

Learning a Visuomotor Transformation in a Local Area of Work Space Produces Directional Biases in Other Areas

MARIA FELICE GHILARDI, JAMES GORDON, AND CLAUDE GHEZ

Center for Neurobiology and Behavior, New York State Psychiatric Institute, and Program in Physical Therapy, College of Physicians and Surgeons, Columbia University, New York, New York 10032; and Istituto di Neuroscienze e Bioimmagini, Consiglio Nazionale delle Ricerche, H. S. Raffaele, Università di Milano, Milano, Italy

SUMMARY AND CONCLUSIONS

1. The dependence of directional biases in reaching movements on the initial position of the hand was studied in normal human subjects moving their unseen hand on a horizontal digitizing tablet to visual targets displayed on a vertical computer screen.

2. When initial hand positions were to the right of midline, movements were systematically biased clockwise. Biases were counterclockwise for starting points to the left. Biases were unaffected by the screen location of the starting and target positions.

3. Vision of the hand in relation to the target before movement, as well as practice with vision of the cursor during the movement, temporarily eliminated these biases. The spatial organization of the biases suggests that, without vision of the limb, the nervous system underestimates the distance of the hand from an axis or plane that includes its most common operating location.

4. To test the hypothesis that such an underestimate might represent an adaptation to a local area of work space or range effect, subjects were trained to reach accurately from right or left positions. After training, movements initiated from other locations, including ones that were previously error free, showed new biases that again represented underestimates of the distance of the initial hand position from the new trained location.

5. We conclude that hand path planning is dependent on learned representations of the location of the hand in the work space.

aim movements from a range of initial positions in the horizontal plane. We find that, in the absence of vision, movements aimed in all directions show directional biases that depend on the initial position of the hand. We then analyze the visual information required for subjects to eliminate these biases and the effect of training in a particular region of work space on biases in other areas. Parts of this study have been published in abstract form (Ghilardi et al. 1991, 1993, 1994).

METHODS

Nineteen neurologically intact subjects (11 men and 8 women) between the ages of 20 and 53 performed reaching movements in a task similar to that described previously (Ghez et al. 1995; Gordon et al. 1994a,b, 1995). They sat facing a vertical computer screen and moved a hand-held cursor with their right arm on a horizontal digitizing tablet located at shoulder level. To reduce gravitational and frictional forces, their performing arm was suspended from the ceiling with cables (Gordon et al. 1994b) or, in later experiments, lifted above the tablet with air jets (Karst and Hasan 1991; Pine et al. 1994). The computer screen displayed the position of the cursor on the tablet along with two circles, indicating a starting and a target location. In most experiments the starting position was displayed in the center of the computer screen located in front of the subject. At the beginning of a trial, subjects were to position the screen cursor in the start circle. Then, after an unpredictable time, a tone was presented, and they were to move the cursor to the target with a "single, uncorrected movement."

Targets were in 12 or 24 equally spaced directions at 7.5 cm from a common starting position (Fig. 1B). Targets were presented pseudorandomly in blocks of trials that precluded the same target from appearing twice in succession. Trial blocks included six reaches to each target. Movements were initiated from three basic starting positions (Fig. 1A). In the *center position*, it was 30–40 cm in front of the subject's sternum. For the *right position*, it was displaced ~40 cm to the right on a mediolateral axis. For the *left position*, it was ~20 cm to the left of the midline. In selected experiments we also examined movements initiated from other locations.

The effects of visual information on directional errors were examined in four conditions. In the standard *No Vision condition*, the screen cursor was blanked during movement, and vision of the limb was blocked. With *Knowledge of Results (KR)*, the hand path was displayed on the screen after each movement. With *Prior Vision*, subjects were shown the position of the target relative to their hand directly on the digitizing tablet before each movement. With *Cursor Feedback*, the screen cursor remained visible during movement.

We then trained subjects to perform accurate movements with

INTRODUCTION

Reaching to visual targets is understood to involve transformations in the neural representation of the intended hand position in space (Flanders et al. 1992). Confirming the results of unitary recordings from motor cortex (Georgopoulos 1991; Georgopoulos et al. 1986, 1989), recent analyses of reaching errors suggest that planning is carried out vectorially, with relatively independent specification of extent and direction (Bock and Arnold 1992; Ghez et al. 1993; Gordon et al. 1994a,b). This implies that movements are planned in a relative coordinate system centered at the initial position of the hand. However, it raises the question of how the brain determines absolute hand position in the work space, because different hand locations will be associated with different configurations of the joints of the arm. One hypothesis is that direction is computed by the brain by integrating visual information about target location and proprioceptive information about hand position and/or arm configuration (Flanders et al. 1992). The present report examines an alternative possibility, namely that vision of the hand is needed to determine hand position and thus limb configuration. We analyze directional errors made when subjects

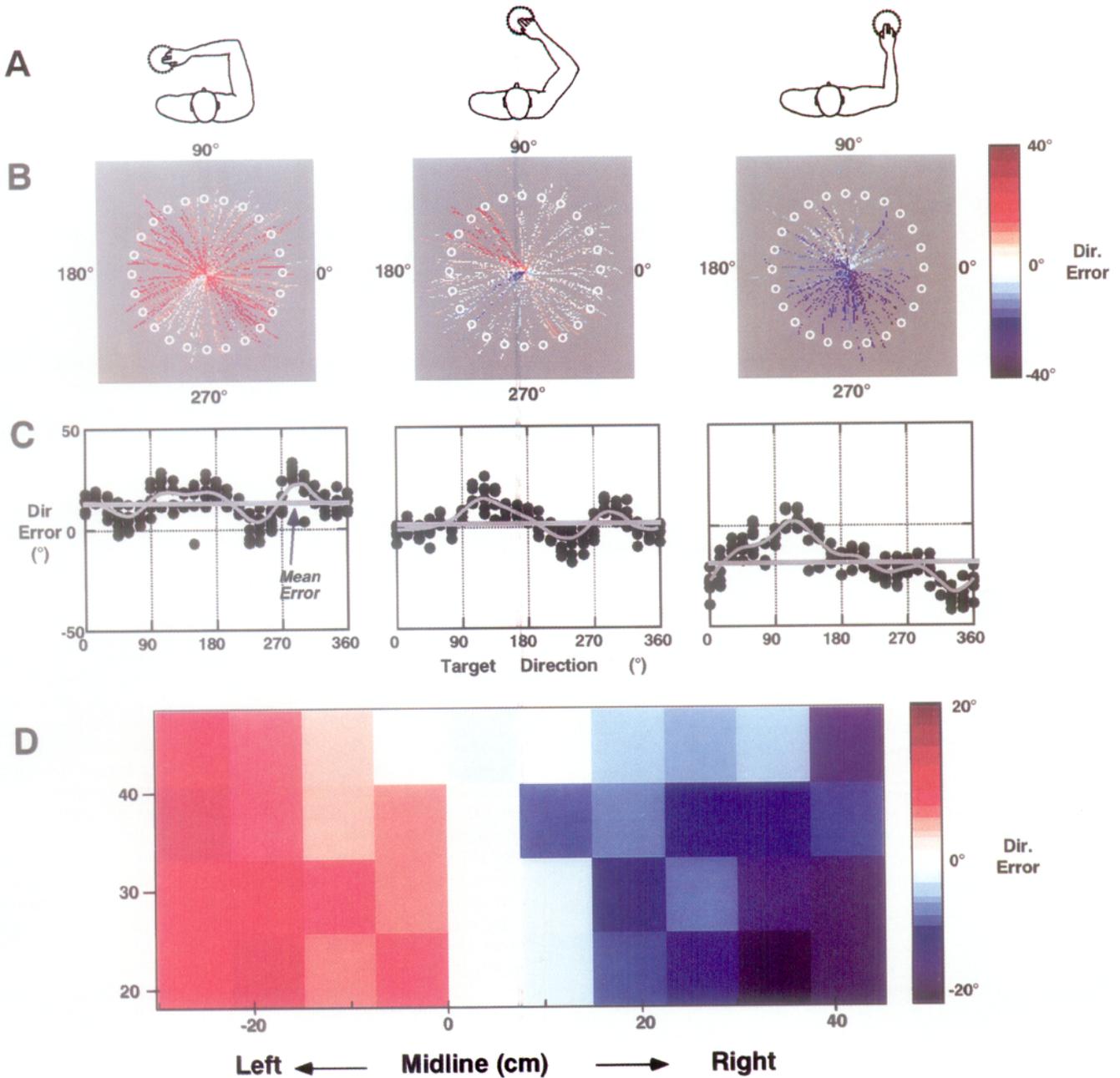


FIG. 1. Directional bias and its dependence on initial hand position. *A*: initial positions of the hand: left, center, and right positions. *B*: hand paths to 24 radial targets from 3 initial positions shown in *A* (*subject MG*). Dots represent hand positions at successive 20-ms intervals and are color coded to indicate direction and magnitude of directional errors (blue, clockwise; red, counterclockwise; white, 0). *C*: directional errors plotted as a function of target direction for data in *B*. Gray lines fitted lines through the data points using locally weighted scatter plot smoother (Cleveland 1979) show systematic directional fluctuations; horizontal gray lines show mean directional errors, or biases. *D*: mean directional errors (see color scale) of movements in 12 directions (target distance 3 cm) from 40 initial hand positions at centers of squares (spaced 7.5 cm apart). Data collected in *subject CG* in single session (480 trials) with the use of 2 tablets placed side by side and 12 equally spaced target directions from each starting position. Both hand positions and target directions were varied in pseudorandom order. Note that for the experiments shown in *B* and *C* the start position was at the center of the screen for all initial positions. For the experiment shown in *D*, the screen displayed the entire work space with a reduced gain by 53%. Thus differences in bias cannot readily be accounted for by differences in gaze orientation.

their hand in either the right or left positions by providing KR, vision of their initial hand position, and cursor feedback. After 72 trials of training in one of the two positions, they were tested in No Vision blocks in which movements were initiated, in pseudorandom order, from center, right, and left positions. To maintain learning effects, each series of 12 test trials was alternated with a

series of 12 training trials in the reference position. Testing was carried out in separate sessions over 2 days. In these adaptation experiments, the screen displayed the entire work space at a reduced gain. Subjects were adapted to this difference in gain with a set of 24 practice trials given before data collection.

Details of the data analysis are described in previous papers

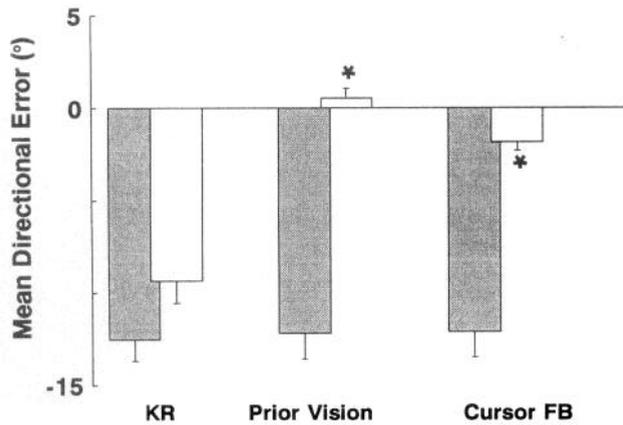


FIG. 2. Effect of visual information on directional bias. Mean directional errors \pm SE for movements starting from the right lateral initial position under No Vision condition (■) are compared with 3 conditions (□): KR ($n = 8$ subjects), Prior Vision ($n = 6$ subjects), and Cursor Feedback ($n = 9$ subjects). Asterisks indicate significant differences (paired t -tests, $P < 0.001$).

(Gordon et al. 1994a,b). Data consisted of x and y coordinates of the hand-held cursor sampled at 200 Hz. Movement direction was defined as the orientation of a straight line from the starting point to the endpoint of the movement. Directional error was computed as the difference between target and movement direction. Clockwise errors were considered negative and counterclockwise errors positive. Directional bias was computed as the mean directional error across all trials for a given hand starting position. In this paper we will describe changes of this type of error only. Other classes of directional errors, i.e., direction-dependent error and variable errors, are reported elsewhere (Ghilardi et al. 1991; Gordon et al. 1995).

RESULTS

Directional biases in reaching depend on the position of the hand in the work space

In movements made from the centered initial position without vision of the limb or cursor, errors in extent and direction were small. However, in all subjects, directions were systematically shifted counterclockwise when movements were initiated from locations to the left of midline, and clockwise when initiated from the right. This can be seen for a representative subject in Fig. 1, *B* and *C*, showing hand paths and directional errors for three initial hand positions. Although paths remained straight and extents did not change substantially with starting position,¹ directional errors showed consistent biases for all target directions. The magnitude of this directional bias varied primarily with the distance of the hand (at the starting point) from a parasagittal plane 3–10 cm to the right of the midline. This is shown in Fig. 1*D* for a different subject, 1 of 3 in whom mean directional error was assessed for 40 locations in the work space. In all subjects the bias-free region was just to the right of the midline.

Directional biases are abolished by prior vision of the hand and target in the work space and by cursor feedback

The directional biases described above were remarkably robust: they were not significantly reduced when KR was provided after each movement (Fig. 2). They were also present for both vertical and horizontal displays in different locations (including in front of the hand). On the other hand, when subjects were allowed to view the locations of the target and of their hand in the work space before each movement, the biases virtually disappeared (Fig. 2). This suggests that the errors occurred because, in the absence of vision, subjects incorrectly estimated the position of their hand when planning movement direction. In addition, subjects were also able to use screen cursor information when presented during

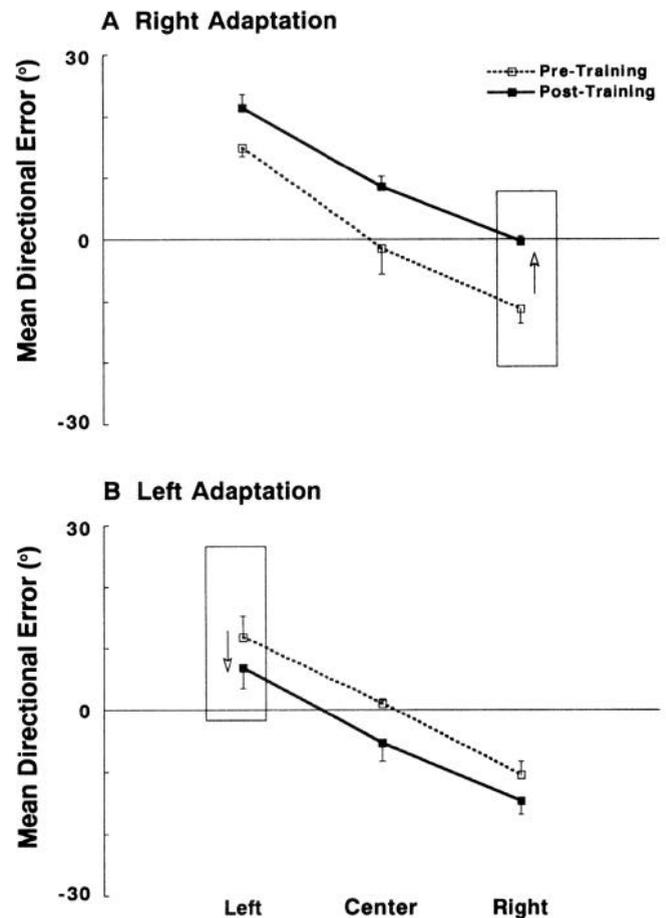


FIG. 3. Training in local areas of work space alters directional biases in others. Mean directional errors and SE with starting point in 3 different locations (left, center, and right). Boxed points indicate side of training (as per Fig. 1*A*). Empty squares and dotted lines are pre-training, filled squares and solid lines are post-training. *A*: training in right starting position ($n = 4$ subjects). Analysis of variance (ANOVA) showed significant effect of training ($P = 0.025$), initial hand position ($P = 0.0001$), but no interaction, indicating a similar shift in directional bias for all 3 locations. *B*: training in left starting position ($n = 3$ subjects). ANOVA showed a significant effect of initial hand position ($P = 0.0017$), but training, because of the small number of subjects, did not reach statistical significance ($P = 0.0632$). Interaction between training and hand location was not significant, indicating that bias shifted by about the same amount for the 3 locations. It should also be noted that the mean pretraining biases the initial position on the right did not differ statistically from those of Fig. 2 (■) in the same position, where the display was centered on the initial hand position.

¹ Although mean extent errors did not vary with initial hand position, the small directional fluctuations in these errors varied in accord with changes in limb inertia, as reported previously (Gordon et al. 1994a).

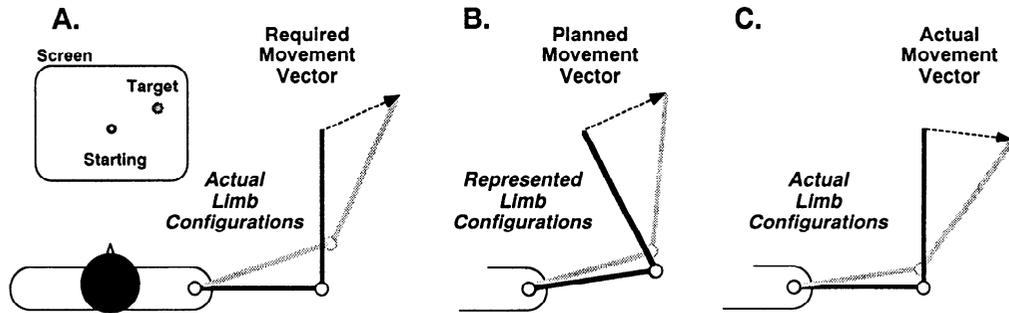


FIG. 4. Hypothesis: directional bias results from error in spatial representation of hand location. Limb configurations at initial position are shown in black; configurations at endpoints in gray. A: direction and extent of intended hand movement are specified correctly from screen information. B: joint commands are computed for hand position represented erroneously closer to midline. C: joint angle changes planned for incorrect position are applied to the actual initial position producing clockwise error.

movement gradually to eliminate directional biases (Fig. 2). The reductions in bias for both prior vision and cursor feedback did not merely reflect corrections during movement because movements remained straight and without curves indicative of adjustments in direction. Indeed, the reductions in mean directional errors were equally evident in measurements of initial direction taken at the time of peak acceleration (not shown). This indicates that the reduction in bias in both conditions reflects an adaptive change in feed-forward commands generating the movements and thus implies that learning has taken place.

Elimination of directional bias through learning is only applied to local areas of the work space

The ability of subjects to adjust their motor commands with practice in a novel area of the work space raised the question of how the underlying sensorimotor transformation was altered. Did subjects learn to perform accurately in an additional region of work space (leaving the bias in other regions unaltered), or did learning shift the bias-free region to a new spatial location? To answer this question, we measured the bias associated with different initial positions after subjects were trained to perform bias-free movements in either the right or left position. The results obtained in four subjects for training on the right are shown in Fig. 3A and for training on the left in Fig. 3B. Training either reduced or abolished preexisting biases; however, the reduction in bias was consistently greater for the right than the left positions. We speculate that this occurred because subjects normally have greater experience performing tasks on the right side of the work space with their right hand.

The effect of training was not, however, limited to the local area of work space where it occurred. It also shifted the biases for other locations. After training in the left position, the average errors in the center and right positions were shifted clockwise. After training in the right position, counterclockwise biases appeared in the center position, and the preexisting bias in the left shoulder position increased. Thus the effect of training was to shift the overall positional dependence of the mean directional errors, leading to the development of bias in locations where none existed previously.

DISCUSSION

Human subjects exhibit consistent directional biases in reaching movements when they cannot see the position of their hand. Although the task here required the subjects to use spatial information presented on a vertical computer screen to plan horizontal arm movements, such a display was not necessary to reveal the biases. Indeed, we have seen similar biases when subjects reach, with their unseen hand, for targets in directions specified by verbal commands (Ghez et al. 1994; Ghilardi et al. 1993). The fact that biases are corrected by viewing the hand indicates that information about limb configuration or about hand location relative to the body are necessary for accurate specification of movement direction. By the same token, these results indicate that proprioception alone does not provide this information. These biases differ from systematic *direction-dependent* directional errors, evident in Fig. 1C (Ghilardi et al. 1991; Graaf 1994; Graaf et al. 1991, 1994), which are not (in subjects with intact proprioception) substantially affected by vision of the hand in the work space (Gordon et al. 1995; Ghilardi et al. 1991).

We have previously provided evidence that subjects program reaching movements in a vectorial space centered at the hand (Gordon et al. 1994a,b). The existence of consistent directional biases supports further the idea that specification of hand direction is, at the level of the initial kinematic plan, independent of movement extent. In this vectorial framework the observed position-dependent biases could occur if subjects planned the elbow and shoulder motions with the use of an inaccurate representation of the initial position of their hand. We hypothesize that subjects correctly derived both extent and direction from information provided on the screen (or from verbal instructions), but specified the rotations of elbow and shoulder incorrectly. Movement directions would be biased in the manner observed if joint kinematics were computed on the basis of a representation of their initial hand position that was closer to the midline than the actual hand position. Directional biases would occur because the changes in joint angles required to move the hand in a given direction differ consistently between the actual and represented hand locations. Figure 4 illustrates this for a single target. If the actual initial position of the hand were located to the right of midline, but were represented by the brain as being closer to midline, the planned shoulder and elbow

movements would lead to a clockwise error as observed. Simulations indicate that a clockwise bias would occur for targets in all directions, whereas a counterclockwise bias would occur for an initial position to the left of midline (Ghilardi et al. 1994).

Because the error-free region includes the habitual location of the hand in daily tasks, we presume that the underestimate of initial distance from the midline represents a range effect centered at this location (Poulton 1975). Like other range effects (Favilla et al. 1990; Hening et al. 1988), this reflects prior experience. In this case we hypothesize that training in a new area sets the reference hand position and perhaps the reference axis as well. The changes in the spatial organization of the biases after learning to move accurately in off-axis regions of work space support this idea. Further experiments are needed to determine whether perceptual representations of hand position derived from proprioceptive cues alone also show drifts (Wann and Ibrahim 1992) in expected directions after occlusion of vision. The present results also stress the importance of adaptation and learning in the accurate specification of movement kinematics. However, generalization of learning to novel regions of work space can lead to unexpected degradation in accuracy in regions where movements were previously accurate. The present data complement the recent demonstrations that planning movement dynamics to take account of intersegmental interactions also depends fundamentally on short-term learning or updating of internal models of limb mechanics (Ghez et al. 1995; Ghez and Sainburg 1995; Shadmehr and Mussa-Ivaldi 1994).

This work was supported by National Institute of Neurological Disorders and Stroke Grant NS-22713 and by the McKnight Foundation.

Address for reprint requests: M. F. Ghilardi, Center for Neurobiology and Behavior, 722 West 168th St., New York, NY 10032.

Received 17 October 1994; accepted in final form 7 February 1995.

REFERENCES

- BOCK, A. AND ARNOLD, K. Motor control prior to movement onset: preparatory mechanisms for pointing at visual targets. *Exp. Brain Res.* 90: 209–216, 1992.
- CLEVELAND, W. S. Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* 74: 829–836, 1979.
- FAVILLA, M., GORDON, J., HENING, W., AND GHEZ, C. Trajectory control in targeted force impulses. VII. Independent setting of amplitude and direction in response preparation. *Exp. Brain Res.* 79: 530–538, 1990.
- FLANDERS, M., HELMS TILLERY, S. I., AND SOECHTING, J. F. Early stages in a sensorimotor transformation. *Behav. Brain Sci.* 15: 309–362, 1992.
- GEORGOPOULOS, A. P. Higher order motor control. *Annu. Rev. Neurosci.* 14: 361–377, 1991.
- GEORGOPOULOS, A. P., LURITO, J. T., PETRIDES, M., SCHWARTZ, A. B., AND MASSEY, J. T. Mental rotation of the neuronal population vector. *Science Wash. DC* 243: 234–236, 1989.
- GEORGOPOULOS, A. P., SCHWARTZ, A. B., AND KETTNER, R. E. Neuronal population coding of movement direction. *Science Wash. DC* 233: 1416–1419, 1986.
- GHEZ, C., GORDON, J., AND GHILARDI, M. F. Programming of extent and direction in human reaching movements. *Biomed. Res.* 14: 1–5, 1993.
- GHEZ, C., GORDON, J., AND GHILARDI, M. F. Impairments of reaching movements in patients without proprioception. II. Effects of visual information on accuracy. *J. Neurophysiol.* 73: 361–372, 1995.
- GHEZ, C., GORDON, J., GHILARDI, M. F., AND SAINBURG, R. Contributions of vision and proprioception to accuracy in limb movements. In: *The Cognitive Neurosciences*, edited by M. S. Gazzaniga. Cambridge, MA: MIT Press, 1994, p. 549–564.
- GHEZ, C. AND SAINBURG, R. Proprioceptive control of interjoint coordination. *Can. J. Physiol. Pharmacol.* 73: 273–284, 1995.
- GHILARDI, M. F., GORDON, J., AND GHEZ, C. Systematic directional errors in planar arm movements are reduced by vision of the arm. *Soc. Neurosci. Abstr.* 17: 1089, 1991.
- GHILARDI, M. F., GORDON, J., AND GHEZ, C. Directional biases in targeted arm movements result from distortions in the representation of the work-space. *Soc. Neurosci. Abstr.* 19: 1686, 1993.
- GHILARDI, M. F., GORDON, J., AND GHEZ, C. Directional biases in arm movements reflect biased estimates of initial hand position. *Soc. Neurosci. Abstr.* 20: 1410, 1994.
- GORDON, J., GHILARDI, M. F., COOPER, S. E., AND GHEZ, C. Accuracy of planar reaching movements. II. Systematic extent errors resulting from inertial anisotropy. *Exp. Brain Res.* 99: 112–130, 1994a.
- GORDON, J., GHILARDI, M. F., AND GHEZ, C. Accuracy of planar reaching movements. I. Independence of direction and extent variability. *Exp. Brain Res.* 99: 97–111, 1994b.
- GORDON, J., GHILARDI, M. F., AND GHEZ, C. Impairment of reaching movements in patients without proprioception. I. Spatial errors. *J. Neurophysiol.* 73: 347–360, 1995.
- GRAAF, J. B. D. *The Initial Direction of Slow Goal-Directed Arm Movements. Deviations as a Means to Study Spatial Representations* (PhD thesis). Delft, The Netherlands: Technische Univ. Delft, 1994.
- GRAAF, J. B. D., SITTING, A. C., AND DENIER VAN DER GON, J. J. Misdirections in slow goal-directed arm movements and pointer-setting tasks. *Exp. Brain Res.* 84: 434–438, 1991.
- GRAAF, J. B. D., SITTING, A. C., AND DENIER VAN DER GON, J. J. Misdirections in slow goal-directed arm movements are not primarily visually based. *Exp. Brain Res.* 99: 464–472, 1994.
- HENING, W., VICARIO, D., AND GHEZ, C. Trajectory control in targeted force impulses. IV. Influences of choice, prior experience and urgency. *Exp. Brain Res.* 71: 103–115, 1988.
- KARST, G. M. AND HASAN, Z. Initiation roles for planar, two joint arm movements: agonist selection for movements throughout the work space. *J. Neurophysiol.* 66: 1579–1593, 1991.
- PINE, Z. M., GORDON, J., AND GHEZ, C. Adaptation to display rotations and altered gains in planar reaching movements. *Soc. Neurosci. Abstr.* 20: 1410, 1994.
- POULTON, E. C. Range effects in experiments on people. *Am. J. Psychol.* 88: 3–32, 1975.
- SHADMENR, R. AND MUSSA-IVALDI, F. A. Adaptive representation of dynamics during learning of a motor task. *J. Neurosci.* 14: 3208–3224, 1994.
- WANN, J. P. AND IBRAHIM, S. F. Does limb proprioception drift? *Exp. Brain Res.* 91: 162–166, 1992.