

Independent learning of internal models for kinematic and dynamic control of reaching

John W. Krakauer¹, Maria-Felice Ghilardi^{2,3} and Claude Ghez³

¹ Department of Neurology, Columbia University College of Physicians and Surgeons, 630 West 168th Street, New York, New York 10032, USA

² INB-CNR, Milan, Italy

³ Center for Neurobiology and Behavior, N.Y.S. Psychiatric Institute, Columbia University, College of Physicians and Surgeons, 1051 Riverside Drive, New York, New York 10032, USA

Correspondence should be addressed to C.G. (cpgl@columbia.edu)

Psychophysical studies of reaching movements suggest that hand kinematics are learned from errors in extent and direction in an extrinsic coordinate system, whereas dynamics are learned from proprioceptive errors in an intrinsic coordinate system. We examined consolidation and interference to determine if these two forms of learning were independent. Learning and consolidation of two novel transformations, a rotated spatial reference frame and altered intersegmental dynamics, did not interfere with each other and consolidated in parallel. Thus separate kinematic and dynamic models were constructed simultaneously based on errors computed in different coordinate frames, and possibly, in different sensory modalities, using separate working-memory systems. These results suggest that computational approaches to motor learning should include two separate performance errors rather than one.

In reaching for objects around us, neural processing transforms visuospatial information about target location into motor commands to specify muscle forces and joint motions that move the hand to the desired location^{1,2}. In reaching movements, extent and direction have different sources of variable³ and systematic errors^{4–6}, suggesting that hand paths are initially planned in vectorial coordinates without taking account of the joint motions⁷. The movement vector is specified as an extent and direction from the initial hand position. Kinematic accuracy depends on learning a scaling factor from errors in extent and reference axes from errors in direction⁸. The learning of new reference axes shows limited generalization⁸ and is coded in extrinsic coordinates (J.W.K., Z. Pine and C.G.; in preparation)^{9,10}. Finally however, vectorial information needs to be transformed into muscle forces for movement to take place. This transformation needs to take account of the biomechanical properties of the moving arm, notably the interaction torques produced at each joint by motions of all the limb segments^{11,12}. The capacity to anticipate these dynamic effects is understood to depend on learning an internal model^{13,14} of musculoskeletal dynamics and of other forces acting on the limb. Proprioceptive feedback is critical for developing dynamic models: in patients with large-fiber sensory neuropathy who lack proprioception, reaching movements show characteristic abnormalities in their trajectories and endpoints. The errors, which vary with movement direction, arise because feed-forward commands to muscles are no longer adapted to the movement-dependent torques resulting from intersegmental interactions^{15–17}. Correspondingly, a proprioceptively deafferented patient that we studied is unable to learn the altered inertial configurations with or without visual feedback (Virji-Babul *et al.*, *Soc. Neurosci. Abstr.* 23, 202, 1997). In contrast, similar

patients can learn the spatial transformations needed for mirror drawing¹⁸. Like learning a novel reference frame, learning of novel dynamics generalizes poorly across directions^{14,19} but is coded in intrinsic rather than Cartesian coordinates^{13,20}. Thus, psychophysical evidence suggests that the coordinate systems and the sensory signals used to learn new internal kinematic models differ from those used to learn new internal models of intersegmental dynamics.

Various computational approaches to motor learning also use sensory feedback about movement errors to train internal models. However, such approaches do not distinguish explicitly between the kinematic and dynamic errors that train internal models, or between the sensory channels that might carry the relevant information²¹.

A series of studies demonstrates consolidation and interference in motor learning^{22,23}: when subjects adapt to a velocity-dependent rotatory force-field acting at the hand, performance improves more rapidly in relearning the same task the next day (consolidation). This improvement did not occur if subjects practiced moving in a second force field rotating in the opposite direction within six hours of learning the first (interference). Learning is thought to take place initially within local regions of cortex in short-term working memory, whereas consolidation involves the redistribution of learned information to other regions for long-term memory storage²³. Interference presumably occurs because a second set of associative pairs competes with the first for limited working-memory space and cancels it²⁴.

To determine whether the learning of hand kinematics and limb dynamics make use of separate working memory systems, we examined consolidation and interference in adapting to novel spatial and inertial perturbations. If the two processes are distinct,

learning novel dynamics should not interfere with the consolidation of a previously learned kinematic transformation. Moreover, it should be possible to learn novel kinematics and dynamics in parallel.

In one task, subjects learned to move their hands to a series of targets while feedback of the hand movements was rotated counterclockwise (CCW) by 30° around the origin, thus requiring subjects to learn a rotated spatial reference frame for kinematic planning.

In the other, subjects learned to move to the same targets when the inertial configurations of their arms were altered by attaching a 1.5-kg mass 25 cm lateral to the forearm¹⁴. This manipulation altered inertial interactions at the elbow and required subjects to learn new internal models of the intersegmental dynamics of their limbs¹⁴. The results demonstrate that the learning of spatial and dynamic models occurs through independent channels.

RESULTS

Learning a rotated reference frame

On each of two successive days, two groups of subjects (1 and 2, see Table 1) learned to move a cursor to a series of targets while the display of their hand path on a computer monitor was rotated CCW by 30°. Typical cursor paths produced when subjects were first exposed to the 30° CCW rotation and at the end of the first day's session are shown in Fig. 1a. During the first cycle, clockwise directional errors equal in magnitude to the imposed rotation are apparent for all eight target directions. These errors were reduced rapidly at first and more slowly thereafter. The time course of the reduction over the training block was well fit by a double exponential function ($r^2 = 0.91$ for group 1 and 0.84 for group 2).

Table 1. Experimental Conditions

Group	Day 1 Training	Day 2 Training
Group 1	30° CCW rotation	30° CCW rotation
Group 2	30° CCW rotation → 30° CW rotation	30° CCW rotation
Group 3	Lateral mass*	Lateral mass*
Group 4	Lateral mass* → medial mass*	Lateral mass*
Group 5	30° CCW rotation → lateral mass*	30° CCW rotation
Group 6	30° CCW rotation plus lateral mass	30° CCW rotation plus lateral mass

* No visual feedback

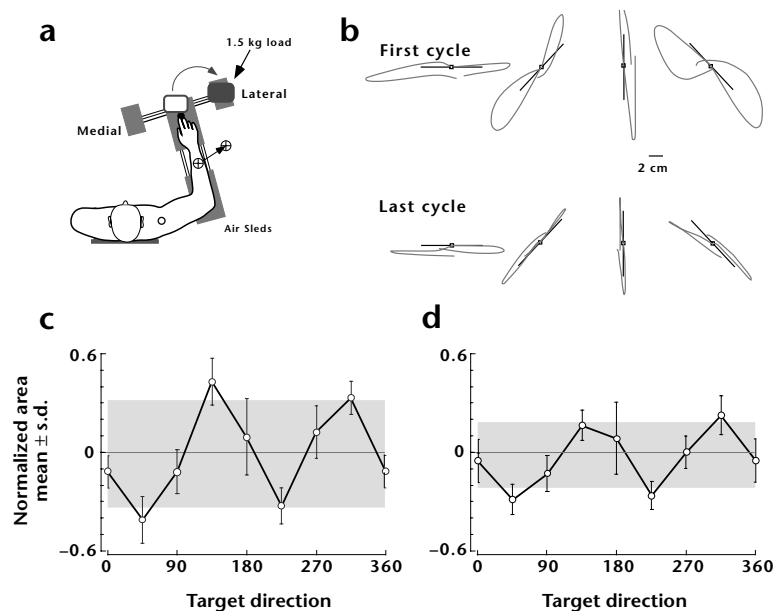
Consistent with prior observations showing local learning of rotations^{8,20}, errors were not reduced over successive targets within each cycle ($r = 0.03$; NS for first 5 cycles), but were reduced only over successive cycles (3.8° per cycle; $r = 0.46$; $p < 0.0001$ for first 5 cycles). Group 2 learned a 30° clockwise rotation 5 minutes after counter-clockwise training. Both groups were retrained 24 hours later, and performance on the 2 days was compared.

Without additional practice between days, group 1 showed substantial retention of the learning achieved on day 1 (Fig. 1b). The mean directional error during the first cycle of movements on day 2 was significantly lower than on the first cycle on day 1 ($17.4 \pm 7.3^\circ$ versus $25.2 \pm 5.2^\circ$), and over cycles 2 and 3, the mean directional error did not differ significantly from the mean error on the last two cycles of day 1 (Fig. 1c). Thus contextual cues, presumably consisting of mismatch between the expected and actual motion of the cursor during the first cycle of movements, provided subjects with the information needed to recall the reference frame they had learned

Fig. 1. Kinematic learning: consolidation and interference. (a) Representative screen-cursor paths for subject SD who experienced the 30° CCW rotation for the first time (cycle 1) and at the end of training (cycle 33). For clarity, in the first cycle, the eight targets are divided into four sets of two targets. (b, d) Learning curves for group 1 and 2. The mean directional error per cycle is plotted against cycle number during the training block on days 1 and 2. Points are means across subjects and fitted to a double exponential function. Gray represents learning on day 1 and black represents learning on day 2. The dashed line represents mean subject performance at the end of the baseline familiarization block. The larger points represent the cycles used in the statistical analyses in c and e. (c, e) Bar charts for Group 1 and 2 showing the mean directional error for the last baseline block (BSL, hatched bar), cycles 2 and 3 (First), and cycles 32 and 33 (Last) on day 1 (gray bars) and day 2 (white bars). Significant differences were found across baseline, day 1 and day 2 (Group 1, ANOVA $F_{4,25} = 31.39$; $p < 0.0001$; Group 2, ANOVA $F_{4,25} = 18.34$; $p < 0.0001$). The horizontal lines indicate significant comparisons at post-hoc analysis.



Fig. 2. Dynamic learning is characterized by reduction in direction-dependent errors. (a) Apparatus for training subjects with a medial or lateral mass. (b) Representative cursor paths for subject AV when he experienced the lateral mass for the first time (cycle 1) and at the end of training (cycle 33). For clarity, the eight targets are divided into four sets of two targets. (c, d) Mean normalized area per target for group 3 subjects over the first (c) and last (d) four cycles on day 1. Error bars represent standard deviations per target across subjects. The gray area represents the standard deviation of the mean error for each target over the target cycle and reflects an error in adapting motor commands to directional changes in inertial dynamics.



on the previous day. In contrast, group 2 showed no significant difference in the learning curves between day 1 and day 2 (Fig. 1d and e). Thus, learning the opposite rotation interfered with consolidation of the previously learned rotation. This retroactive interference is the kinematic counterpart of that reported in learning a dynamic perturbation²².

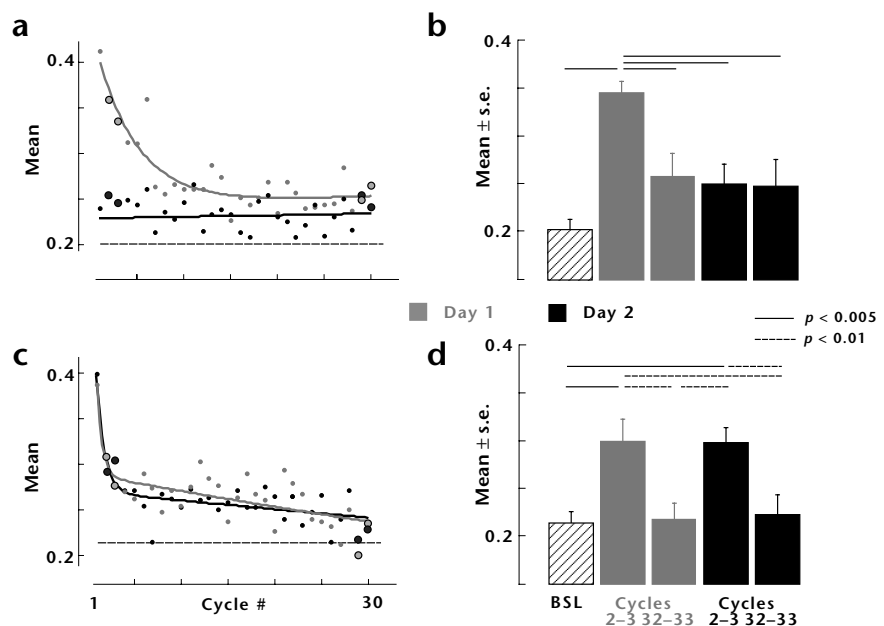
Learning a new dynamic internal model

Attaching a load medial or lateral to the longitudinal axis of the forearm displaces the center of mass of the forearm segment, causing large changes in elbow interaction torques. The new inertial configuration results in large errors in initial direction and in highly curved trajectories¹⁴. Because hand movements in different directions are associated with different relative motions of the elbow and shoulder, inertial errors vary systematically with direction. With practice, however, subjects model these novel intersegmental dynamics and generate appropriate anticipatory muscle torques to produce a straight path¹⁴.

Subjects in groups 3 and 4 learned to move a lateral load (Fig. 2a) without visual feedback on two successive days: on day 1 group 3 was exposed only to the lateral load, whereas group 4 also learned a medial load five minutes later (see Table 1). Initially, subjects showed increased trajectory curvature, increases in the area circumscribed by the path and initial directional areas, all of which varied systematically with movement direction (Fig. 2b). The directional variation in

normalized area, which we quantified as the standard deviation of the means across directions within each cycle, represents an error in dynamic planning and is reduced with practice (gray area in Fig. 2c). On day 2, subjects in group 3 fully retained the learning achieved on day 1 (Fig. 3a and b); there was no significant difference in the directional variation of normalized area of cycles 2 and 3 on day 2 and the last 2 cycles on day 1. Presumably, moving the load to the starting position provided subjects with enough contextual information about the dynamic conditions of the task for them to select the appropriate model of inertial dynamics. As in learning a rotated reference frame, adaptation to a dynamic perturbation opposite to the one just learned interfered completely with consolidation. The performance and rate of learning were identical on day 1 and 2 (Fig. 3c and d).

Fig. 3. Dynamic learning: consolidation and interference. (a, c). Learning curves for group 3 and 4. The mean standard deviation of the normalized area per cycle is plotted against cycle number during the training block on days 1 and 2. Points are means across subjects and are fitted to a double exponential function and single exponential on day 2. Symbols as in Fig. 1 b and d. (b, d). Bar charts for Group 3 and 4 showing the mean \pm standard deviation of the normalized area. Symbols as in Fig. 1 c and e. Significant differences were found across baseline, day 1 and day 2 (Group 3, ANOVA $F_{4,25} = 7.23$; $p = 0.0005$; Group 4, ANOVA $F_{4,25} = 5.40$; $p = 0.0028$). The horizontal lines indicate significant comparisons at *post-hoc* analysis.



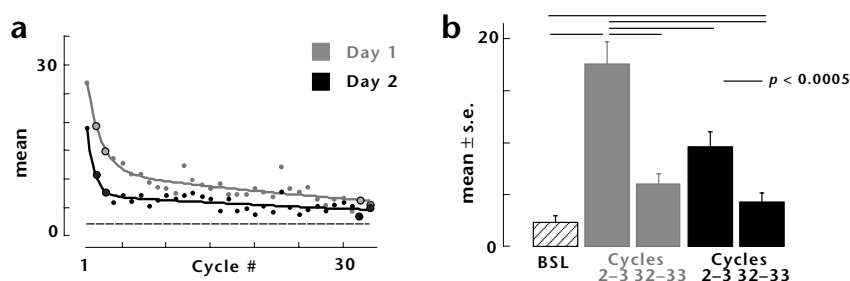


Fig. 4. Consolidation after consecutive learning of kinematics and dynamics. **(a)** Learning curves for group 5. Symbols as in Fig. 1b and d. **(b)** Bar charts for Group 5. Same key as in Fig. 1c and e. Significant differences were found across baseline, day 1 and day 2 (ANOVA $F_{4,25} = 19.45$; $p < 0.0001$). The horizontal lines indicate significant comparisons at *post-hoc* analysis.

Kinematics and dynamics are learned independently

To determine if the learning of a rotated reference frame and an altered mass distribution are independent, we first asked whether the learning of a lateral mass would interfere with subjects' consolidation of a newly learned rotated reference frame. Group 5 practiced and learned to move a laterally displaced load in the absence of visual feedback 5 minutes after learning a 30° rotation. This dynamic learning was quantitatively similar to that of subjects in groups 3 and 4. This did not interfere with the retention of kinematic learning on day 2, which was not significantly different from that seen for group 1 ($p = 0.52$; Fig. 4). This is consistent with independence of kinematics from dynamics.

Next, we asked if adaptation to rotation or to a lateral mass is reduced when the two are learned concurrently. Figure 5 shows the results of this experiment in subject group 6, who experienced both the rotation and the lateral mass concomitantly on day 1 and day 2. The reductions in directional error (Fig. 5a and b) and in the directional variation of normalized area over time (Fig. 5c and d) did not differ statistically from those of subjects learning each separately in groups 1, 2 and 3 (directional error, $F_3 = 0.89$, $p = 0.465$; normalized area variation, $F_2 = 0.3$, $p = 0.745$). (In all cases, comparisons were of differences between cycles 2 and 3 at the beginning, and 32 and 33 at the end of the training blocks.) Thus, concomitant learning of the lateral mass did not interfere with the learning of CCW rotation or *vice versa*. It should be noted that, unlike group 3 who learned the lateral mass alone, group 6 had visual feedback of the cursor motion on the screen during this dual learning. The parallel learning of a novel visuomotor transformation and a novel inertial configuration in the presence of visual feedback makes it unlikely that the lack of

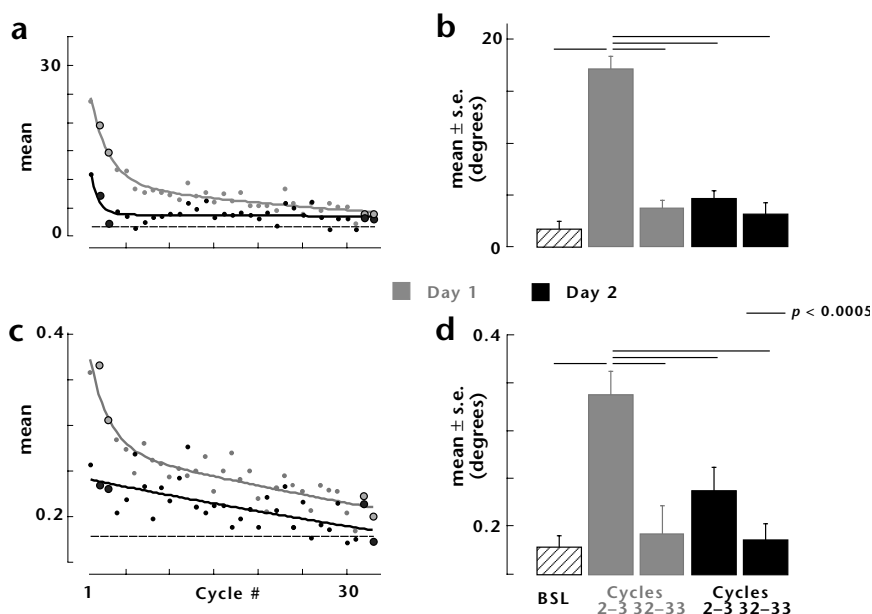
interference observed in serial learning above (group 5) resulted from differences in the sensory channels providing feedback. Moreover, since adding visual feedback did not increase the rate at which a novel dynamic configuration was learned, it is likely that proprioception alone provided the information needed to learn the new inertial dynamics.

DISCUSSION

The present observations demonstrate three main points. First, there is consolidation in the learning of novel kinematics and dynamics. Second, learning of another kinematic or dynamic model with conflicting sensorimotor mappings interferes with the consolidation of previously learned models of the same type. Third, the learning of novel intersegmental dynamics does not interfere with the consolidation of a newly learned kinematic transformation, and the two can be learned concurrently at the same rate as singly. This indicates that the learning of kinematics and dynamics are independent.

Current views of learning posit that both error storage and processing occur in working memory²⁵. For motor learning, this would suggest that the storage of movement errors and the computation of an internal model also take place in working memory. Such learning is interfered with when a perturbation requires learning a new model in which opposite corrective adjustments are necessary to counter the same feedback signal²⁴. In this case, there is a conflict in the adaptive changes required by error signals in the two conditions. Interference with consolidation seen in

Fig. 5. Kinematics and dynamics are learned in parallel. **(a, c)** Learning curves for group 6. The mean directional error per cycle **(a)** and mean standard deviation of the normalized area per cycle **(c)** are plotted against cycle number during the training block on days 1 and 2. Symbols as in Fig. 1b and d. **(b, d)** Bar charts for Group 6 showing the mean directional error and the mean standard deviation of the normalized area. Symbols as in Fig. 1c and e. Significant differences were found across baseline, day 1 and day 2 (mean directional error: ANOVA $F_{4,25} = 42.56$; $p < 0.0001$; mean standard deviation of the normalized area: ANOVA $F_{4,25} = 8.44$; $p = 0.0004$). The horizontal lines indicate significant comparisons at *post-hoc* analysis.



our experiments presumably reflects this process since the biases induced by the two rotations and the dynamic errors¹⁴ produced by the medial and lateral masses were opposite.

With the kinematic perturbation, learning required using directional errors, which could only be detected visually in Cartesian space, to rotate the spatial representation of the target relative to the hand. Although subjects might have used either visual or proprioceptive feedback in adapting to the lateral mass, subjects were able to learn this with proprioception alone. Moreover, subjects who were exposed to both perturbations with visual feedback learned the new dynamics and kinematics concurrently at the same rate as when they were learned separately. Therefore, it seems that vision is unnecessary and does not enhance proprioceptive learning of the new internal dynamic model.

The lack of interference in consolidating a newly learned kinematic model by learning a new dynamic model and concurrent learning of the two indicate that kinematic and dynamic errors are stored and processed in distinct working memory systems. This could occur because sensory channels are different, or because errors are coded in different coordinate systems.

It may be thought that the lack of interference across kinematic and dynamic learning tasks might have occurred not because errors in extrinsic and intrinsic coordinates are processed through different channels, but because context was sufficiently different to 'label' distinct working memory systems. Indeed, this is predicted by a computational model²⁶. However, this is unlikely to account for our results, since learning in the dual task, in which contextual differences do not apply, occurred in parallel without interference or delays.

Functional imaging data are consistent with a separation in the systems mediating the learning of kinematic and dynamic transformations. Thus, in subjects using the right arm, adaptation to lateral displacing prisms or screen-cursor rotations is associated with activation in posterior parietal areas^{27,28}, whose inputs are predominantly visual. In contrast, initial learning of novel force fields²³ is associated with activity in right dorsolateral prefrontal cortex, whereas consolidation is correlated with activity in left posterior parietal cortex, left dorsal premotor cortex and right anterior cerebellar cortex. We speculate that models of dynamics might be encoded directly in the arm area of primary motor cortex since proprioceptive information from the arm reaches this area at a short latency^{29,30}. Nevertheless, specific comparisons will require using comparable motor tasks and controlling the sources and modalities of sensory feedback, as well as studies in animals to identify the neural networks underlying these processes.

In current computational approaches to motor learning, inverse and forward models are both trained using a single performance criterion, which necessarily combines kinematic and dynamic errors²¹. Our results propose that future models should include two independent sources of error, kinematic and dynamic, computed in different reference frames and, possibly, in different sensory modalities.

METHODS

Six groups of 6 naive subjects (aged 19 to 36; 30 males, 6 females) were paid to participate in the study and signed an institutionally-approved consent form. Subjects moved a hand cursor on a horizontal digitizing tablet (sampling rate, 200 Hz) at shoulder level from a central starting point to a series of peripheral targets displayed on a computer monitor along with a screen cursor. Subjects' shoulders and wrists were restrained and their forearms were supported on an airslid system equipped with a rigid outrigger to which masses could be attached 25 cm medial or lateral to the forearm. An opaque shield prevented subjects from seeing their arms and hands at all times. In all experiments, the target set consisted of

8 circles arrayed radially at 4.2 cm from the same starting point in the center. Targets were presented every 1.5 seconds with a tone and in a predictable CCW order.

Subjects were instructed to make straight and uncorrected out-and-back movements, with sharply reversing direction within each target and in synchrony with the tone (timed response task), pausing briefly in the center before initiating the next movement. If the movement reached the target within a time window of 320 ms before and after each tone, the target turned gray, signaling a successful hit.

All subjects were initially familiarized with the apparatus and task during an initial block of 33 cycles of 8 targets in the absence of any perturbations (cursor feedback gain, 1:1; leftward hand movement produced leftward cursor movement). The six different groups of subjects were exposed to two types of perturbation which occurred concurrently or separately on each of two successive days. In the first, a kinematic perturbation, whereby the screen cursor was rotated by $\pm 30^\circ$, was imposed unexpectedly at the time of presentation of the first target and after subjects hand aligned the cursor in the center. In the second, a dynamic perturbation, whereby a 1.5-kg mass was placed medially or laterally to the forearm on an outrigger attached to an airslid¹⁴ (Fig. 2a), subjects had proprioceptive information about the impedance of the system before being presented with any target. All conditions were experienced in blocks of 33 cycles. The experimental protocol for all groups is outlined in Table 1.

For each movement (from the onset of the change in hand velocity in the start circle to the velocity minimum when it returned near the starting position) we determined the hand locations and bin numbers at various critical points in the trajectory. The directional error for each movement was taken as the difference between the direction of the target from the initial hand position and the direction of the hand at the peak outward velocity from the same initial point³. We used the mean directional error over each cycle of eight movements to measure the time course of adaptation to the kinematic perturbation.

Changes in hand path curvature were assessed by calculating the normalized area: the area enclosed by the hand path divided by the squared path length. To identify systematic direction-dependent changes, indicative of dynamic errors, we then computed the standard deviation of the mean errors for each target over each target cycle. The novel mass distribution also induced direction-dependent variations in initial direction; however, because subjects are unable to compensate for this error without visual feedback, we did not use this error here²⁰.

Differences between conditions and across days were assessed using analysis of variance (ANOVA) followed by Bonferroni-Dunn tests. *Post-hoc* tests were considered significant at $p < 0.005$.

ACKNOWLEDGEMENTS

We thank Cathleen Song and Thomas Frontera for technical assistance with the experiments and the data analysis and Walton Comer and Hao Huang for computer software. Supported by NS 22713 and NS 01961.

RECEIVED 22 JULY; ACCEPTED 9 SEPTEMBER 1999

1. Flanders, M., Helms Tillery, S. I. & Soechting, J. F. Early stages in a sensorimotor transformation. *Behav. Brain Sci.* 15, 309–362 (1992).
2. Desmurget, M., Pelisson, D., Rossetti, Y. & Prablanc, C. From eye to hand: planning goal-directed movements. *Neurosci. Biobehav. Rev.* 22, 761–788 (1998).
3. Gordon, J., Ghilardi, M. F. & Ghez, C. Accuracy of planar reaching movements. I. Independence of direction and extent variability. *Exp. Brain Res.* 99, 97–111 (1994).
4. Ghilardi, M. F., Gordon, J. & Ghez, C. Learning a visuomotor transformation in a local area of work space produces directional biases in other areas. *J. Neurophysiol.* 73, 2535–2539 (1995).
5. Gordon, J., Ghilardi, M. F., Cooper, S. E. & Ghez, C. Accuracy of planar reaching movements. II. Systematic extent errors resulting from inertial anisotropy. *Exp. Brain Res.* 99, 112–130 (1994).
6. Vindras, P. & Viviani, P. Frames of reference and control parameters in visuomanual pointing. *J. Exp. Psychol.* 24, 1–23 (1998).
7. Morasso, P. Spatial control of arm movements. *Exp. Brain Res.* 42, 223–227 (1981).
8. Pine, Z. M., Krakauer, J., Gordon, J. & Ghez, C. Learning of scaling factors and reference axes for reaching movements. *Neuroreport* 7, 2357–2361 (1996).

9. Wolpert, D. M., Ghahramani, Z. & Jordan, M. Are arm trajectories planned in kinematic or dynamic coordinates? An adaptation study. *Exp Brain Res.* **103**, 460–470 (1995).
10. Flanagan, J. R. & Rao, A. K. Trajectory adaptation to a nonlinear visuomotor transformation: evidence of motion planning in visually perceived space. *J. Neurophysiol.* **74**, 2174–2178 (1995).
11. Hollerbach, J. M. & Flash, T. Dynamic interactions between limb segments during planar arm movement. *Biol. Cybern.* **44**, 67–77 (1982).
12. Hoy, M. G. & Zernicke, R. F. The role of intersegmental dynamics during rapid limb oscillations. *J. Biomech.* **19**, 867–877 (1986).
13. Shadmehr, R. & Mussa-Ivaldi, F. A. Adaptive representation of dynamics during learning of a motor task. *J. Neurosci.* **14**, 3208–3224 (1994).
14. Sainburg, R. L., Ghez, C. & Kalakian, D. Intersegmental dynamics are controlled by sequential anticipatory, error correction, and postural mechanisms. *J. Neurophysiol.* **81**, 1045–1056 (1999).
15. Ghez, C., Gordon, J., Ghilardi, M. F., Christakos, C. N. & Cooper, S. E. Roles of proprioceptive input in the programming of arm trajectories. *Cold Spring Harb. Symp. Quant. Biol.* **55**, 837–847 (1990).
16. Gordon, J., Ghilardi, M. F. & Ghez, C. Impairments of reaching movements in patients without proprioception. I. Spatial errors. *J. Neurophysiol.* (1995).
17. Sainburg, R. L., Ghilardi, M. F., Poizner, H. & Ghez, C. The control of limb dynamics in normal subjects and patients without proprioception. *J. Neurophysiol.* **73**, 820–835 (1995).
18. Lajoie, Y. *et al.* Mirror drawing in a deafferented patient and normal subjects: visuoproprioceptive conflict. *Neurology* **42**, 1104–1106 (1992).
19. Gandolfo, F., Mussa-Ivaldi, F. A. & Bizzi, E. Motor learning by field approximation. *Proc. Natl. Acad. Sci. USA* **93**, 3843–3846 (1996).
20. Ghez, C., Krakauer, J. W., Sainburg, R. & Ghilardi, M. F. in *The Cognitive Neurosciences* 2nd edn. (ed. Gazzaniga, M.) 501–514 (MIT Press, Cambridge, Massachusetts, in press).
21. Jordan, M. I. in *Handbook of Perception and Action, V. II Motor Skills* Vol. 2 (eds. Heuer, H. & Keele, S. W.) 71–118 (Academic, San Diego, 1996).
22. Shadmehr, R. & Brashers-Krug, T. Functional stages in the formation of human long-term motor memory. *J. Neurosci.* **17**, 409–419 (1997).
23. Shadmehr, R. & Holcomb, H. H. Neural correlates of motor memory consolidation. *Science* **277**, 821–825 (1997).
24. Baddeley, A. D. *Working Memory* (Clarendon, Oxford, 1986).
25. Baddeley, A. Working memory. *Science* **255**, 556–559 (1992).
26. Wolpert, D. M. & Kawato, M. Multiple paired forward and inverse models for motor control. *Neural Net.* **11**, 1317–1329 (1998).
27. Clower, D., Hoffman, J., Votaw, J., Faber, T. & Woods, R. Role of posterior parietal cortex in the recalibration of visually guided reaching. *Nature* **383**, 618–621 (1996).
28. Moeller, J. R. *et al.* in *Quantitative Functional Brain Imaging with Positron Emission Tomography* (eds. Carson, R., Daube-Witherspoon, M. & Herscovitch, P.) 165–172
29. Asanuma, H. & Mackel, R. Direct and indirect sensory input pathways to the motor cortex; its structure and function in relation to learning of motor skills. *Jpn. J. Physiol.* **39**, 1–19 (1989).
30. Asanuma, H. Functional role of sensory inputs to the motor cortex. *Prog. Neurobiol.* **16**, 241–262 (1981).