp_{end}), peak velocity (Disp_{vel}), and peak acceleration (Disp_{accel}). Note the hypermetria of Disp_{end} and Disp_{vel} of untrained slices relative to trained reaches (white vs. gray fill in right pair of bars). Note also that hypermetria develops between peak acceleration and peak velocity. Similar values were obtained after rotation training. In slice training, ANOVA found no significant difference in movement extent across tasks at peak acceleration, peak velocity, or peak extent during baseline and after rotation training. In contrast, after reach training, both in baseline and after rotation training, slice extents and peak velocity points were significantly hypermetric, whereas peak acceleration points were not different. Here, as in Figs. 3–5, error bars indicate \pm SD and asterisks indicate statistically significant differences ($P < 0.05$).

$29.9 \pm 4.2^\circ$, respectively; $P = 0.11$; Fig. 4*B*). However, whereas slices remained straight, reaches often became curved in the course of positional training in reaching (Fig. 4*A*, *left* vs. *right*), much as we found previously with movements in eight target directions (Scheidt and Ghez 2007). Two-way ANOVA showed significant main effects of training condition (reaching vs. slicing; $P = 0.001$) and training block (baseline vs. test; $P = 0.015$) on curvature estimated as the difference between final and initial directions (see METHODS); no interactions were observed. We were surprised to find that, for subjects learning the rotation while slicing, test slices (made without feedback) curved back toward the unadapted final position, and drifted further toward the unadapted 270° target during final postural stabilization (Fig. 4*A*, *left*, filled arrow). This did not occur in the immediately preceding “refresher” trials within which test trials were interleaved. Refresher movements made with continuous cursor feedback terminated accurately at the rotated location (Fig. 4*A*, *left*, gray paths and empty arrow). Correspondingly, endpoints were more displaced horizontally to the left with visual feedback than without (5.1 ± 0.2 vs. 1.6 ± 1.0 cm, $P < 0.001$; Fig. 4*C*). Thus the subjects who trained while slicing adapted their reversal points to the imposed visuomotor

rotation but did not do so for their final stabilized hand positions. This was despite the presence of continuous visual feedback during training, which provided error information for the outward and return phases of movement. The discussion below proposes that this result is caused by differences in spatial reference frames for planning movement reversals and final positions, which require learning opposite coordinate rotations.

As was the case at baseline, displacing the hand's initial position to the right shifted the location of slice reversals to the right (3.38 ± 0.38 cm) but not reach endpoints (0.6 ± 0.8 cm; slice vs. reach; $P < 0.0001$; Fig. 4, *D* and *E*). In addition, final hand positions of slicing movements were displaced less than reversals in the same trials. We used a mixed model, two-way repeated-measures ANOVA to assess the effect of shifting initial hand position on slicing movements across target locations (reversal vs. final position) and experimental blocks (baseline vs. training). ANOVA revealed significant main effects of target ($F_{(1,23)} = 16.89$, $P < 0.001$) but not of training condition ($F_{(1,23)} = 0.32$, $P = 0.58$).

Generalization of learning from the trained 90° target to the untrained 45° target also differed between slicing and reaching

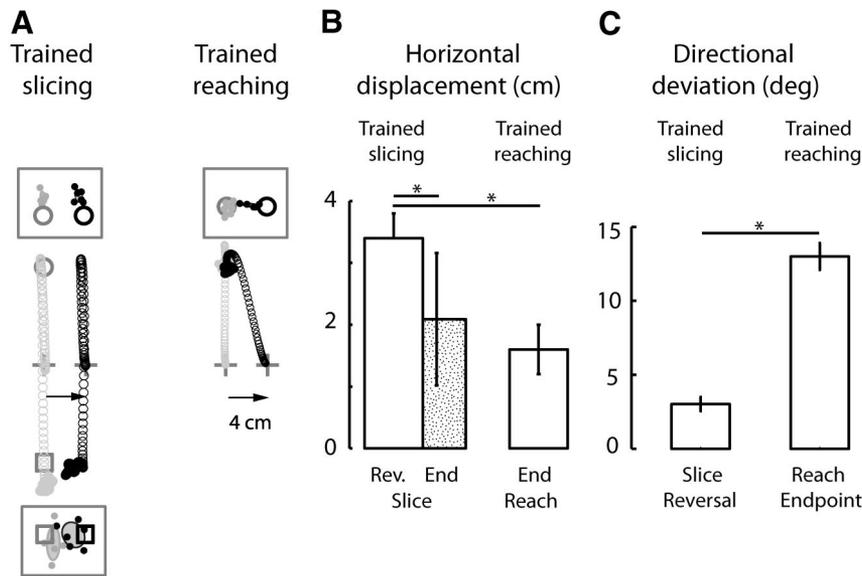


FIG. 3. Baseline performance. Effects of shifting initial position and target direction on slicing and reaching. *A* and *D*: hand paths of slicing and reaching movements made by representative subjects receiving baseline training in either slicing (*left*) or reaching (*right*) tasks. *Insets*: centroids of distributions and fitted 95% confidence ellipses for slice reversals and reach endpoints for all subjects (above paths) and for slice endpoints (below paths). *A*: gray, control path from practiced initial position. Black: test trial (i.e., a trial performed without cursor feedback) with the initial hand position displaced to right. Note that hand paths of displaced slice remains parallel to practiced slice, reversing far from practiced target (*left*), whereas displaced reach deviates in the CCW direction and terminates close to target (*right*). Note also that the final position of the displaced slice gravitates toward the practiced final slice position. *B*: mean horizontal displacements (\pm SD) at reversals points (white) and final endpoints of displaced slices (*left*) and at endpoints of displaced reaches. *C*: mean directional deviations (\pm SD) for slice reversals (*left*) and reach endpoints (*right*) in trials with displaced starting hand positions.

(Fig. 4, *F* and *G*). After slice training, directional deviations were markedly lower for the untrained target than for the trained target (-11.0 ± 3.1 vs. $-26.1 \pm 2.7^\circ$, $P < 0.001$). Whereas learned deviations were also smaller for the untrained 45° movements after reach training (-18.0 ± 3.9 vs. $-29.9 \pm 4.2^\circ$, $P < 0.015$), this difference was significantly less than that found for slicing ($P = 0.007$). This difference suggests that learning trajectory reversals and final positions may be represented in different coordinate systems.

As we had found previously in our study of reaching and slicing to targets in eight directions (Scheidt and Ghez 2007), adaptation acquired during slice training transferred incompletely to reaching (-26.1 ± 3.0 vs. $-21.44 \pm 5.7^\circ$; paired *t*-test: $P = 0.027$; Fig. 5, *A*, *left*, and *B*) and reach training transferred only partially to the reversals of slicing movements (-29.9 ± 4.2 vs. $-11.3 \pm 5.7^\circ$; $P = 0.004$; Fig. 5, *A*, *right*, and *B*).

A new finding documented here is that the final positions of test slices (aimed for the target at 270°) were deviated CCW from baseline after reach training (Fig. 5*B*; $P < 0.001$). This would not be expected if subjects had learned to compensate for the CCW cursor rotation by a counter-rotation of final positions about the hand's initial location. Rather, this rotation is opposite to the adaptive deviations present for the other targets in reaching and also is in the opposite direction to the adaptive deviations of reversals during slice training.

This finding is not consistent with the application of a common hand-centered coordinate rotation for final positions at the 90° , 45° , and 270° targets. We therefore considered whether reach training may have induced adaptation in the spatial representation of final positions in a reference frame centered elsewhere than at the hand. Two possibilities seemed plausible: a shoulder-centered representation corresponding to proprioceptive coordinates (Flanders and Soechting 1990; van Beers et al. 1998), and an "eye-centered" representation (Vetter et al. 1999) possibly coding the intended position relative to the direction of gaze. Figure 6*A* shows pooled endpoint distributions and the corresponding 95% confidence ellipses for the final positions observed at the 90° , 45° , and 270° targets. The

centroids of these distributions were used to compute the adaptive deviations of the three targets in reference frames centered at the hand (Fig. 6*B*), the shoulder (Fig. 6*C*), and a point between the two eyes (the cyclopean eye) (Fig. 6*D*). Adaptive deviations computed relative to either the shoulder or to the cyclopean eye were all deviated in the same direction and differed by only small amounts whereas adaptive deviations about the hand varied dramatically across targets. Either shoulder or head-centered frames would explain the improved transfer of rotation learning to the 45° target in reaching versus slicing, because, as shown in Fig. 6*E*, the angular separation between trained and untrained targets in either of these frames would be considerably smaller than that in the hand-centered frame. Consequently, the relative decrease in generalization of rotation learning for reaches to the 45° target would be smaller than that for the reversal point of slices which have been shown previously to be represented in hand-centered coordinates (Krakauer et al. 2000) (see Fig. 4, *F* and *G*). However, these simple analyses cannot resolve whether the shoulder or the head is more likely to be the origin of a common rotation or whether other spatial locations might serve equally well as origins for adaptive rotation of the spatial representation for intended final positions.

We therefore computed the likelihood that each point in peripersonal space could represent the origin of a coordinate frame about which the set of three distributions of final hand positions observed before training could be transformed by a common rotation into the ones observed after training (see METHODS and APPENDIX). Figure 6*F* maps the log likelihoods for each point together with the contour of an idealized subject together with the endpoint distributions for each of the three targets at baseline (white ellipses) and after reach adaptation (gray ellipses). The darkest blue regions have the highest likelihood of representing a common origin (i.e., the negative log likelihood is lowest and the unexplained variance in the data is least). Red regions have the lowest likelihood. Points with the highest likelihood representing the origin of a common learned rotation are contained in a single continuous region whose base extends from the subject's trunk to an apex just beyond the 270° target.

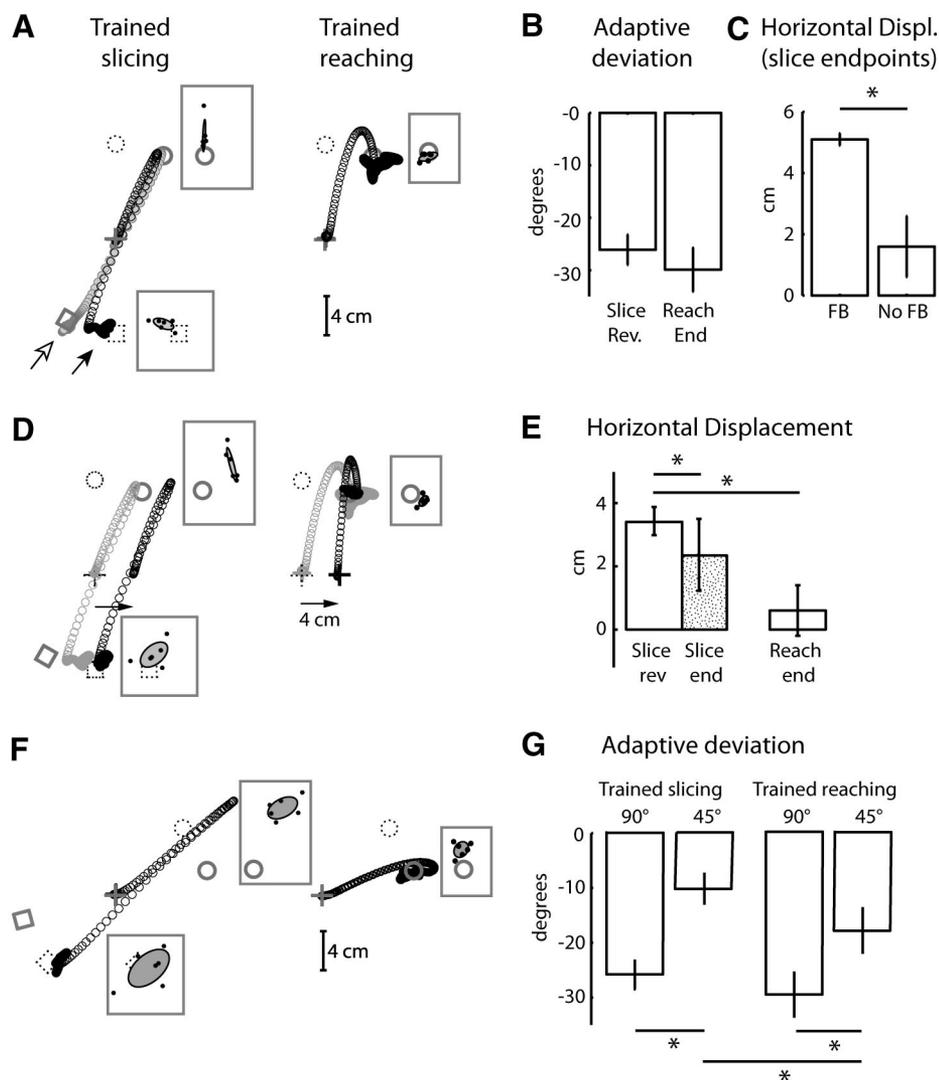


FIG. 4. Adaptation in slicing and reaching and effects of shifts in initial position and target direction. *A*, *D*, and *F*: hand paths of slicing and reaching movements made by representative subjects after rotation training either in slicing (*left*) or reaching (*right*) tasks. *Insets*: centroids of distributions and fitted 95% confidence ellipses for slice reversals and reach endpoints for all subjects (above paths) and for slice endpoints (below paths). *A*: black: test trial performed without cursor feedback; gray: preceding refresher trial performed with cursor feedback. Note slight angular deviation of return phase and terminal drift of test slice toward the unadapted location (black arrow) but not of preceding slice movement made with cursor feedback (white arrow). Note also curvature and bend in the test reaching movement performed after reach training. *B*: mean directional deviations measured as the change in direction of vectors from the origin to reversal points of slices or the final position of reaches. *C*: displacement of final position of slices after adaptation for refresher movements made with feedback (*left*) is greater than in test movements made without feedback (*right*). The latter terminate close to the position at baseline. *D*: hand paths of test slice and reach movements from displaced initial hand position. *E*: mean horizontal displacements at reversals points (white) and final endpoints of slices (*left*) and at endpoints of reaches (*right*). *F*: hand paths of test slice and reach movements to the untrained 45° target. *G*: generalization of visuomotor learning to movements toward a target in the untrained 45° direction. Directional deviations are less for untrained 45° target than for trained (90°) target for both slice reversals (*left*) and reach endpoints (*right*). Transfer of directional deviations (generalization) is significantly lower for reversal points of slices than for endpoints of reaches.

Although this blue region appears quite broad and extends beyond the subject, the model converges on a single point ("m" in the figure) located midway between the subject's head and the nearest target. Around this point, regions of equal likelihood form successively larger ellipses before splaying out in the region behind the subject. The ellipses are clearly aligned along an axis passing through the subject's head between the eyes. We next performed a bootstrap analysis (Efron and Tibshirani 1998) by taking random samples with replacement from our dataset, such that this sample had the same size as the original dataset (but likely containing some points more than once). We recalculated the optimal origin from our model and repeated this procedure 10,000 times. The results of this bootstrap analysis, shown in Fig. 6G, indicate that the computed centers of the common rotation all fall within an ellipsoid extending from the nearest target to a region that includes the entire head (and the cyclopean eye). The data are therefore consistent with a common rotation around an eye- or a gaze-centered reference frame. Because none of the bootstrap origins are located at either the hand's starting point or the shoulder, our data are not consistent with common rotations about either of those points.

DISCUSSION

In our previous study, we proposed that the kinematics of normal reaching movements reflect the superimposition of two sequential control actions. The first dominates as the hand is launched along an intended straight trajectory, whereas the second dominates later to terminate movement and stabilize the hand at an intended location (Scheidt and Ghez 2007). Those conclusions were based on findings of limited transfer of visuomotor learning between two tasks that required subjects to align either trajectory reversals or final positions with common spatial targets and on observations of dramatic differences in hand path in the two tasks. Both were replicated in computer simulations implementing the proposed sequential control. The present findings extend our previous results. First, displacing the initial position of the hand had different effects on both the accuracy and direction of movements to reversal points and final positions during slicing movements. The final positions of slices showed a similar lack of sensitivity to displacement and changes in direction found for endpoints of reaching movements. These were consistent with our model and thus confirm the conclusions of our earlier study (see Introduction) and are in line with previous reports suggesting dif-

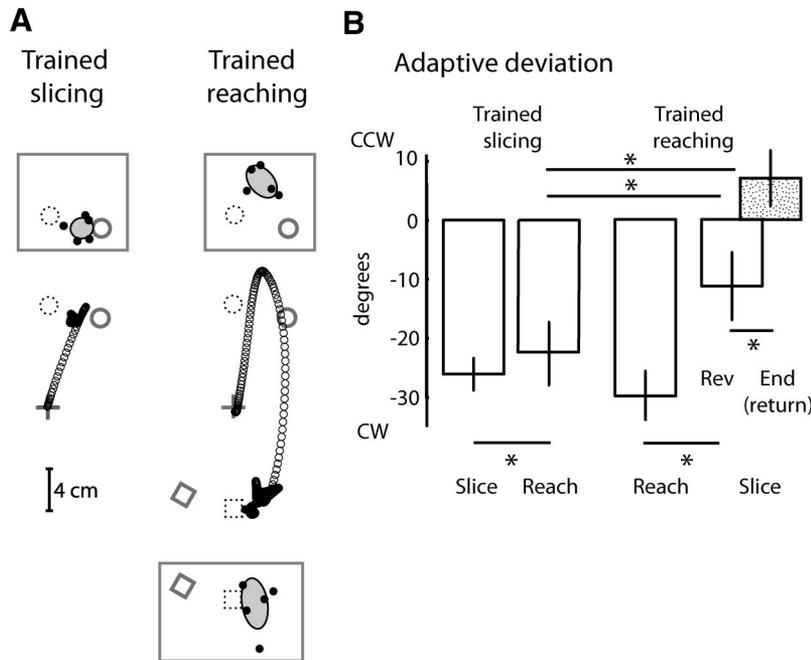


FIG. 5. Transfer of visuomotor adaptation across tasks. *A*: hand paths of reaches made after adaptation in slicing (*left*) and of slices made after adaptation in reaching (*right*). *Insets* are as in previous figures. *B*: *left*: directional deviations of reversals of trained slices and of endpoints of untrained reaches after slice training. *Right*: directional deviations for endpoints of reaches and of reversal points (open) and final positions (stippled) of slices after reach training. Note that in *A* and *B*, final positions of slices performed after reach training are deviated CCW instead of CW relative to origin (i.e., the hand's starting point).

ferences in the feedforward planning of trajectory and final hand position in reaching (Bagesteiro and Sainburg 2002, 2003; Dizio and Lackner 1995; Sainburg 2002; Sainburg et al. 1999). Second, we found differences in how visuomotor learning generalizes across the workspace depending on whether visual feedback pertained to the reversal point in slicing (i.e., the point indicating movement direction and extent) or the hand's final position (i.e., the location of the hand's stabilized position in both slicing and reaching). Thus target location is represented in different reference frames for planning the hand's trajectory to the reversal point and to its final position. For planning trajectory reversals, the target location is represented in a reference frame with its origin located at the initial position of the hand, whereas in planning final positions, the target is instead represented in a reference frame having its origin located at the head or the eyes. We propose that adaptive changes in hand trajectory and final position are driven by kinematic errors that subjects represent in these different coordinate systems. As discussed in the following text, our findings challenge the view that the entire movement trajectory, including the final position, reflects a unitary planning process.

Differences in the control of trajectory and final equilibrium position

The slicing task used here resolves a potential confound in our previous report (Scheidt and Ghez 2007), showing conclusively that slicing and reaching were not controlled using separate cued motor programs but rather that specific features within each task were controlled differentially. In that study, we inferred that accuracy of trajectory reversals and stable final positions are supported by different adaptive mechanisms by examining transfer of visuomotor rotations between slicing and reaching tasks. Although all subjects learned both tasks, separate groups of subjects learned the visuomotor rotation in

slicing or in reaching. In slicing, subjects were to return their hand to the starting position after reversing direction at the target. Because the cursor motion was rotated around the starting position, visuomotor learning did not require learning a new position at which to terminate movement. This was no longer the case in the slicing task used here, because subjects returned their hands past the origin to stop at a second target closer to the body. Thus in adapting to the visuomotor rotation, the slicing task encouraged learning of both a rotated reversal point and a terminal position about which to stabilize the hand. The addition of a second target allowed us to determine the effects of training on reversal points and final positions within the same subjects performing the same task under the same feedback conditions. The differential effects of shifting initial hand position on trajectory directions and final positions in slicing and reaching comprise a double dissociation that cannot be attributed to differences in feedback (available continuously in slicing but only after stabilization in reaching). Rather, the differences must have reflected the specific feature of movement that subjects were planning (and adjusting during training) to reverse direction or to terminate movement accurately on target.

Because slice trajectories remained rectilinear and parallel to the trained direction when the hand's initial position was shifted, subjects apparently implemented the practiced trajectory plan without accounting for the change in initial condition. To do so, they had to alter the joint torques generated in the course of movement to compensate for the change in initial position (Wang and Sainburg 2005) and could only have done so here using proprioceptive information. As a consequence, reversal points became inaccurate. In reaches and in the return movements of slices, however, trajectories no longer remained rectilinear but curved toward the target, compensating for the imposed changes in initial position. This equifinality (Kelso and Holt 1980) is predicted in our model by the implementation of an impedance controller centered at the final equilibrium position, which acts as an attractor for the hand at the

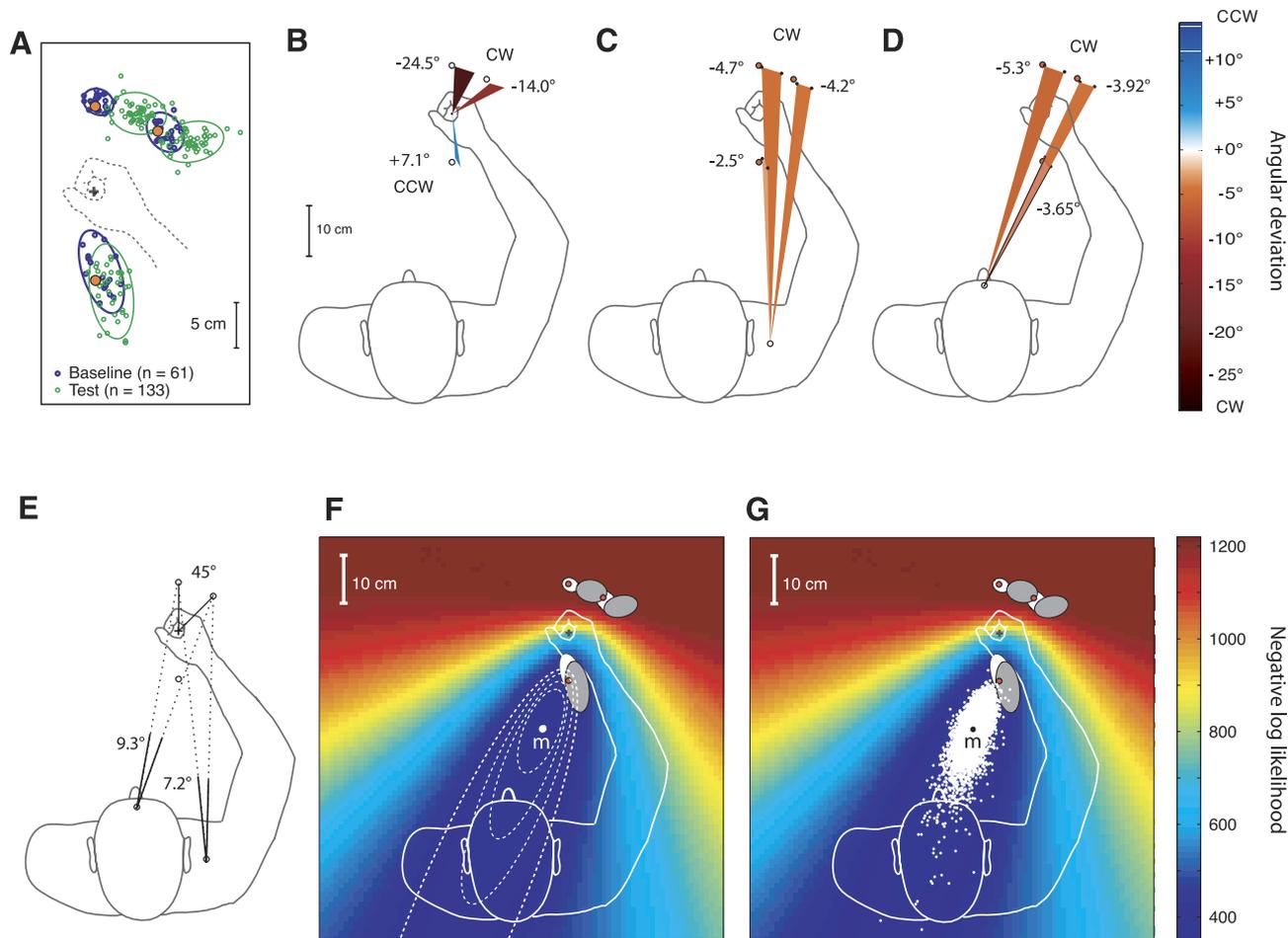


FIG. 6. Generalization of visuomotor adaptation of final hand positions: relative likelihood of origins under a common rotational transformation. *A*: dataset used to evaluate ability of different origins in peripersonal space to account for our experimental findings in reaching. Blue circles correspond to final positions recorded from test movements in baseline block, whereas green dots correspond to final positions recorded from test movements in test block. 95% confidence ellipses fitted to endpoint distributions are shown for pre- and post-training trials for each target. *B–D*: mean directional deviations induced by reach training at 90° target, as computed relative to movement origin, shoulder, and cyclopean eye, respectively. For clarity, only centers of distributions are shown (solid black dots), as well as the targets and starting position. The closer the angular difference between baseline and test angles are to each other, the more likely the point is to be an origin for a common rotation. *E*: angular separation of target at 45° relative to origin computed relative to head (at cyclopean eye) and shoulder. *F*: log-likelihood map of spatial locus of a common origin for final position remapping under a common rotational transformation. Blue regions correspond to locations with least amount of unexplained variance, with lower numbers indicating a higher likelihood (i.e., blue areas are more likely origins than red areas). White dotted contours outline areas of equal likelihood. Point “m” denotes minimum value over entire space. Negative log likelihood values for the hypothesis that each location served as the origin for a common rotation were as follows: for hand, 788; for shoulder, 458; for cyclopean eye, 376. *G*: bootstrap analysis superimposed on relative likelihood map. In *F* and *G*, target locations are depicted as orange-filled black circles and the hand’s starting position as a + sign. 95% confidence ellipses fitted to endpoint distributions are shown for baseline (white) and test trials (gray) for the 3 target locations.

intended endpoint as predicted in earlier equilibrium control models (Asatryan and Feldman 1965; Polit and Bizzi 1978; see Scheidt and Ghez 2007). It should be noted that equifinality was not observed in a recent study of the effects of displacing the hand in horizontal reaching movements (Vindras et al. 2005). However, differences in instructions and task conditions can account for the different observations. In the study by Vindras et al. (2005), subjects were not provided visual feedback after the movement. Thus they could neither correct endpoint errors nor reduce them adaptively in successive trials and would not have been motivated to do so even without the hand displacements. In contrast, subjects performing our reaching task were instructed to be as accurate as possible and were provided with visual feedback of errors in stabilized hand position. They were also explicitly instructed to correct residual errors at the end of the trial. Both factors likely favored

optimizing terminal accuracy independent of initial hand position. Furthermore, the environmental perturbations we imposed required subjects to co-contract their arm muscles to stabilize their hand at movement endpoints (cf. Scheidt and Ghez 2007). This increase in terminal joint stiffness enhanced the mechanical effectiveness of the planned equilibrium positions in our study.

Differences in spatial reference frames for planning trajectories and final positions

An earlier study of spatial generalization of visuomotor rotation learning in slicing movements showed that target distance and direction are represented in a coordinate system having its origin at the hand’s starting position (Krakauer et al. 2000). After learning to reverse direction accurately at a single target, movements to targets in the same direction but at

different distances remained straight and accurate in extent. In contrast, learned angular deviations decreased rapidly as the difference between trained and test target directions increased. The steep drop in the adaptive deviations found here for slice reversals aimed to the 45° target was similar to that found previously (Krakauer et al. 2000). Although a decrease in adaptive deviation was also present for reaches to the 45° target after reach training to the 90° target, it was substantially (and significantly) less than with slicing training. Greater transfer of learning in reaching to this untrained target is readily understood if one considers generalization to be a function of the angular separation between the trained and untrained targets computed relative to the head or shoulder, as opposed to the hand (Fig. 6E). The conclusion that slice reversals and reach endpoints were planned in different coordinate frames was further confirmed by the finding that the movement endpoints that were to terminate at the 270° target were rotated in the opposite (CCW) direction from the CW rotation learned for the trained target. This could not be accounted for by a common rotation around the hand. Instead, using the entire dataset, we found that a CW rotation centered in a region that included the head could account for the changes in endpoint distributions of reaches to all three targets. Our model did not consider the possible decay in generalization with angular separation, however, because we had data for only three targets, and did not want the number of independent model parameters to exceed the number of targets. Further experiments using a larger number of targets will be needed to determine the magnitude of this effect and to explore the effects of gaze direction and/or shoulder orientation. Nevertheless, our results showed unambiguously that the nervous system uses separate coordinate systems to plan trajectories and final stabilized positions.

Our findings for aimed final positions matches the pattern of generalization found in 3D positioning tasks in experiments sampling a larger number of test target locations (Vetter et al. 1999). In particular, the results of our analyses are more consistent with an eye-centered coordinate frame rather than with a shoulder-centered system as we had expected originally. This is consistent with the distributions of spatial errors described in studies of 3D pointing (Admiraal et al. 2003; Crawford et al. 2004; Flanders and Soechting 1990; McIntyre et al. 1997; Soechting and Flanders 1989), and with those described in studies of virtual object orientation (van den Dobbelen et al. 2001, 2003, 2004).

A surprising finding here was that, after rotation training in slicing, catch trials without visual feedback showed complete adaptation for reversal points but not for final positions. Therefore when the cursor was visible, subjects relied on feedforward mechanisms to control movement to the reversal point but must then have relied on visual corrections to terminate movement. Because subjects had experienced visual feedback both at reversals and endpoints, they might have been expected to learn the visuomotor rotation for both the 90° reversal point and 270° final position equally well. Indeed, we have previously shown that subjects have no difficulty learning a 30° CW cursor rotation about the hand's starting point for slicing movements made to two, four, or eight targets uniformly distributed about that common origin (Krakauer et al. 2000; Scheidt and Ghez 2007). However, to terminate movement accurately at the 270° target in this experiment, subjects would have had to learn a CCW rotation of the intended final position

relative to the head or the eyes. This corresponds to a coordinate rotation in the opposite direction from the CW rotation required for the reversal target. Because learning a visuomotor rotation in one direction is known to interfere with learning a visuomotor rotation in the opposite direction within a single task and spatial reference frame (cf. Bock et al. 2001; Krakauer et al. 2000; Wigmore et al. 2002), it is also possible that interference may arise even when the spatial reference frames are different. This is because the sensory consequences of movement predicted using the trajectory and positional controllers would be in conflict, and thus the failure of subjects to learn to redirect their movements CCW to the final position could be attributable to anterograde and/or retrograde interference produced by learning the conflicting rotations for the reversal and final targets.

Performance errors driving adaptive adjustments in trajectory and position

Improvement in spatial accuracy over successive trials is driven by kinematic errors that subjects experience in the course of practice (Scheidt et al. 2000, 2001). Sensory signals arising during hand movements do not themselves provide this information directly. Instead, errors are estimated by comparing the actual and predicted sensory consequences of the motor commands (Wolpert 1997). Computational approaches propose that sensory predictions arise by simulating the effects of intended commands through forward models (Wolpert 1997; Wolpert et al. 1995). To be compared, however, it is essential that predicted and actual feedback information both be represented in the same reference frame. In this study, both the spatial target and performance feedback were presented visually. Thus the finding of different origins for planned reversals and final positions suggests that subjects also predicted the visual consequences of movements (i.e., reversal and stabilized positions) in different reference frames.

Because vision provides salient cues about trajectory curvature and directional errors, the presence of visual feedback during movement in slicing might have been responsible for differences in hand path kinematics for reaching and slicing. However, findings from our previous study (Scheidt and Ghez 2007) suggest that this is unlikely to fully account for differences in linearity and/or the different spatial representations of reversal points and final positions observed here. Specifically, in *experiment 2* of that previous study, subjects successfully adapted slicing movements when only the reversal point of movement was provided as visual feedback of performance error. Importantly, hand paths remained substantially straighter than in the reach task as they did in this study, indicating that continuous visual feedback is not necessary to maintain linearity. Why should linearity be regulated adaptively and maintained for reversals but not for stabilized positions? Because some of our findings differ with prior studies in horizontal movements, we present the following speculative remarks to sketch the main elements of our working hypothesis.

We hypothesize that differences in trajectory characteristics and learned coordinate frames emerge from differences in the costs associated with achieving accurate performance in the two task conditions (Kording and Wolpert 2004, 2006; Tassinari et al. 2006). A critical difference between movements made to a transient via-point for reversing direction from ones

made to achieve a stable position on arrival was the addition of a stringent criterion for temporal precision: to accurately reverse direction as the hand reached the target, subjects had to predict precisely when the hand would reach the desired spatial location. This was not the case in reaching where only the stabilized position had to be predicted. We propose that by maintaining hand paths straight and by using information about the hand's starting position, subjects were able to partition endpoint variability into errors of extent and direction. Each could then be compensated adaptively by simple control laws: extent errors in slicing could be corrected by varying the time of the return stroke, whereas directional errors could be corrected by a compensatory change in movement direction (see next paragraph for consideration of point-to-point movements). More specifically, if neural controllers apply stereotyped joint torques for outgoing and return segments as we postulated in the formulation of our heuristic model (Scheidt and Ghez 2007), extent errors at reversal points would be critically dependent on the timing of the return stroke. Delaying the return segment would increase movement extent (and produce hypermetria) while shortening the delay from the initial stroke would reduce extent (and produce hypometria) for targets at a set distance. In contrast, adjustments to movement direction require subjects to use information about the hand's initial position to plan movement vector direction: the knowledge of initial hand position is needed to solve the credit assignment problem resolving movement errors into errors of direction and extent. In the experiments described here, as in most experiments, this information was provided by an explicit home target and by cursor position feedback. In some experimental situations, however, subjects may obtain this information combining proprioceptive and visual input (Sober and Sabes 2003, 2005). With multiple target locations and a common origin for movements, it may be possible to obtain this information implicitly (i.e., in the absence of explicit visual cues) by considering the effects of successive adjustments on accuracy. This would not be possible if initial position varied from trial to trial.

In our reaching task, subjects were only provided with visual feedback after movement termination. The precise timing of target acquisition in relation to the prior trajectory was neither critical nor was it prominently contained in the visual feedback signal, because random hand displacements had been introduced by the perturbation for 1.5 s before visual feedback presentation. Furthermore, it is known that adaptive adjustments of movement trajectories in response to terminal errors decrease substantially when a delay elapses between the movement and visual feedback (Kitazawa et al. 1995). Accuracy was primarily dependent on the subject's ability to develop stiffness about the desired equilibrium position and to maintain this position through proprioceptive feedback. Because our task required subjects to then correct residual errors once the cursor became visible, subjects are likely to have directed their attention to (and visually fixated on) the target in anticipation of the cursor becoming visible. This is typical when aiming pointing movements in 3D space (see Crawford et al. 2004 for a review) where gaze shifts and accuracy covary with endpoints (Admiraal et al. 2003), and accuracy is degraded when gaze is made to deviate from the target (Henriques et al. 2003). Because subjects had no explicit visual cue indicating their starting position, gaze direction provided the only reliable

reference for subjects to estimate errors at movement endpoints. Even in the absence of destabilizing perturbation, increasing stiffness would facilitate identification of an appropriate control law for driving adaptive adjustments in final positions relative to the center of gaze (Jordan and Rumelhart 1992; Wolpert et al. 1998). This could therefore account for a pattern of generalization consistent with head- or eye-centered coordinates, as observed here and in 3D studies (Vetter et al. 1999).

Increasing joint stiffness at the intended equilibrium position in the reaching paradigm used here was necessary to counter effects the perturbations. However, increasing stiffness in unperturbed conditions would also be desirable to compensate for uncertain loads (Franklin et al. 2004), as well as to facilitate identification of an appropriate adaptive strategy in visual space. As control laws are learned to enable adjustments in trajectory direction and extent, an optimal control framework would predict that terminal stiffness should be progressively minimized to reduce energetic costs. This would favor increasing the dominance of a hand-centered or vectorial trajectory, over a terminal position control plan in determining hand kinematics, because improvement in state estimates improve the subject's ability to accurately predict hand trajectories. We posit that this accounts for the hand-centered error distributions typically observed in planar horizontal movements (Brown et al. 2003; Rossetti et al. 1995; Sainburg et al. 2003; Vindras et al. 2005; Wang and Sainburg 2005). The interplay of optimization objectives, however, would be expected to have different outcomes in three dimensional movements because of the larger numbers of degrees of freedom to be controlled. Furthermore gravitational loads may sufficiently alter the topography of the solution space to result in the positional controller playing a dominant role. These factors may be expected to favor greater reliance on controlling final position with higher limb impedances at the expense of stereotypical trajectories, as well as accounting for the typical head- or eye- centered coordinates observed experimentally in 3D movements.

Concluding remarks

Our experimental findings show that the brain plans and represents movements to the same visual locations in peripersonal space differently when the task calls for achieving this spatial goal transiently but with a high degree of temporal precision and when the goal is to maintain a stable posture at the end of movement. This contradicts the common assumption that the neural control of reaching relies on a unified spatial model to specify both trajectories and final positions (Asatryan and Feldman 1965; Feldman 1966, 1986; Flash and Hogan 1985; Gribble and Ostry 2000; Harris and Wolpert 1998). We speculate that differences in trajectory kinematics and learned coordinate frames reflect different cost functions for achieving accurate reversals and stable endpoints. Both would be influenced by uncertainty and variation in initial and final positions and by the specific information provided by sensory feedback. The use of separate representations in planning and regulating different features of movement, such as reversals and final positions, raises the question of how these representations may be brought into register or calibrated. Such a calibration is frequently assumed to occur automatically or implicitly (Sober and Sabes 2003). However, the hypermetria of slice trajectories

after calibration of reaching movements, found both here and in our previous study, suggests instead that “combining separate sources of concurrent sensory information does not necessarily lead to their mutual calibration” (Smeets et al. 2006). Moreover, trajectory planning mechanisms do not appear to be informed of impedance changes associated with the upcoming positional plan (cf. Fig. 2C). As discussed above, these findings raise a number of issues for future experiments.

The demonstration that separate populations of neurons in overlapping loci of primate motor cortex govern movement trajectory and posture (Kurtzer et al. 2005) points to likely substrates for implementing these controls in parallel through connections with spinal circuitry. Although the brain maintains spatial representations of target location in eye-centered, shoulder-centered, and hand-centered reference frames in premotor and parietal areas (Battaglia-Mayer et al. 2000, 2001; Buneo et al. 2002; Lacquaniti et al. 1995), whether these representation play different roles in different tasks or during the course of learning has not been resolved. Restricting visual feedback to specific task features and correlating performance with neural activity during adaptive learning of different tasks, as was done here psychophysically, could provide significant insights into the contributions of these circuits to the optimization of motor performance during different learning tasks.

APPENDIX

We evaluated whether the distributions of final hand positions about the test targets at 90, 45, and 270° collected during baseline practice could be transformed into the respective distributions observed after reach task adaptation using a common rotation θ around an origin $p_o = \{x_o, y_o\}$. We considered p_o to be the origin of the coordinate frame within which final position adaptation occurred (i.e., the point in space we wished to localize). We first computed the sample mean vector μ_j and sample covariance matrix Σ_j for the baseline data $\{q_1, \dots, q_m\}_j$ obtained about each target ($j = \{1, 2, 3\}$). We next considered how the μ 's and Σ 's would transform under a rotation θ about p_o . We define a transformation matrix R that applies a CCW rotation θ about the origin

$$R = \begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix} \tag{A1}$$

Rotating μ_j about p_o results in the transformed mean vectors μ_j^* :

$$\mu_j^* = R(\mu_j - p_o) + p_o \tag{A2}$$

while the transformed covariance matrices Σ_j^* are specified by

$$\Sigma_j^* = R \Sigma_j R^T \tag{A3}$$

We computed the probability of observing each postadaptation set of final hand positions $\{r_1, \dots, r_m\}_j$ for each target j as a transformed version of the respective unadapted baseline distribution of endpoints assuming an origin p_o . The probability of observing the group corresponding to target j is defined by the following equation

$$\text{prob}(r_{1j}, \dots, r_{mj} | \mu_j, \Sigma_j, p_o, \theta) \propto \prod_{i=1}^m \left[(\Sigma_j^*)^{-\frac{1}{2}} \cdot e^{-\frac{1}{2}(r_{ij} - \mu_j^*)(\Sigma_j^*)^{-1}(r_{ij} - \mu_j^*)} \right] \tag{A4}$$

The probability of observing all three endpoint distributions is simply the product of the individual probabilities for each target (DeGroot and Schervish 2001). Taking the log of the resulting equation results, after some simplification, in

$$\text{prob}(\text{data} | \mu_j, \Sigma_j, p_o, \theta) \propto - \sum_{j=1}^3 \sum_{i=1}^{m_j} (r_{ij} - \mu_j^*)(\Sigma_j^*)^{-1}(r_{ij} - \mu_j^*) \tag{A5}$$

In this computation, we assume that the transformed groups have the same variances as the baseline groups. We considered adding an additional scaling variable in Eq. A3 to account for differences in variance, but the small number of targets compared with the number of parameters in the model did not seem to justify the added complexity.

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