

Remapping Hand Movements in a Novel Geometrical Environment

Kristine M. Mosier,¹ Robert A. Scheidt,² Santiago Acosta,³ and Ferdinando A. Mussa-Ivaldi^{3,4}

¹Department of Radiology, Indiana University School of Medicine, Indianapolis, Indiana; ²Department of Biomedical Engineering, Marquette University, Milwaukee, Wisconsin; ³Sensory Motor Performance Program, Rehabilitation Institute of Chicago, and ⁴Department of Physiology, Northwestern University, Feinberg School of Medicine, Chicago, Illinois

Submitted 14 April 2005; accepted in final form 28 August 2005

Mosier, Kristine M., Robert A. Scheidt, Santiago Acosta, and Ferdinando A. Mussa-Ivaldi. Remapping hand movements in a novel geometrical environment. *J Neurophysiol* 94: 4362–4372, 2005. First published September 7, 2005; doi:10.1152/jn.00380.2005. The issue of how the Euclidean properties of space are represented in the nervous system is a main focus in the study of visual perception, but is equally relevant to motor learning. The goal of our experiments was to investigate how the properties of space guide the remapping of motor coordination. Subjects wore an instrumented data glove that recorded the finger motions. Signals generated by the glove operated a remotely controlled endpoint: a cursor on a computer monitor. The subjects were instructed to execute movements of this endpoint with controlled motions of the fingers. This required inverting a highly redundant map from fingers to cursor motions. We found that 1) after training with visual feedback of the final error (but not of the ongoing cursor motion), subjects learned to map cursor locations into configurations of the fingers; 2) extended practice of movement led to more rectilinear cursor movement, a trend facilitated by training under continuous visual feedback of cursor motions; 3) with practice, subjects reduced motion in the degrees of freedom that did not contribute to the movements of the cursor; 4) with practice, subjects reduced variability of both cursor and hand movements; and 5) the reduction of errors and the increase in linearity generalized beyond the set of movements used for training. These findings suggest that subjects not only learned to produce novel coordinated movement to control the placement of the cursor, but they also developed a representation of the Euclidean space on which hand movements were remapped.

INTRODUCTION

The defining property of Euclidean spaces is that the length of a segment does not depend on the segment's orientation or position. This property is essential to capture the nature and motions of rigid bodies (Goldstein 1980), which are defined by the invariance of the distances between their points. The measure of distance (the metric) is of vital importance in constructing a map between the visual representation of space and the motor commands controlling movements within that space.

The ability of the visual system to capture the Euclidean nature of space has been extensively studied (Hatfield 2003; Shepard 2001), whereas fewer studies have examined the representation of space in the motor system (Bernstein 1967; Rossetti 1998). These studies emphasize that visual perception and motor action are independent but highly interconnected. The visual representation of space from retinal coordinates is

believed to be transformed into motor commands by dorsal pathways, whereas objects within space are thought to be represented by ventral pathways, with multiple interconnections between the two pathways (Goodale and Milner 1992; Milner and Goodale 1993). In contrast, little is known about how the fundamental geometrical properties of space are represented by the motor system. We easily formulate and execute motor plans such as “move the hand 10 cm to the right,” despite the fact that this action requires widely varying muscle activations and segmental coordination, depending on the hand's initial position. This clearly demonstrates that the motor system is able to capture the Euclidean properties of the space in which actions take place.

The purpose of our studies was to understand how the motor system learns to represent a new space. We asked subjects to move between target locations on a computer screen using an instrumented data glove that converted finger motions into cursor motions. The screen had a well-defined Euclidean metric: the distance between any two points is the length of the straight segment that joins them. In contrast, there is no obvious or “natural” definition of distance in finger articulation space (i.e., between two gestures of the hand). We observed how two features of motor behavior evolved in the course of learning this novel task: 1) the shape of the cursor trajectories and 2) the variability of both hand and cursor motions.

Our hypotheses centered on two questions. First, we asked whether subjects learn the Euclidean metric of the controlled endpoint by organizing coordination of finger motions to generate straighter motions of the cursor (i.e., movements of minimum Euclidean length). The second question is whether practice leads to more accurate targeting, at the expense of more variable trajectories (Todorov and Jordan 2002) or, alternatively, does the entire movement profile become less variable, suggesting that the control system is attempting to become both more accurate in reaching the target and more consistent in producing finger and/or cursor trajectories (Flash and Hogan 1985; Hogan 1984)? We will show that when subjects learn to control an overabundant set of hand signals in the presence of a novel transformation between these signals and the controlled endpoint, they become both more accurate in the task and more consistent in their finger and cursor motions. This finding is not consistent with the model of motor control proposing that the motor system increases variability in the redundant degrees of freedom to improve accuracy of the motor task.

Address for reprint requests and other correspondence: F. A. Mussa-Ivaldi, Department of Physiology (M211), Northwestern University, Feinberg School of Medicine, 303 East Chicago Ave., Chicago, IL 60611 (E-mail: sandro@northwestern.edu).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

METHODS

Twenty-seven adult subjects participated in this investigation after providing written informed consent approved by Northwestern University's Institutional Review Board. Each subject wore a right- or left-handed CyberGlove (Immersion, San Jose, CA), from which 19 joint angle measurements were recorded from flexion of the phalangeal joints (proximal, middle, and distal), abduction of the thumb and fingers, and wrist flexion/extension and abduction/adduction. CyberGlove signals were sampled at a rate of 20/s in all procedures with the exception of the generalization experiment, where the rate was 50/s. The 19-dimensional (19-D) vector of glove signals encoding the configuration of the fingers was mapped onto the two-dimensional (2-D) (x, y) coordinates of a computer screen using a linear transformation

$$\begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} a_{x,1} & a_{x,2} & \dots & a_{x,19} \\ a_{y,1} & a_{y,2} & \dots & a_{y,19} \end{bmatrix} \cdot \begin{bmatrix} h_1 \\ h_2 \\ \dots \\ h_{19} \end{bmatrix} = A \cdot h \quad (1)$$

where $p = [x, y]^T$ indicates the point on the monitor, $h = [h_1, h_2, \dots, h_{19}]^T$ is the "glove signal vector," and A is the matrix of mapping coefficients, $[A]_{i,j} = a_{i,j}$.

The mapping was calibrated before the start of each experiment session by asking the subject to assume four different hand configurations (gestures) and then establishing a correspondence between these configurations and the four vertices of a rectangular workspace on the computer screen (Fig. 1). The mapping coefficients ($a_{i,j}[r]$)

were determined by the following procedure. Let $P = [p^{(1)}, p^{(2)}, \dots, p^{(4)}]^T = [x^{(1)}, y^{(1)}, x^{(2)}, y^{(2)}, \dots, x^{(4)}, y^{(4)}]^T$ indicate the eight-dimensional vector of screen coordinates at the four vertices. Let $h^{(1)}, h^{(2)}, \dots, h^{(4)}$ indicate the corresponding 19-D glove signal vectors at these postures. Collect the vectors in the 8×38 data matrix

$$H = \begin{bmatrix} h_1^{(1)} & \dots & h_{19}^{(1)} & 0 & \dots & 0 \\ 0 & \dots & 0 & h_1^{(1)} & \dots & h_{19}^{(1)} \\ \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ h_1^{(4)} & \dots & h_{19}^{(4)} & 0 & \dots & 0 \\ 0 & \dots & 0 & h_1^{(4)} & \dots & h_{19}^{(4)} \end{bmatrix}$$

and the unknown coefficients of A into a 38-dimensional vector, $a = [a_{1,1}, a_{1,2}, \dots, a_{1,19}, a_{2,1}, a_{2,2}, \dots, a_{2,19}]^T$. Using this notation, the coefficients are estimated by $a = H^+P$, where H^+ is the Moore-Penrose pseudoinverse of H . This procedure corresponds to the selection of the minimum norm parameter vector a , consistent with the calibration postures.

All subjects used the same calibration postures. After calibration, any point within the rectangular workspace could be reached by assuming a hand posture that was a linear interpolation of the four calibration postures. These postures were chosen empirically, based on the requirement that all points inside the workspace be reachable and that, whereas each gesture of the hand mapped into a single point on the screen, each screen location corresponded to multiple hand gestures.

After calibration, subjects practiced moving the cursor using finger motions for 5 min. After this acquaintance phase, they then made

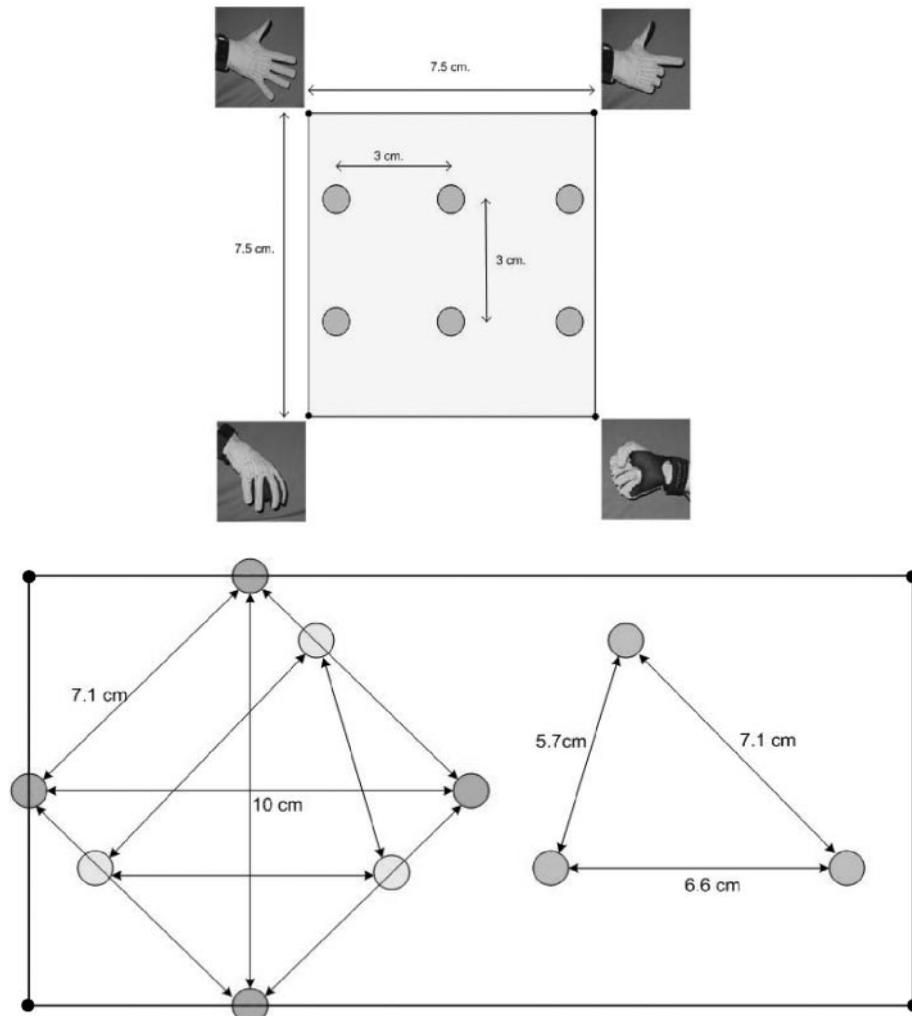


FIG. 1. Calibration and targets. *Top*: target layout and postures used to set up the map from glove signals to monitor coordinates. Each calibration posture corresponds to a corner of the rectangular region on the monitor. Subjects were aware of this correspondence. This target layout was used in the main experiment. *Bottom*: target locations for the generalization experiment. Three sets of targets were used: one training set (diamond pattern on the left) and 2 test sets (triangular patterns). Targets in the triangular pattern inside the training diamond are the interpolation set. Three targets on the right are the extrapolation set. Subjects practiced reaching movements over the training set and then were asked to perform movements in the 2 test sets (see text for details). Four calibration postures (*top*) were used to calibrate the corners of the larger rectangular workspace in the generalization experiment.

either No Vision (NV) or Vision (V) movements. NV movements consisted of the following steps:

- 1) Subjects positioned the cursor inside the initial target.
- 2) On presentation of a new target, the cursor vanished.
- 3) Subjects were required to place and hold the (invisible) cursor inside the new target using a single rapid movement of the fingers. This reaching was to be completed within 2 s of target presentation.
- 4) The cursor reappeared when the hand was at rest after this movement.
- 5) Errors in final position were to be corrected by moving the cursor to the target under visual guidance.
- 6) Once inside the target the procedure was repeated starting from step 2.

V movements followed the same sequence of events as NV movements, except that in steps 2 and 3, cursor presentation was maintained throughout the movement.

Two sets of experiments were conducted to explore: 1) how subjects learn to control cursor motion on the computer screen using a highly redundant actuator system (the hand) and 2) whether this learning generalizes to new target locations requiring novel combinations of hand postures.

In the first set of experiments, a single trial involved a total of 30 reaching movements between six targets (five movements per target) in pseudorandom order. Although glove and cursor data were collected throughout the entire experiment, only those collected during the rapid initial hand movement (steps 2 and 3) were analyzed and are discussed here.

Each subject participated in one of three protocols: P1, P2, and P3. In protocol P1, they repeated 10 NV trials in a single session that lasted about 1 h. Subjects in protocols P2 and P3 participated in four experimental sessions on four consecutive days. Subjects executed the same total number of movements in conditions P2 and P3. On each day, subjects in both protocols performed ten trials during an hour-long session. P2 subjects engaged in only NV trials. P3 subjects alternated V and NV trials, in the following order: NV–V–V–NV–V–V–NV–V–V–NV. For comparison between both groups, only data for the rapid initial movements in the NV trials common to both protocols (trials 1, 4, 7, and 10) are analyzed and discussed here. The V and NV movements in the remaining trials were used only to provide different training contexts for the two protocols. Subjects in both protocols received some amount of training under visual feedback. However, for those in P2, visual guidance was limited to corrective movements, which were typically shorter and generally slower than the initial target-reaching movements.

The second set of experiments explored how learning generalizes to new targets requiring novel combinations of hand postures. Seven subjects participated in two consecutive sessions, 6 h apart. Three sets of targets were used (Fig. 1): four training targets, three “interpolation” targets, and three “extrapolation” targets. The calibration was performed as in the basic experiment, by asking subjects to execute the four hand gestures shown in Fig. 1 (*top*), in correspondence with the four corners of the large rectangular workspace. These gestures were the same as for the first experiment. However, the training and test workspace were different. Therefore the calibration resulted in a different mapping from glove signals to cursor coordinates. At the beginning of the first session, subjects performed 30 NV movements to both the interpolation and extrapolation sets. These movements provided a baseline for evaluating learning effects induced by practicing over the training targets. Subjects then performed 500 practice movements over the training set. This practice period lasted about 1 h and was conducted with continuous cursor feedback. Immediately after this training, subjects made 30 NV movements each to the interpolation and extrapolation targets. A second session took place after a 6-h pause after the first session, to assess the consolidation of learning induced by the first training period. Here again, subjects were asked to execute 30 NV movements to the interpolation and extrapolation sets.

Data analysis

Signals from each of the bend sensors and the coordinates of the cursor relative to the origin of the screen were acquired and transferred off-line for analysis. Preprocessing of the data was carried out to extract the first, open-loop movement component. Movement onset and termination were identified by applying a velocity threshold (0.5 cm/s) to the cursor speed profile. Only movements with a simple speed profile, preceded and followed by a prolonged period of rest, were accepted for further analysis. We measured and analyzed four aspects of performance.

1) *Final endpoint error*: The Euclidean distance between the cursor position at movement’s end and the target center.

2) *Aspect ratio* (a measure of linearity): The ratio of maximum lateral excursion to the distance between start and end positions of the cursor. A straight segment has a zero aspect ratio.

3) *Redundant motion*: The vector h of data glove signals is uniquely decomposed into two orthogonal vectors: $h = h_T + h_N$, such that $p = A \cdot h_T$ and $0 = A \cdot h_N$ (where $p = [x, y]^T$). The “task” vector h_T has the minimum Euclidean length among all possible vectors that map into p . The “null” vector h_N belongs to the “null space” of A . Task and null vectors are obtained by projection operators derived from the Moore–Penrose inverse of A : $A^+ = A^T \cdot (A \cdot A^T)^{-1}$. Specifically, $h_T = T(A) \cdot h$, with $T(A) = A^+ \cdot A$, $h_N = N(A) \cdot h$, where $N(A) = [I_{19} - T(A)]$ and I_{19} is the 19-D identity matrix. This decomposition is analogous to the decomposition into controlled and uncontrolled manifolds (Scholz and Schoner 1999). Here, however, the analysis is greatly simplified because the glove-to-screen transformation is linear. Thus the task and null components are defined over proper subspaces of the glove-signal space rather than over curved manifolds. For each reaching movement, we used the projection operators $N(A)$ and $T(A)$ to derive the null-space and task-space components of the glove signals. We then calculated the movement length in task and null subspaces, where the latter is the component of finger motion that does not contribute to cursor motion. Both h_T and h_N are 19-D glove vectors within subspaces “embedded” in the glove signal space. The units that we used for the components of these vectors (G.S.U. for glove signal units) is the resolution of the numerical values generated by the CyberGlove sensors, each ranging between 0 and 255.

4) *Movement variability*: To assess the consistency of performance from movement to movement, it is desirable to align movements in time in a way that does not require scaling of the motion variables themselves. To do so, we identified the onset of movement (OM) by first scanning each cursor speed profile forward in time to identify when cursor speed was >10 cm/s, and then scanning backward until reaching a speed <0.5 cm/s. After aligning (with respect to OM) all of the movements to be analyzed, the movement records were truncated to the same total duration [end of movement (EM)], defined so that the slowest movement was represented in its entirety along with a brief period of postmovement rest. We required sufficiently long rest periods during data collection to ensure that, after truncation, all records contained the whole initial movement followed by some amount of samples at zero velocity. Finally, sampling times were normalized for each set of movements by setting $OM = 0$ and $EM = 1$. For each pair of start and end targets and each experimental session, the covariance matrices of the cursor movements and of the glove signals were derived at each sample instant using MATLAB (function: cov). Three signals were considered for this analysis: 1) the total glove signal, $h(t)$; 2) the null-space projection, $h_N(t)$; and 3) the task-space projection, $h_T(t)$.

Statistical testing

Learning trends were determined by considering how individual and group measures evolved within sessions and across multiple days. Before statistical testing, each of the performance measures described

above required correction for nonnormality (skew) in their distributions arising from the fact that these measures are strictly nonnegative. A Box-Cox transformation [$T_\lambda(y) = (y^\lambda - 1)/(\lambda y^{\lambda-1})$] was used to correct for distribution skew within the Minitab v13 computing environment (Box and Cox 1964). One- and two-way ANOVAs were conducted on the transformed data to evaluate training effects within a day and across days for each subject group. Post hoc Tukey *t*-tests were conducted to identify significant changes in performance ($P < 0.05$) within and across days when ANOVA revealed a significant main effect.

Inclusion criteria

The vast majority of subjects were able to learn the cursor manipulation tasks described above. The mere fact that this learning occurred is not by itself surprising. However, to evaluate *how* learning evolves, it is necessary that learning occurs in the first place. Thus only 23 of 27 subjects (85%) who demonstrated consistent error reduction with practice were included in the analyses.

Handedness

Of the 23 included subjects (15 males, 8 females; 20 right-hand dominant, three left-hand dominant), 14 used their dominant hand and nine used the nondominant hand. Although hand dominance had an effect on final error, ANOVAs found no main effect of hand dominance on the other statistics analyzed, and accounting for hand dominance did not affect the results on learning trends that form the primary focus of this report.

RESULTS

Training without vision

As subjects practiced controlling cursor movement by hand gestures, cursor trajectories became more consistent (Fig. 2;

training and test movements without vision within a single session), indicating that subjects learned the finger coordination patterns required of this novel task. A set of trajectories between two targets and their speed profiles are shown in *A* and *C* for a representative subject. Average motion and speed, together with the SD are shown in *B* and *D*. The markedly curved trajectories apparently reflect sequential execution of submovements, one directed toward the target below the starting position, followed by a correction toward the final target (dark black circles). The six plots on the *right* of Fig. 2 show average movements by the same subject in three sets of trials early in training (Part 1) and in the last three set of trials (Part 2). Although the reduction of final error apparent in the *top 2 plots* labeled Part 1 and Part 2 does not correspond to a straightening of cursor motion, variability is reduced from Part 1 to Part 2.

Figure 3, *A* and *E* shows the learning trend for the whole population after 1 h of training without visual feedback on a single day (*A*) and after 4 days of training (*E*, dotted line). Subjects reduced the final error after training and this reduction was highly significant both across trials in day 1 of training [one-way ANOVA: $F(9,90) = 3.66$, $P = 0.001$] as well as across days and trial order within days [two-way ANOVA main effects by day: $F(3,200) = 31.64$; $P < 0.0005$; by trial order: $F(9,200) = 2.10$; $P = 0.031$]. Trends for individual subjects were very similar to the plots shown in Fig. 3, *A* and *E* (data not shown). No interaction effects reached statistical significance at the $P = 0.05$ level. Subjects clearly learned to make increasingly accurate movements of the cursor using hand motions that did not require ongoing visual feedback of cursor movement.

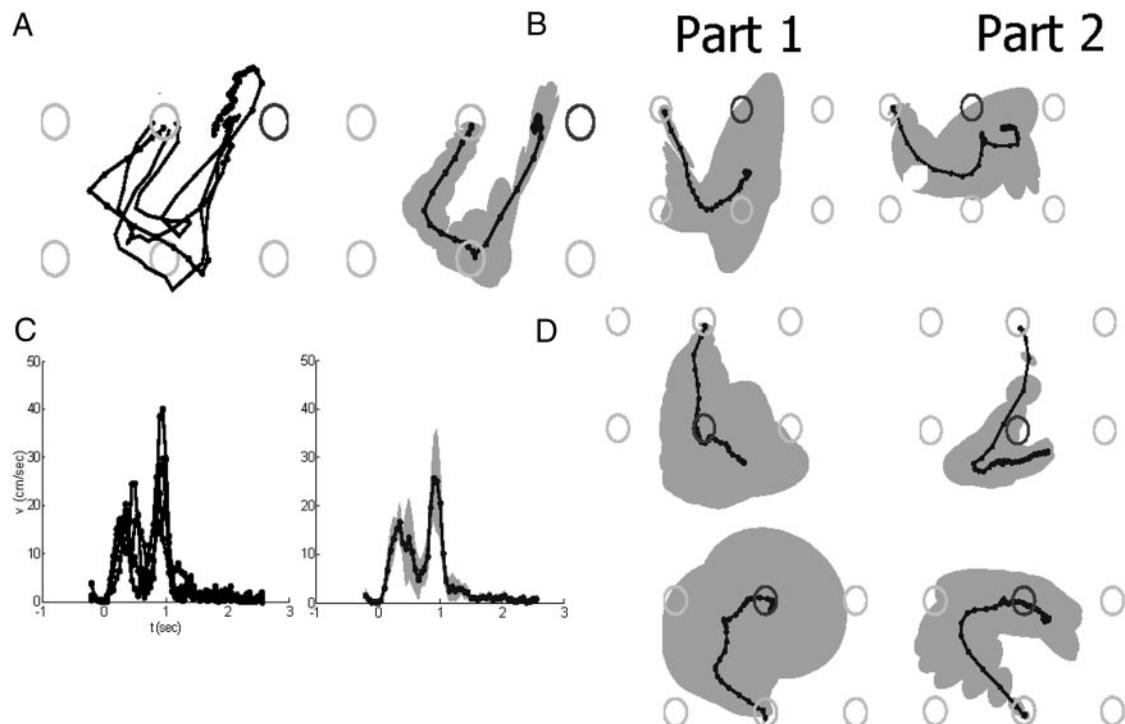


FIG. 2. Trajectories from a representative subject (S4 from group P1). *A* and *C*: 4 cursor trajectories and speed profiles obtained during movements toward the dark black circle in the first part of this single session experiment. *B* and *D*: corresponding average trajectories and speed profiles over this limited set of movements. Gray regions around each point in *B* are SD ellipses. *Right*: 6 plots show examples of average trajectories and SDs obtained in the first half of the experiment (Part 1, trials 1–5) and from the second half (Part 2, trials 6–10). Note the decrease in shaded area for similar movements from Part 1 to Part 2. Only the final target was visible to the subject during each movement.

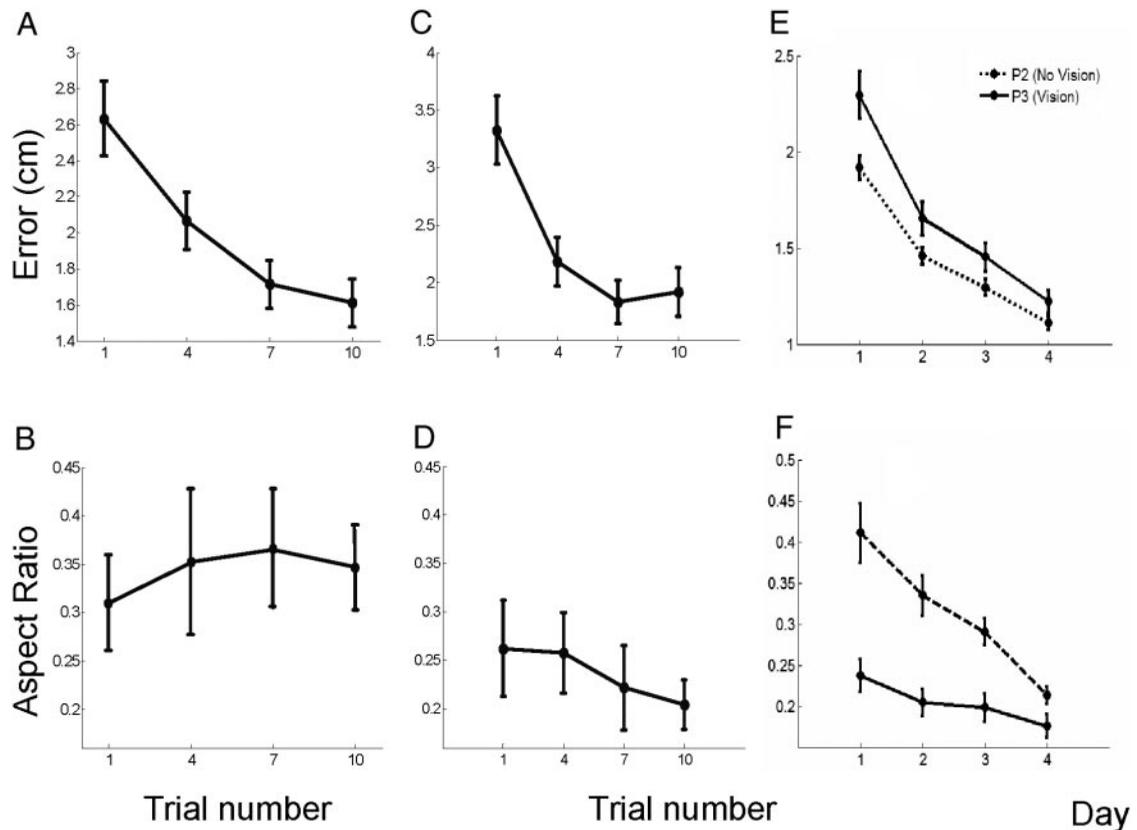


FIG. 3. Final error and trajectory linearity. Training without and with continuous visual feedback of movement leads to a progressive reduction in target reaching error. *A*: protocol P1 (No vision). Ensemble average of the final error over 10 subjects in a single (first) session of practice. *B*: protocol P1. Ensemble average of the linearity measure over 10 subjects in a single session of practice. *C*: protocol P3 (Vision). Ensemble average of the final error over 6 subjects in a single (first) session of practice. *D*: protocol P3. Ensemble average of the linearity measure over 6 subjects in a single (first) session of practice. Error (*E*) and linearity (*F*) over 4 days of practice. Each data point in these graphs was obtained from the ensemble average across 6 subjects in each group and across a whole session. Dotted lines: subjects in group P2 (No vision). Solid lines: subjects in group P3 (Vision). Error bars: 95% confidence intervals.

Training with vision

The six subjects in protocol P3 performed a set of training trials with continuous vision, alternated with test trials with no vision that were identical to those performed by P1 and P2 subjects. The learning results after 1 day (Fig. 3*C*) and 4 days (Fig. 3*E*) of practice were similar to those of subjects trained without vision. There was a significant and large decrease in final error within day 1 of training [one-way ANOVA: $F(3,20) = 4.90$; $P = 0.01$] and after 4 days of training and by trial order within days [two-way ANOVA main effects by day: $F(3,80) = 26.82$; $P < 0.0005$; by trial order: $F(3,80) = 9.86$; $P < 0.0005$]. No interaction effects reached statistical significance at the $P = 0.05$ level.

It is apparent that subjects in the P2 and P3 protocols showed a remarkably similar trend in error reduction (Fig. 3*E*): practicing with or without continuous visual feedback led to similar accuracy of the feed-forward movements. Subjects in the P3 protocol, however, had a slightly but significantly larger error than subjects in the P2 protocol for day 1 ($P = 0.026$). This initial lower performance may be explained by the fact that these subjects trained with continuous visual feedback, a condition different from the no-vision condition of the test trials. Also, note that learning did not appear to be complete at the end of the experiment because both P2 and P3 groups had large residual errors on the last day.

Linearity of cursor trajectories

The finding that subjects learned to bring the cursor closer to the target is not surprising and it is reported here merely to show that, albeit difficult, the task was learnable. The goal of this study is to observe changes in motor behavior that were not explicitly instructed.

Subjects in this study were not required to move the cursor along any specified trajectory. Earlier studies of planar, goal-directed reaching have shown that straight trajectories of the controlled endpoint—either the hand or a displayed cursor—are an invariant and spontaneous kinematic property of movements (Flash and Hogan 1985; Morasso 1981; Soechting and Laquaniti 1981). This characteristic is robust, being resistant to a broad range of physical and visuomotor perturbations (Dingwell et al. 2002; Flanagan and Rao 1995; Shadmehr and Mussa-Ivaldi 1994; Wolpert et al. 1995). Under the coordinate transformation used in this study, there was no intrinsic geometrical or mechanical constraint that would naturally induce straight-line cursor movements (see also Fig. 2). Indeed, after a single session of training without vision of the cursor (Fig. 3*B*), subjects did not tend toward straighter motions [ANOVA with trials as a factor: $F(9,90) = 0.21$, $P = 0.99$]. However, the linearity of cursor trajectories increased (and aspect ratio decreased) across days of training without ongoing visual feedback (Fig. 3*F*). For P2 subjects trained without visual feedback, two-way ANOVAs found a significant main effect by

day [$F(3,200) = 9.61$; $P < 0.0005$] but no main effect by trial order within days [$F(9,200) = 0.10$; $P > 0.9$].

P3 subjects, on the other hand, appear to show a trend toward more rectilinear cursor motions (Fig. 3D) after a single day of training, suggested by slightly smaller aspect ratio values (compare Fig. 3, B and D). This trend, however, is not statistically significant between the beginning and end of a 1-day session. Similar to the P2 subjects, P3 subjects demonstrated increasingly rectilinear cursor motions after 4 days of training (Fig. 3F) with no significant effect of trial order within days [two-way ANOVA main effects by day: $F(3,80) = 3.22$; $P = 0.027$; by trial order: $F(3,80) = 0.75$; $P = 0.525$]. The ensemble-averaged linearity measure follows a different trend over the 4 days of training in the two groups (P2 and P3, Fig. 3F): the subjects trained under the vision condition generate, on the whole, straighter movements. This is particularly evident in day 1, although the difference between the two groups is reduced by day 4.

In summary, extended training led to the generation of straighter and increasingly accurate motions in both groups. Furthermore, the presence of continuous visual feedback during movements enhanced the tendency toward straighter cursor motions. In contrast, continuous visual feedback of cursor motion did not appear to have an effect on learning to translate the desired cursor positions into postures of the hand.

Control of redundancy

Subjects learned to generate finger configurations that positioned the cursor at distinct target locations within the 2-D task space. In so doing, they became experts at solving the ill-posed problem (Hadamard 1902) of mapping a desired 2-D vector into a higher-dimensional signal vector: but did they also learn to partition the space of hand and finger

degrees of freedom into the combinations that are relevant to the task and those not relevant? We addressed this question by projecting the 19-D vector of glove signals into a 2-D task-relevant subspace (the “task” subspace) and its orthogonal (17-D) null space (see METHODS). We asked whether subjects learned with practice to reduce the amount of null- and task-space motions (Fig. 4). In the course of four sessions all P2 and P3 subjects reduced the amount of motion both in the null subspace and in the task subspace. For both subspaces, the amount of motion was smaller in P3 subjects who trained under continuous visual feedback. For null-space motion, two-way ANOVA found significant main effects comparing protocols [$F(1,92) = 6.08$; $P = 0.015$] and by comparing day 1 and day 4 within each protocol [$F(1,92) = 17.89$; $P < 0.0005$]. For task-space motion, use of two-way ANOVAs again found significant main effects by protocol [$F(3,80) = 18.30$; $P < 0.0005$] and by day [$F(3,80) = 11.95$; $P = 0.001$]. No interaction effects reached statistical significance at the $P = 0.05$ level for either analysis. The ratio of null-to-task motion was smaller for the P2 group. Two-way ANOVAs found significant main effects comparing protocols [$F(1,92) = 8.32$; $P = 0.005$] as well as days [$F(1,92) = 6.44$; $P = 0.013$]. The larger Null/Task ratio in subjects of the P3 group may reflect the stronger tendency of these subjects to produce straight movements of the cursor. On day 4, subjects trained with no vision made movements that were on average 26.5% longer in task subspace than movements by subjects trained with vision. In contrast, null-space motions by subjects training without vision on day 4 were only 12.7% longer than the null-space motion for P3 subjects. We conclude that continuous vision of cursor motion led to a smaller amount of unnecessary null-space motion and facilitated the tendency to make more rectilinear cursor trajectories, with a stronger influence on the latter effect.

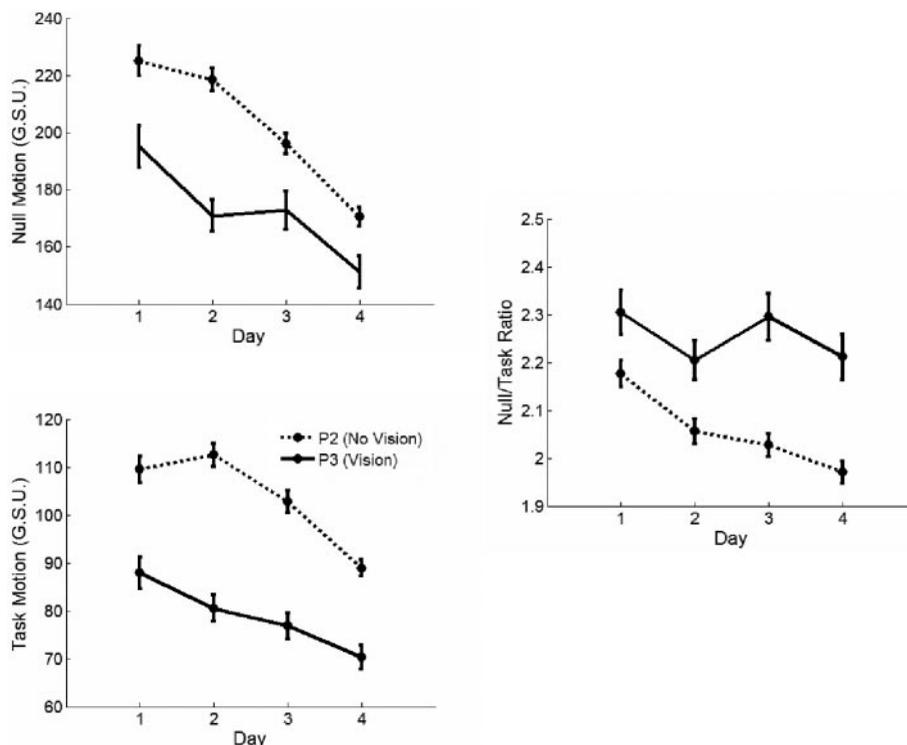


FIG. 4. Control of redundancy: length of movements. Trends over 4 days of practice. Each data point in these graphs was obtained from the ensemble average across 6 subjects in each group and across a whole session. Dotted lines: P2 subjects. Solid lines: P3 subjects. *Top left*: length of movements in the null subspace. *Bottom left*: length of movements in the task subspace. *Right*: ratio of null space length to task-space length.

Variability

Scholz, Schoner, and others (Latash et al. 2001; Scholz and Schoner 1999; Todorov and Jordan 2002) argued that, to obtain a more stable performance within a controlled manifold, the nervous system may transfer as much variance as possible to degrees of freedom orthogonal to that manifold (i.e., the uncontrolled manifold). In our case, the controlled and uncontrolled manifolds correspond to the task and null subspaces, respectively. Todorov and Jordan (2002) further formalized this concept and proposed that an optimal control law takes advantage of redundancy by increasing variability in task-irrelevant dimensions to decrease variability in the task-relevant dimensions. Optimal feedback control, as proposed by these authors, is consistent with a “minimum intervention principle,” according to which the “deviations from the average trajectory are corrected only when they interfere with task performance” (Todorov and Jordan 2002). In our case, task performance is, by construction, measured by final accuracy. Although one cannot rule out that a subject might be following some implicit, self-imposed task, the explicit instructions and “knowledge of results” feedback were strictly confined to the accuracy of reaching. A minimum intervention principle predicts that movement variability is maximal at some point between the initial and final targets so that accuracy of the final position may be achieved. Our data are only partially consistent, if at all, with such hypotheses.

The plots in Figure 5A show the average cursor trajectories between two targets executed by one subject—S11 of the P2 group—in four subsequent days. The shadowed areas around the mean trajectories are generated by the SD ellipsoids. The two plots in Fig. 5C show, for the same movements, the norm of the average SD (i.e., the largest eigenvalue of the 2×2 SD matrix) and the average velocity profile, versus normalized

time (see METHODS). Because subjects were required to maintain the cursor in a small area around the starting target before a new target was presented, the variability is minimal at the beginning of the movement. It is apparent that the SD decreases across subsequent days of training. Perhaps consistent with the minimum intervention hypothesis, the variability on days 2 and 4 peaks midway between onset and termination of movement. Figure 5, B and D shows the ensemble-averaged trajectories and variability profiles, for the same movement, across the entire group of P2 subjects. The group data display the same trend of decreased variability on subsequent days. Similar observations were obtained when all movements were considered for both P2 and P3 groups. Multivariate and subsequent one-way ANOVAs found significant effect across days on the cursor variability [$F(3,20) = 6.33$; $P < 0.003$] but not cursor speed [$F(3,20) = 0.50$; $P < 0.689$] for P2 subjects. P3 subjects demonstrated a similar effect of training across days on cursor variability [$F(3,20) = 4.96$; $P < 0.01$], with no significant change in cursor speed across days [$F(3,20) = 0.10$; $P < 0.961$].

We also derived the temporal profiles of SD about the average glove signal trajectory through glove, task, and null spaces for all movements and all P2 and P3 subjects (Fig. 6). The trend toward reduction of variability from day 1 to day 4 is particularly evident for null-space motion, which is not consistent with the hypothesis that subjects learn to shift the movement variance to degrees of freedom that do not contribute to task performance. On the contrary, all the results of our experiment suggest that subjects learn to generate less-variable trajectories, with a decreased amount of variance as training proceeds. Note that, although the task-space projections of the glove signals (which correspond to the cursor motions) have very little variance at the start of movement, the glove signals

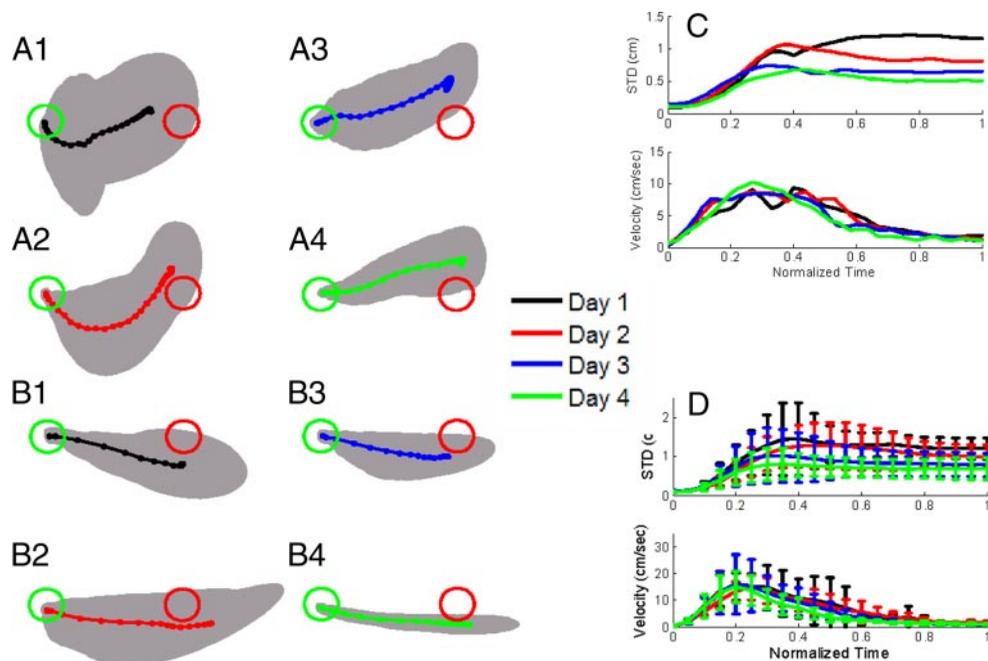


FIG. 5. Analysis of variability: cursor. A1, A2, A3, A4: average trajectories between 2 targets from one subject (S11) in 4 consecutive days. Different colors are different days. Shaded areas are SD ellipsoids about each point. B1, B2, B3, B4: average trajectories between 2 targets from all subjects in the P2 group in 4 consecutive days. C, top: norm of the SD for the 4 movements in the A plots vs. normalized movement time (see METHODS). Bottom: speed profiles for the same 4 movements vs. normalized time. D, top: ensemble averages over P2 subjects of the norm of the SD for the 4 movements in the B plots vs. normalized movement time. Bottom: Ensemble averages over P2 subjects of the speed profiles for the same 4 movements vs. normalized time. Error bars are 95% confidence intervals.

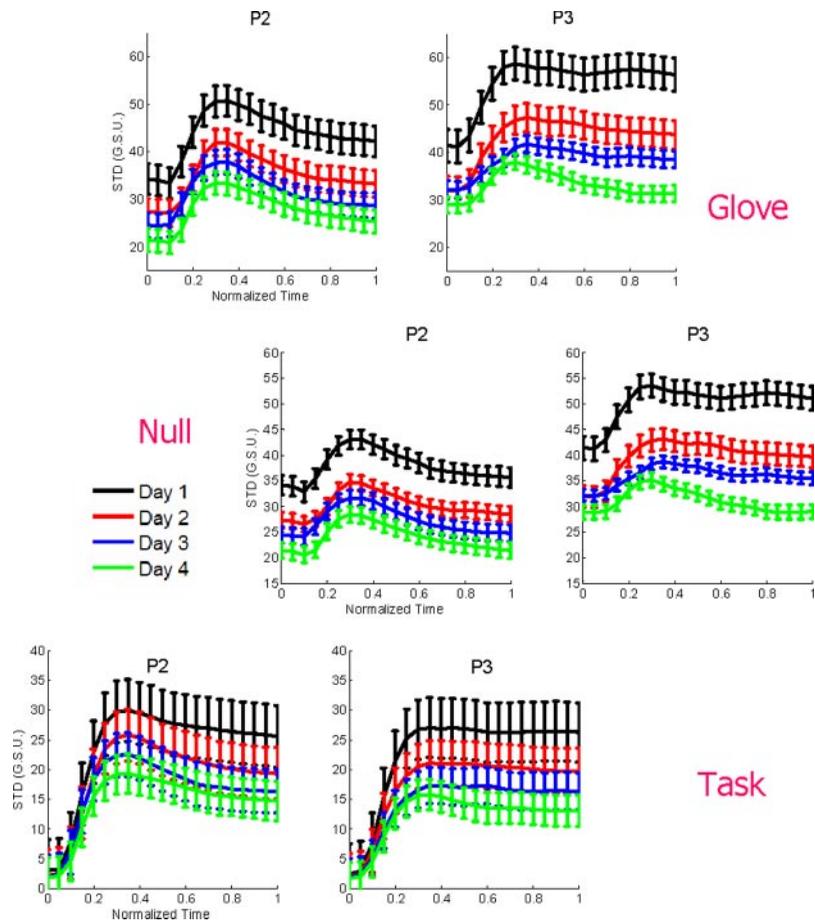


FIG. 6. Analysis of variability: glove signals. Cumulative analysis for all movements. Colors represent different days. Each trace was obtained from the average across all data from all subjects in a group and all movements in each day. *Top*: total glove signals. *Middle*: null-subspace projections. *Bottom*: task subspace projections. *Left*: P2 subjects. *Right*: P3 subjects. Error bars are 95% confidence intervals.

and their null-space projections have a significant amount of initial variance. Initial task-space variance is only 5 to 10% of initial null-space variance compared across days. This initial variance is regularly and almost uniformly decreasing from day 1 to day 4. Multivariate ANOVA found significant effect of both protocol and days of training for both final null- and task-space variability. Subsequent two-way analyses found significant effect of both protocol [$F(1,40) = 17.96$; $P < 0.0005$] and days of training [$F(3,40) = 8.43$; $P < 0.0005$] for final null-space variance, with variability considerably higher when subjects were provided with continuous visual feedback during training, and variability decreasing across days of training. Two-way ANOVA also found a similar, significant effect of days of training [$F(3,40) = 3.05$; $P < 0.039$] for final task-space variance, but no effect of protocol was observed [$F(1,40) = 0.61$; $P < 0.440$]. Because the initial variance is associated with hand configuration at the starting target, its reduction indicates the tendency to form a consistent inverse map from screen positions to hand configurations, thus effectively reducing the degree of redundancy associated with the reaching task.

One finding that appears consistent with the minimum-intervention principle is that the null-space variability is pronounced about midway through motions made by P2 subjects. These movements are “open-loop” in the sense that subjects do not receive feedback of cursor motion during movement. Any variation in the path and timing of movements may be responsible for the increased variability in the middle of movement. In contrast, subjects who trained with continuous visual feed-

back generated a more uniform variance along the movement, although a maximum of variability also appears in the null-space motion of P3 subjects on day 4.

In summary, subjects showed a tendency to distribute variance of motion in a nonuniform way along the movement. In particular, we found evidence that variance in some instances reached a peak midway between start and end position, consistent with the minimum intervention principle of Todorov and Jordan (2002). However, at the same time subjects learned through practice to reduce the amount of variability both in the task and in the null subspaces with extended training. Taken together, our data reveal the mutual presence of two trends, which need not to be in reciprocal contrast: on one hand, subjects learned to produce more regular and rectilinear trajectories, consistent with the development of a representation of the space in which the cursor moved. This is demonstrated by the general reduction of variability across days. On the other hand, subjects—particularly those who trained without visual feedback—also had a tendency to allow a somewhat greater variability of movement between initial position and end target.

Generalization

We explored how learning of a novel geometrical environment generalizes beyond the trained task-space targets in a fourth set of experiments. Subjects practiced movements over a set of four targets and were tested over two different sets of three targets (Fig. 1). One set of test trajectories, the “interpolation” set, was included within the region of the training

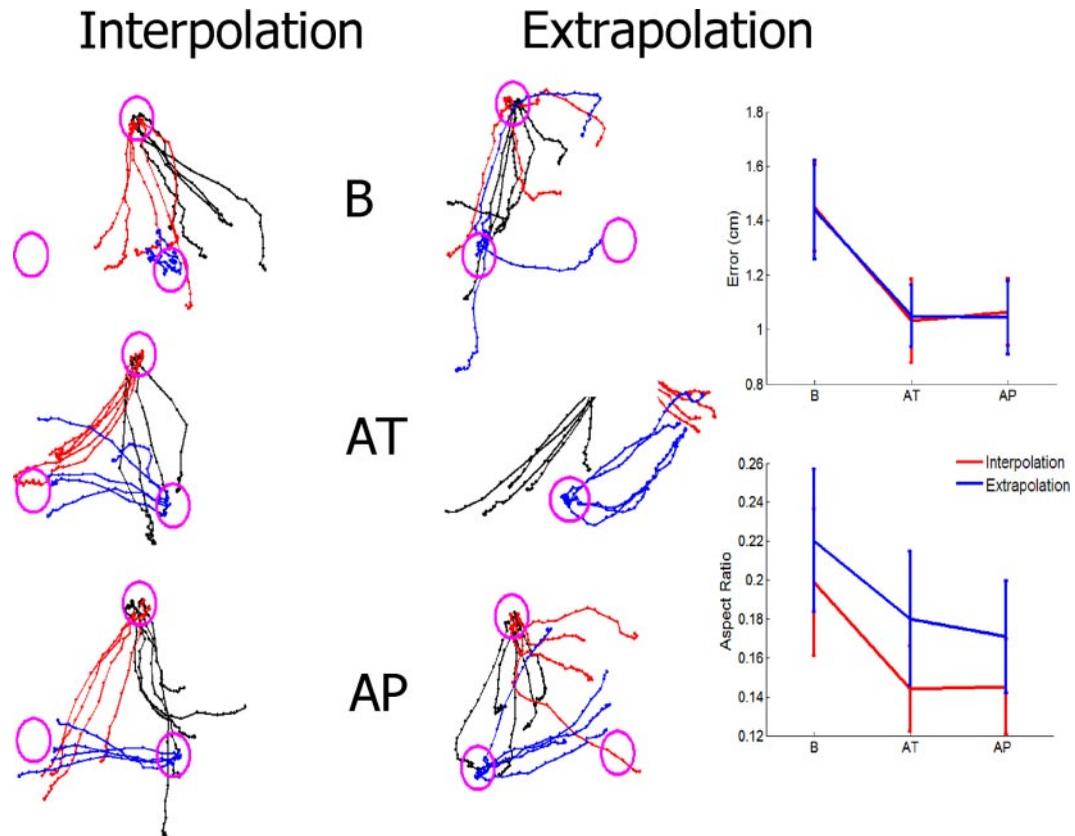


FIG. 7. Generalization experiment. *Left and middle*: examples of cursor trajectories from one subject, G10. In each pane, trajectories with the same colors have the same start and end targets. Interpolation (*left*) and extrapolation (*right*) trajectories are plotted in the baseline (B) phase, immediately after training (AT) over the training targets, and after a 6-h pause (AP). *Right*: error (*top*) and aspect ratio (*bottom*) averaged across subjects and movements in each phase. Red lines refer to the interpolation targets and blue lines to the extrapolation targets. Error bars are 95% confidence intervals.

trajectories; the other set, the “extrapolation” set, was external to the training region. Subjects performed a set of baseline (B) trials at the beginning of the experiment. Immediately after training (AT), the average final errors were significantly reduced for both the interpolation and the extrapolation targets (Fig. 7) and the learning persisted across a 5- to 6-h pause (AP). Multivariate ANOVA found significant effect of training period (B, AT, AP) on both final error and aspect ratio with no significant difference in performance between interpolation and extrapolation. Subsequent ANOVA and Tukey *t*-test found significant reduction in endpoint error with practice when tested over novel targets [$F(2,39) = 9.33$; $P < 0.0005$] with no significant difference between performance immediately after training and after a 6-h pause. A similar reduction in aspect ratio was observed: ANOVA and Tukey *t*-test found significant reduction in aspect ratio over novel targets [$F(2,39) = 3.61$; $P < 0.037$] with no significant difference between performance immediately after training and after a 6-h pause. Thus the pattern of learning observed in this study is not limited to the set of targets over which subjects were trained, but extends over a wider region of space.

DISCUSSION

We have developed a novel experimental paradigm in which subjects must reorganize finger coordination to control the positioning of a cursor on a computer screen. Subjects successfully learned this task by mapping target screen locations into

finger postures. This learning generalized within the trained region of the task space, as well as to targets outside the trained region. Because of the high degree of kinematic redundancy in our task, this is an example of a solution to an ill-posed problem (Hadamard 1902; Tikhonov and Arsenin 1977). Remarkably, subjects developed more rectilinear cursor trajectories with extended practice. This tendency was clearly enhanced by training with continuous visual feedback of cursor motion. Furthermore, the temporal trend of the final error was considerably different from the temporal trend of linearity: the substantial and significant reduction of final error that was observed in the first session was not matched by a corresponding straightening of the trajectories, which took place only across multiple sessions. Thus the adaptive modification of cursor trajectory was not guided by the pattern of final errors and of subsequent corrections.

Studies of reaching arm movements have revealed a consistent tendency of subjects to generate straight trajectories of the hand (Flash and Hogan 1985; Morasso 1981; Soechting and Laquaniti 1981; Viviani and Terzuolo 1980). Other studies (Flanagan and Rao 1995; Wolpert et al. 1995) have demonstrated, as shown here, a tendency to produce rectilinear movements of a controlled endpoint, in the presence of a map that alters the relation between movement of the hand and movement of the controlled cursor. In particular, Flanagan and Rao (1995) considered a map in which subjects were presented with a Cartesian display of the shoulder and elbow angle. With practice, subjects learned to enforce rectilinear motions in joint

space at the expense of curvilinear movements of the hand. Rectilinear endpoint movements may reflect a strategy of trajectory planning by the CNS, which has been modeled mathematically through the optimization of smoothness (Flash and Hogan 1985; Hogan 1984). Alternative accounts have also been proposed, based on optimization of dynamical criteria (Uno et al. 1989) and of final error in the presence of signal-dependent noise (Harris and Wolpert 1998). But what is the functional value of straightness of the hand path or, more generally, of endpoint motions? To address this question, we observe that the physical space in which endpoint movements take place has a fundamental property, summarized by the concept of Euclidean symmetry (Goldstein 1980; Weyl 1966). This reflects the fact that space is effectively a container of rigid bodies whose size is invariant by translations and rotation. The essential primitive of Euclidean symmetry is the straight segment (the path with minimum Euclidean length between any two points). The tendency to generate straight reaching movements makes sense from a functional perspective, because living organisms must ultimately be proficient at operating inside the Euclidean geometry of ordinary space.

The novel and arbitrary linear mapping used to transform glove signals into cursor locations allowed us to examine how the CNS learns to represent and control the redundant transformation from hand to cursor space, without the confounding effects of previously experienced movements. Other studies have proposed to resolve redundancy by decomposing movement variables into null-space and controlled variables, typically through some form of the generalized inverse. For example, the concept of controlled and uncontrolled manifolds used by Scholz and Schöner (1999) is, in fact, an application of the generalized inverse. Generalized inverses have been familiar for a long time to robotic researchers investigating the control of kinematically redundant manipulators (Baillieul 1985; Baker and Wampler 1988; Burdick 1989; Klein and Huang 1983). They allow one to regularize the inversion of ill-conditioned linear maps by minimizing a quadratic form (Ben-Israel and Greville 1980). In particular, for an underconstrained linear transformation, the Moore–Penrose pseudoinverse finds a unique inverse map that satisfies the additional requirement of minimizing the (Euclidean) norm of the solution vector among infinite alternatives. It has been well established that this type of operation fails to produce repeatable (or, more technically, integrable) motions when applied in differential form to nonlinear kinematic transformations, as for example, in attempting to invert the transformation from joint angles to endpoint coordinates of a redundant arm (Klein and Huang 1983; Mussa-Ivaldi and Hogan 1991; Shamir and Yomdin 1988). This is a rather important issue that has often been overlooked in studies of biological motor control. However, this issue does not affect our investigation because we use a linear transformation from glove to screen coordinates. In our case, the pseudoinverse generates a family of regular inverse solutions. The map we use has the property of affine transformations in that it maps straight lines into straight lines. Because hand configurations and glove signals are related by a nonlinear isomorphism, rectilinear motions of the cursor on the monitor are not compatible with rectilinear motions in the space of finger-joint coordinates. However, the generation of well-behaved inverse maps from desired screen coordinates to finger configurations circumvents the challenge to derive a

repeatable inverse map that would be associated with a nonlinear map from glove signals to screen coordinates. The investigation of how more complex maps may be learned is deserving of a separate study.

The null space generated by our glove-cursor map had effectively 17 dimensions ($19 - 2$). We observed a marked tendency of subjects to reduce the amount of motion in this null space (Fig. 4). The selective reduction of null-space motion is particularly important because it may reveal how the Euclidean metric of the task space (the monitor) is effectively “imported” into the coordination of hand. The tendency to generate finger motions with smaller null-space components suggests that the movements tend to remain confined to subspaces that are minimum-norm images of the cursor space. This observation provides us with further evidence that the motor system is effectively capturing the metric structure of the controlled space and that it uses this metric as a basis to form coordinated motions of the fingers.

It is possible that the tendency to produce straighter trajectories arises as a result of the presence of implicit intermediate points, which subjects place between targets when training with continuous feedback. These intermediate positions (akin to a “desired trajectory”) might be preserved when movements are executed without continuous visual feedback. This is unlikely, however, because a generic inverse map from cursor positions to hand gestures is not sufficient to induce rectilinear motions: nearby cursor positions can map into radically different finger configurations. Instead, we have observed a general tendency of subjects to reduce the amount of finger motion (Fig. 4), again suggesting that they are learning trajectories, not just final positions or by points.

Our data also show a strong and progressive decrease of movement variability from day to day along the entire motion. This is in sharp contrast with the hypothesis that, through practice, subjects learn to export increasing amounts of variability into the null space to achieve a less-variable task execution. Because this hypothesis has supporting evidence in a variety of natural tasks (Balasubramaniam et al. 2000; Cole and Abbs 1986; Latash et al. 2001), it is possible our finding stems from the unusual nature of the task at hand. Under such novel conditions, the control system may be mostly concerned with formation of an internal model of the metric properties of task space—consistent with increasingly repeatable performance and trajectories.

Another factor that could contribute to our findings stems from the well-documented presence of synergies and of biomechanical couplings among fingers (Lang and Schieber 2004; Schieber 1991; Zatsiorsky et al. 2000). For example, Zatsiorsky et al. (2000) described the tendency of fingers to generate forces as a consequence of activation in other fingers, a phenomenon that was described as “enslaving.” In other studies, Soechting and coworkers (Jerde et al. 2003; Santello et al. 1998) demonstrated that a small number of principal components can account for much of the variance in postures and movements of the hand during fingerspelling and other tasks. To the extent that the patterns of synergy and coupling that are present in natural tasks are preserved in a new mapping, one may expect to see that a reduction of variability in task coordinates would be mirrored by a similar reduction in null-space coordinates.

Our results parallel, in part, patterns of motor learning observed in primates whose motor cortical activities controlled a cursor on a computer screen by a brain-machine interface (BMI) (Serruya et al. 2002; Taylor et al. 2002). In both cases, the nervous system must learn to select the degrees of freedom that are most relevant to the desired movement. By controlling the amount of dimensionality reduction, our paradigm allows us to explore by simple and noninvasive means the mechanisms by which feed-forward control of a highly redundant system is reorganized when presented with a novel coordinate transformation. An important difference between our experimental conditions and the operation of a BMI is the presence of proprioception of hand configuration for subjects engaged in our task. There is no such sensory input for the neural activities in a population of the cerebral cortex. Although proprioceptive information certainly facilitates the task of creating a new map, it may not be necessary for map formation because in both cases the neural controller must reorganize the natural pattern of commands and activities to cope with a novel geometrical environment.

An unavoidable limit of this study stems from the use of only one particular type of hand-to-screen mapping. Understanding in more general terms the impact of this mapping on motor learning and performance is an important goal for future studies. This is a difficult problem because, even in the simple case presented here, the space of possible linear maps is spanned by 38 parameters. However, the same hand postures were used at different screen coordinates in the learning and generalization experiments and thus the resulting maps differed. Nevertheless we observed similar learning trends in the two experiments; thus the learning of rectilinear movements is not contingent on one particular hand-to-screen mapping.

ACKNOWLEDGMENTS

We are grateful to C. Ghez, K. Lynch, L. Miller, and to the anonymous reviewers for many insightful comments.

GRANTS

This work was supported by National Institutes of Health Grants NS-35673 and R24 HD-39627, National Science Foundation Grant 0238442, Whitaker Grant RG010157, and by the Falk Medical Research Trust.

REFERENCES

- Baillieul J.** Kinematic programming alternatives for redundant manipulators. *Proc IEEE Int Conf Robot Autom* 722–728, 1985.
- Baker DR and Wampler CW.** On the inverse kinematics of redundant manipulators. *Int J Robot Res* 7: 3–21, 1988.
- Balashramaniam R, Riley MA, and Turvey MT.** Specificity of postural sway to the demands of a precision task. *Gait Posture* 11: 12–24, 2000.
- Ben-Israel A and Greville TNE.** *Generalized Inverses: Theory and Application*. New York: Wiley, 1980.
- Bernstein N.** *The Coordination and Regulation of Movement*. Oxford, UK: Pergamon Press, 1967.
- Box GEP and Cox DR.** An analysis of transformations. *J R Stat Soc Ser B* 26: 211–246, 1964.
- Burdick JW.** On the inverse kinematics of redundant manipulators: characterization of the self-motion manifolds. *Proc 1989 IEEE Int Conf Robot Autom* 264–270, 1989.
- Cole KJ and Abbs JH.** Coordination of three-joint digit movements for rapid finger-thumb grasp. *J Neurophysiol* 55: 1407–1423, 1986.
- Dingwell JB, Mah CD, and Mussa-Ivaldi FA.** Manipulating objects with internal degrees of freedom: evidence for model-based control. *J Neurophysiol* 88: 222–235, 2002.
- Flanagan JR and Rao AK.** Trajectory adaptation to a nonlinear visuomotor transformation: evidence of motion planning in visually perceived space. *J Neurophysiol* 74: 2174–2178, 1995.
- Flash T and Hogan N.** The coordination of arm movements: an experimentally confirmed mathematical model. *J Neurosci* 5: 1688–1703, 1985.
- Goldstein H.** *Classical Mechanics*. Reading, MA: Addison-Wesley, 1980.
- Goodale MA and Milner AD.** Separate visual pathways for perception and action. *Trends Neurosci* 15: 20–25, 1992.
- Hadamard J.** Sur les problèmes aux dérivées partielles et leur signification physique. *Princeton Univ Bull* 49–52, 1902.
- Harris CM and Wolpert DM.** Signal-dependent noise determines motor planning. *Nature* 394: 780–784, 1998.
- Hatfield G.** Representation and constraints: the inverse problem and the structure of visual space. *Acta Psychol* 114: 355–378, 2003.
- Hogan N.** An organizing principle for a class of voluntary movements. *J Neurosci* 4: 2745–2754, 1984.
- Jerde TE, Soechting JF, and Flanders M.** Biological constraints simplify the recognition of hand shapes. *IEEE Trans Biomed Eng* 50: 265–269, 2003.
- Klein CA and Huang CH.** Review of pseudoinverse control for use with kinematically redundant manipulators. *IEEE Trans Syst Man Cybern* 13: 245–250, 1983.
- Lang CE and Schieber MH.** Human finger independence: limitations due to passive mechanical coupling versus active neuromuscular control. *J Neurophysiol* 92: 2802–2810, 2004.
- Latash ML, Scholz JF, Danion F, and Schoner G.** Structure of motor variability in marginally redundant multifinger force production tasks. *Exp Brain Res* 141: 153–165, 2001.
- Milner AD and Goodale MA.** Visual pathways to perception and action. *Prog Brain Res* 95: 317–337, 1993.
- Morasso P.** Spatial control of arm movements. *Exp Brain Res* 42: 223–227, 1981.
- Mussa-Ivaldi FA and Hogan N.** Integrable solutions of kinematic redundancy via impedance control. *Int J Robot Res* 10: 481–491, 1991.
- Rossetti Y.** Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Conscious Cogn* 7: 520–558, 1998.
- Santello M, Flanders M, and Soechting JF.** Postural hand synergies for tool use. *J Neurosci* 18: 10105–10115, 1998.
- Schieber MH.** Individuated movements of rhesus monkeys: means of quantifying the independence of digits. *J Neurophysiol* 65: 1381–1391, 1991.
- Scholz JP and Schoner G.** The uncontrolled manifold concept: identifying control variables for a functional task. *Exp Brain Res* 126: 289–306, 1999.
- Serruya MD, Hatsopoulos NG, Paninski L, Fellows MR, and Donoghue JP.** Instant neural control of a movement signal. *Nature* 416: 141–142, 2002.
- Shadmehr R and Mussa-Ivaldi FA.** Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14: 3208–3224, 1994.
- Shamir T and Yomdin Y.** Repeatability of redundant manipulators: mathematical solution of the problem. *IEEE Trans Autom Contr* 33: 1004–1009, 1988.
- Shepard RN.** Perceptual-cognitive universals as reflections of the world. *Behav Brain Sci* 24: 581–601, 2001.
- Soechting JF and Laquaniti F.** Modification of trajectory of a pointing movement in response to a change in target location. *J Neurophysiol* 49: 548–564, 1981.
- Taylor DM, Tillery SI, and Schwartz AB.** Direct cortical control of 3D neuroprosthetic devices. *Science* 296: 1829–1832, 2002.
- Tikhonov AN and Arsenin VY.** *Solutions of Ill-posed Problems*. Washington, DC: W. H. Winston, 1977.
- Todorov E and Jordan MI.** Optimal feedback control as a theory of motor coordination. *Nat Neurosci* 5: 1226–1235, 2002.
- Uno Y, Kawato M, and Suzuki R.** Formation and control of optimal trajectory in human multijoint arm movement. *Biol Cybern* 61: 89–101, 1989.
- Viviani P and Terzuolo CA.** Space-time invariance in learned motor skills. In: *Tutorials in Motor Behaviour*, edited by Stelmach GE and Requin J. Amsterdam: North-Holland, 1980, p. 525–533.
- Weyl H.** *Symmetry*. Princeton, NJ: Princeton Univ. Press, 1966.
- Wolpert DM, Ghahramani Z, and Jordan MI.** Are arm trajectories planned in kinematic or dynamic coordinates? An adaptation study. *Exp Brain Res* 103: 460–470, 1995.
- Zatsiorsky VM, Li ZM, and Latash ML.** Enslaving effects in multi-finger force production. *Exp Brain Res* 131: 187–195, 2000.