Rapid Adaptation to Coriolis Force Perturbations of Arm Trajectory

JAMES R. LACKNER AND PAUL DIZIO
Brandeis University, Waltham, Massachusetts 02254-9110

SUMMARY AND CONCLUSIONS

1. Forward reaching movements made during body rotation generate tangential Coriolis forces that are proportional to the cross product of the angular velocity of rotation and the linear velocity of the arm. Coriolis forces are inertial forces that do not involve mechanical contact. Virtually no constant centrifugal forces will be present in the background when motion of the arm generates transient Coriolis forces if the radius of body rotation is small.

2. We measured the trajectories of arm movements made in darkness to a visual target that was extinguished as movement began. The reaching movements were made prerotation, during rotation at 10 rpm in a fully enclosed rotating room, and postrotation. During testing the subject was seated at the center of the room and pointed radially. Neither visual nor tactile feedback about movement accuracy was present.

3. In experiment 1, subjects reached at a fast or slow rate and their hands made contact with a horizontal surface at the end of the reach. Their initial perrotary movements were highly significantly deviated relative to prerotation in both trajectories and endpoints in the direction of the transient Coriolis forces that had been generated during the reaches. Despite the absence of visual and tactile feedback about reaching accuracy, all subjects rapidly regained straight movement trajectories and accurate endpoints. Postrotation, transient errors of opposite sign were present for both trajectories and endpoints.

4. In a second experiment the conditions were identical except that subjects pointed just above the location of the extinguished target so that no surface contact was involved. All subjects showed significant initial perrotation deviations of trajectories and endpoints in the direction of the transient Coriolis forces. With repeated reaches the trajectories, as viewed from above, again became straight, but there was only partial restoration of endpoint accuracy, so that subjects reached in a straight line to the wrong place. Aftereffects of opposite sign were transiently present in the postrotary movements.

5. These observations fail to support current equilibrium point models, both α and λ, of movement control. Such theories would not predict endpoint errors under our experimental conditions, in which the Coriolis force is absent at the beginning and end of a movement. Our results indicate that detailed aspects of movement trajectory are being continuously monitored on the basis of proprioceptive feedback in relation to motor commands. Adaptive compensations can be initiated after one perturbation despite the absence of either visual or tactile feedback about movement trajectory and endpoint error. Moreover, movement trajectory and endpoint can be remapped independently.

6. We interpret these results as emphasizing that movement trajectory and endpoint are continuously monitored. A model illustrating how this might be done is presented; it shows how proprioceptive, motor, and somatosensory factors could be used in updating movement control and compensating for changes in effective limb inertia and dynamics.

INTRODUCTION

Perturbing movement trajectories and studying reflexive, programmed, and voluntary responses—the load compensation paradigm—is an important tool in studies of motor coordination. Its use has contributed to the development of equilibrium-point theories of the planning and execution of limb movements (Bizzi et al. 1976; Cooke 1979; Feldman 1966a,b; Kelso 1977). In this paper we present a new perturbation paradigm employing an "artificial gravity" environment. With it we have observed reaching errors and subsequent adaptation patterns that differ from those observed with previous paradigms. The differences in results and techniques suggest that existing equilibrium-point models exaggerate the functional significance of the springlike behavior of intact muscle systems and overlook inertial and contact forces as aspects of the controlled system. Our findings also emphasize the role of continuous monitoring and control of movement trajectory.

From a mechanical perspective, combinations of muscle length and force produce posture and movement. The nervous system could control posture and movement by regulating just one of these variables if it could anticipate the dynamic mechanical and reflexive influences of the other. This, however, is a formidable computational task unless muscle stiffness is high (Houk and Rymer 1981). The increment in muscle force varies systematically with change in length (Matthews 1959; Rack and Westbury 1969, 1974) and the rate of force change seems to depend on the level of efferent innervation (Agarwal and Gottlieb 1977; Hoffer and Andreassen 1981; Joyce et al. 1969; Nichols and Houk 1976). Theoretically, therefore, a set of parameters related to the stiffness among all the muscles influencing an otherwise unloaded joint could be neurally specified; the joint would then come to rest, mechanically, at the posture where the sum of torques around it would be 0. In some equilibrium-point theories only stiffness per se is regulated (Bizzi 1980); others also incorporate a neurally specified threshold length for elicitation of the stiffness response (Feldman 1966a,b, 1974). In both of these views posture is an equilibrium position.

Such theories also emphasize equilibrium behavior in describing how the nervous system generates movement trajectories (Bizzi et al. 1982, 1984, 1991; Feldman 1966a,b; Hogan 1984). They propose that movements are planned as virtual trajectories—an evolving series of equilibrium points that would bring about a corresponding series of equilibrium postures if there were sufficiently long dwell times between each equilibrium point in the series. For unloaded movements made on a natural time scale, the only points in the actual trajectory predicted to match the virtual trajec-

tory are the start and end points, where the central commands dwell for maintenance of posture. In between, the system is not at equilibrium and the virtual trajectory is only one of many determinants of the actual trajectory (cf. Bizzi et al. 1992 and Feldman 1986 for reviews).

One appeal of such theories is that the nervous system in planning movement endpoints needs not take account of factors such as viscosity and limb mass and moment of inertia or transient external loads that affect mechanical dynamics because they do not affect equilibrium behavior. This idea has been empirically tested by Bizzi and colleagues, who have shown that subjects moving a manipulandum to a target will exert forces toward and ultimately go to the target position even when the movement trajectory is briefly deflected past the target by external forces applied to the manipulandum. This is true both of intact humans (Mussa-Ivaldi et al. 1985) and monkeys (Bizzi et al. 1984) with deafferented limbs. Feldman (1980) has shown similar patterns of springlike behavior and endpoint accuracy in humans whose arms are secured in a cradle used to perturb the arm. Such observations suggest that the terminus of a movement is programmed and that the detailed trajectory need not be continuously monitored and updated during movement execution.

All load compensation and trajectory perturbation experiments used to test equilibrium point models have involved mechanical interference through the application of contact forces to the surface of the perturbed limb. Such contact activates somatosensory and proprioceptive receptors that may provide information about the direction and magnitude of the perturbing force. Subjects instructed not to resist the perturbations (Feldman 1980; Mussa-Ivaldi et al. 1985) may be unable to comply fully and may generate goal-directed forces that resemble springlike forces. Even in experiments on animals with limbs deafferented by dorsal rhizotomies (Bizzi et al. 1976, 1978, 1984), some spatially significant signals may be conveyed through the intact ventral roots and certainly by reaction forces acting on non-deafferented parts of the body involved in postural support, e.g. on the torso and buttocks.

The only experiments that have studied mechanical perturbations of reaches without local contact cues have been performed in parabolic flight (Bock et al. 1992; Fisk et al. 1993) or in centrifuges (Cohen 1970). In these experiments the perturbation consisted of an altered background gravitoinertial force level between 1 and 2 g. This force field affected the whole body before, during, and after a reach, making it up to twice as heavy as normal. In the experiments described here we designed a paradigm in which arm reaching trajectories could be transiently perturbed without any local contact forces and without significant increases in gravitoinertial force level. Our approach was to determine the influence of Coriolis forces on the accuracy of unrestricted pointing movements to a visual target that was extinguished as the movement began. To generate the Coriolis forces we had subjects point while they sat at the center of rotation in a fully enclosed room turning at 10 rpm.

Limb movements in a rotating reference frame generate Coriolis forces that are the cross product of the angular velocity of the reference frame and the linear velocity of the limb relative to the reference frame. Our subjects were at
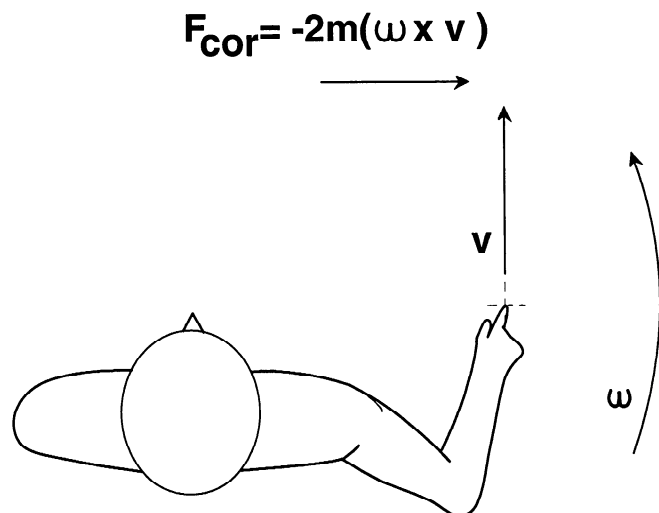
$$F_{cor} = -2m(\omega \times v)$$

FIG. 1. Schematic illustration of the Coriolis forces (F_{cor}) generated during reaching movements of the arm in a rotating room. F_{cor} is proportional to the cross product of the room's angular velocity (ω) and the arm's linear velocity within the room (v). F_{cor} is to the subject's right when the arm is moving forward during counterclockwise rotation. F_{cor} is 0 when the arm is not moving. In our experiment the starting position for reaches was directly on the axis of rotation so neither the hand nor any other part of the body was exposed to significant centrifugal forces.

the center of rotation and reached radially outward during counterclockwise rotation, generating a tangential Coriolis force that accelerated the arm rightward (see Fig. 1). Coriolis forces are inertial forces that do not involve mechanical contact. Accordingly, when an unconstrained reaching movement is made during rotation, the arm will be deflected by the Coriolis force but there will be no tactile cues on its surface signaling the presence of the force. Because the Coriolis force is proportional to the velocity of the arm movement it will be small for a slow movement, large for a fast one, and 0 before the movement and at the end of the movement.

In our experiments the hand moved from the center of the room to radial distances of ~35 cm from start to end. This added a centrifugal force that increased the net background gravitoinertial force on the hand from a normal terrestrial 1 g level to only 1.00076 g. All other parts of the body, which did not move, were exposed to steady gravitoinertial forces proportional to their distances from the center of the room. The maximum distance was ~55 cm at the toes, generating a force of only 1.00189 g.

Vestibular stimulation that might have affected tonic or phasic reflex activity or visual localization was not present in our experiment. Otolith activity was normal because the head was virtually on the axis of rotation where the gravitoinertial force level was 1 g. We waited for >1 min after the room had reached a constant velocity before reaching movements were made; consequently, any canal discharge generated by acceleration of the room would have equilibrated.

Thus with our paradigm there is virtually nothing abnormal about the sensorimotor conditions except the Coriolis force acting on the arm when it is moving, and the nature of this force is not reflected in external contact cues on the arm. The subjects in our experiment pointed to visual targets that were extinguished when a movement began so that there was no visual information about endpoint or trajec-

tory. The targets were embedded in a smooth surface so there was no tactile information about endpoint accuracy. The subjects were instructed to touch the remembered target position in one smooth continuous movement.

Equilibrium position models of motor control have to predict that movements made in a rotating environment under such circumstances should accurately reach their intended endpoints because the Coriolis forces are transient. At the end of the movement the Coriolis force has gone to 0 so that no abnormal external forces are acting on the arm or any other part of the body. Consequently, the movements should achieve their intended goals as determined by the length-tension characteristics of the involved muscles specified by the virtual trajectory. Rightward loading and subsequent unloading by the Coriolis forces might lead to hysteresis, a slight residual rightward deviation of endpoint (Mussa-Ivaldi et al. 1989).

Equilibrium position models also predict that if the goal is only to reach a specific endpoint then there should be no adaptation in a series of reaches made in a rotating environment. Although the trajectories of movements might be distorted, the endgoals should not be, so adaptation is neither required nor predicted. Adaptation of the initially distorted trajectory without endpoint errors at any time would reveal that limb mass and moment of inertia are taken into account, a task from which equilibrium point control ought to relieve the nervous system.

In summary, our goals were to measure endpoint and trajectory errors of the initial reaches made under the influence of transient Coriolis forces and to measure adaptation in a series of reaches. We used two movement speeds: a slow one $\sim$700 ms in duration, and a fast one of $\sim$400 ms. These rates were chosen because slow movements are thought to involve muscle spindle feedback during their ongoing execution, whereas fast ones may involve open-loop drive, i.e., triphasic patterns of agonist burst, antagonist brake, and agonist hold signals (Hallett et al. 1975). As a consequence, one might expect load compensation reflexes to be elicited or preprogrammed reactions to be triggered when slow movements are deflected by the Coriolis forces but not when fast movements are deflected (Rack 1981).

Parts of this work have been presented in preliminary form at the 1992 and 1993 Annual meetings of the Society for Neuroscience (DiZio and Lackner 1992, 1993; Lackner and DiZio 1992, 1993).

METHODS

Movements with terminal contact

SUBJECTS. Twenty-four subjects participated; 11 were tested making slow arm movements and 13 were tested making fast arm movements. They were without sensorimotor anomalies that could have affected their reaching behavior. All were naive with regard to the goals of the experiment and were unfamiliar with the characteristics of rotating environments.

APPARATUS. Testing took place in the Graybiel Laboratory's rotating room, a fully enclosed chamber 6.7 m diam. The subject was seated in a chair with a head rest near the center of rotation. The right hand rested on a horizontal surface that projected forward at waist level. A light-emitting diode (LED) embedded in
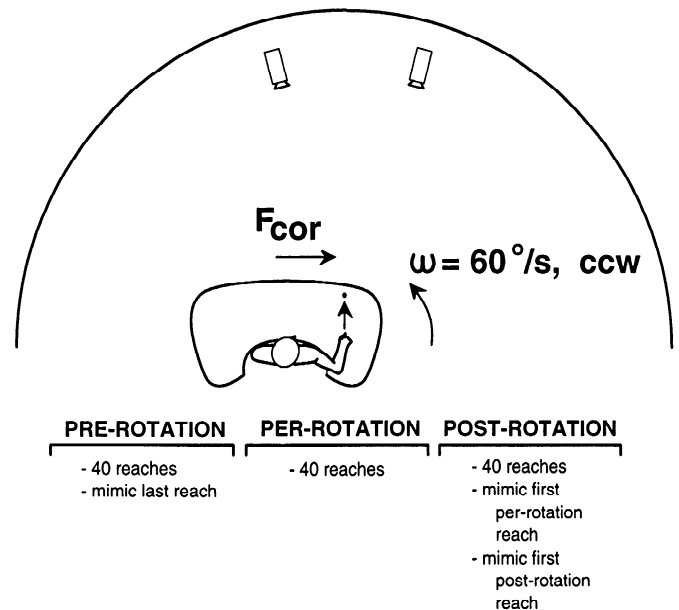

FIG. 2. Schematic illustration of the experimental paradigm. The experiment was conducted inside a rotating room. Subjects were seated at the center of the room and reached forward in a parasagittal plane for a target that disappeared at movement onset. Reaches were executed in complete darkness, the target was beneath the Plexiglas work surface, and return movements were made in the air and slowly so there was no visual or tactile feedback. Subjects made 40 reaching movements before, during, and after rotation at 60°/s counterclockwise (ccw). Acceleration and deceleration lasted 60 s and an additional 60 s elapsed before any movements were made. Subjects mimicked in light what they had felt their arms do in darkness in each condition. Mimics of the prerotation reaches were performed just after the prerotation series of reaches. Mimics of the per- and postrotation reaches were delayed until the room was stationary again and readaptation to normal conditions had been achieved.

this Plexiglas surface served as the target to which the subject could point. During testing the room lights were extinguished and the single LED was the only object ever visible to the subject. Before the beginning of a reaching movement the subject's right index finger depressed a microswitch that maintained illumination of the LED. The microswitch provided a start position that was slightly to the right of body midline and coincident with the axis of rotation of the room; the target light was 35 cm away, straight ahead of the start position. When ready, the subject lifted the finger, thereby extinguishing the LED, and in one continuous movement pointed to the remembered position of the target. The subject touched the Plexiglas panel but received no tactile feedback about the accuracy of the pointing movement because the target lay beneath the smooth surface. An infrared emitter was taped to the tip of the subject's index finger; its position was monitored by a WATSMART motion recording system that registered movements in the subject's workspace. The sampling rate was 50 Hz. Figure 2 illustrates the experimental situation.

PROCEDURE. An experimental session was divided into prerotation, perrotation, and postrotation components. During each part, 40 pointing movements were made to the target. Subjects were instructed to reach and touch the location of the target in one continuous natural movement without stopping and to hold the index finger there for 1 s before lifting it and slowly bringing it back in the air toward the body. The appropriate movement speed was demonstrated in the light to the subject by the experimenter. The subject then practiced pointing several times until the experimenter was satisfied that the correct cadence for slow or fast movements, as appropriate, had been achieved. The 11 subjects who made slow movements were attempting to achieve a movement

duration of ~700 ms; the 13 subjects making fast movements were attempting to achieve a movement duration of ~400 ms. Then there were several practice trials in darkness with the target LED extinguished at the onset of the reaching movement. In experimental trials the subjects were given a 30-s rest after every self-paced eight movements to minimize fatigue. Throughout the experiment the subject's head was stabilized by a contoured head rest and the subject avoided making any head or body movements besides the pointing movements.

After 40 prerotation movements had been completed, the rotating room was accelerated at $1°/s^2$ to a constant velocity of $60°/s$ counterclockwise. During acceleration and for 1 min afterward, the subject sat quietly, not making arm or head movements. This delay period allowed the horizontal semicircular canals that were activated during acceleration to return to their resting background discharge levels. Subjects were warned that their movements might feel odd and reminded that their sole task was to touch the location of the target LED in one smooth continuous movement with the same overall speed and stiffness of the arm as during the prerotation period. Reaching movements were then made to the target as during prerotation. The subject was instructed to remember what the first movement made during rotation felt like so that he or she could reproduce it at the very end of the experiment. After completion of 40 movements the rotating room was decelerated to rest at $1°/s^2$ and 1 min was allowed to elapse before 40 postrotation reaches were made to the target. After completion of the 40 postrotation reaches the subject mimicked what the first perrotation reach had felt like, and we recorded it when the subject was satisfied that it was right. Then the subject mimicked how the first postrotation movement had felt.

DATA ANALYSIS. The endpoint and duration of every reaching trial were determined by a program that located the position and the time when the finger stopped, arbitrarily defined as when velocity of the filtered (5 Hz) signal first fell to 0. The maximum leftward and rightward positions of the finger's trajectory and the peak forward velocity of the movement were found using binary search algorithms. Our main interest was in how these variables changed in the per- and postrotation periods relative to the prerotation period. To obtain a prerotation baseline that was free of random error, we averaged each variable over a subject's last eight prerotation reaches. Statistical tests were performed on the changes from baseline measured for each subject's per- and postrotation reaches.

Movements without terminal contact cues

One possible reason for endpoint errors during rotation may be the terminal contact of the index finger with the target board surface. Perhaps friction prevented lateral motion of the arm to the target that would otherwise have occurred owing to equilibrium point control. To evaluate this possibility we conducted a second experiment in which the subjects did not touch the target board at the end of a reaching movement but pointed in the air just above the target location. The absence of contact meant that there was no possibility of friction preventing the hand from moving to its programmed endpoint. The design of the experiment was otherwise identical to the first. Fourteen individuals who had not taken part in the first experiment and who had no known sensorimotor anomalies participated. Seven performed slow movements and seven fast movements. The subjects were instructed to point ~1 in. above the target with their fingers at the same distance and angular position (azimuth) as the target. All of them found it comfortable to point in this fashion and not unnatural or constraining. Otherwise the instructions were the same as in the experiments with contact.
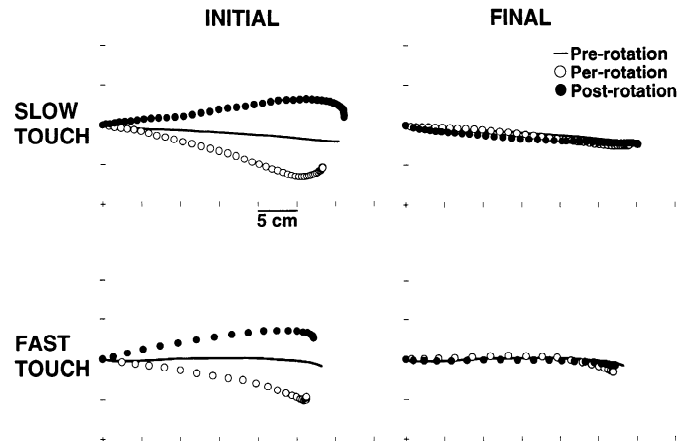

FIG. 3. Top view of the average trajectories for slow ($n = 11$) and fast ($n = 13$) reaches where subjects touched the work surface at the end of the movement. The first (INITIAL) and last (FINAL) movements of each 40 movement sequence pre-, per-, and postrotation are shown. Movements were originally sampled at 50 Hz but were rescaled before averaging to equate movements of different durations.

RESULTS

Slow movements with terminal contact

PREROTARY REACHES. Every subject made nearly straight reaches toward the target before rotation commenced. The trajectories deviated a maximum of only 8 mm left and 5 mm right of a straight line between the start position and endpoint. The average endpoint of the subjects' reaches fell 3 mm to the left of the target and 30 mm short of it. The average prerotation movement duration was 660 ms and the peak velocity was 825 mm/s.

PERROTARY REACHES. Every subject on the first perrotary movement was grossly more inaccurate in pointing to the target location than prerotation. The lateral errors were always in the direction of the Coriolis forces (rightward) generated by the reaches. An error developed as the forward velocity of a reach increased, paralleling the buildup of the Coriolis force that was proportional to the velocity of the arm. As the arm slowed down toward the end of the reach, the hand tended to hook slightly back toward the target. Thus there were trajectory deviations and endpoint errors in the initial reaching movements. For the initial perrotary reach the average lateral endpoint error in relation to prerotation reaches was 41 mm rightward; the average peak trajectory deviation of the initial reaches was 56 mm rightward. Subjects also tended to undershoot the distance of the target more than prerotation. Figure 3 illustrates the movement trajectories.

Within three to four perrotary reaching movements every subject showed increased accuracy. Figure 4 shows all movement endpoints and peak trajectory positions averaged across subjects and plotted sequentially. The perrotary lateral endpoint errors diminished quasiexponentially as successive pointing movements were made and the trajectory errors diminished in parallel. By the end of the perrotary period, movement endpoints and trajectories were indistinguishable from those of the prerotation period, being deviated only 7 mm in the direction of the Coriolis forces for endpoint and 10 mm for peak trajectory deviation. Figure 4 also shows that the peak velocity and thus the peak

SLOW-TOUCH

Lateral endpoint and trajectory errors

Peak Velocity

FAST-TOUCH

Lateral endpoint and trajectory errors
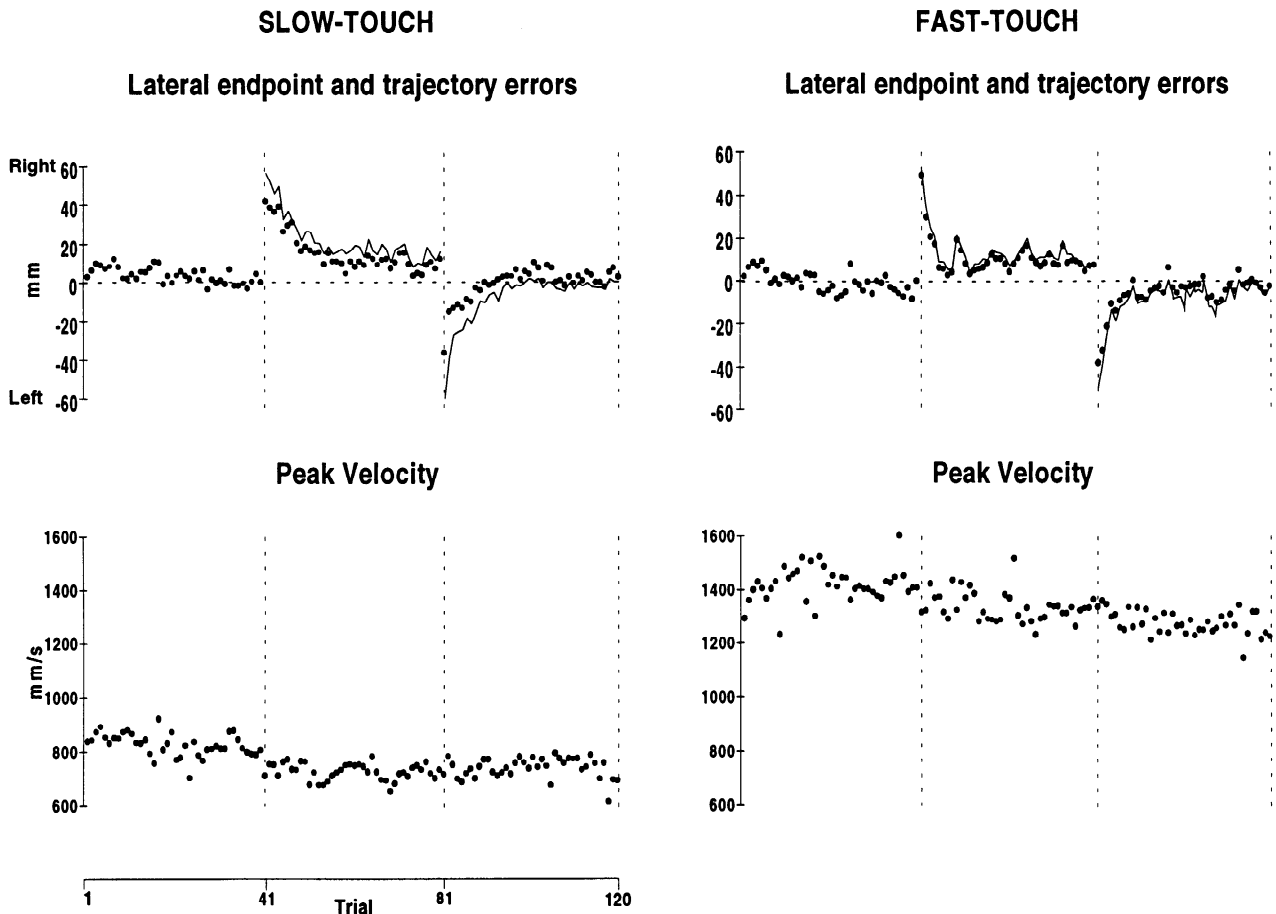
Peak Velocity

FIG. 4. Plots of movement parameters for all 120 reaches of the experiment, averaged for the slow ($n = 11$) and fast ($n = 13$) movements with terminal contact. *Top plots*: dots represent lateral endpoint positions; lines represent the peak lateral trajectory positions. *Bottom plots*: peak velocity of each movement in the horizontal plane.

Coriolis force were virtually constant throughout the perrotation period.

POSTROTARY REACHES. Each subject's first postrotary reach was inaccurate. The magnitudes of the lateral endpoint errors were comparable for initial per and postrotary movements but their directions were opposite. The average endpoint error was 36 mm left of the prerotation baseline. Moreover, the trajectories of the first postrotary reaches were virtually mirror images of the trajectories of the first perrotary movements, with the peak trajectory deviation being 61 mm leftward. In initial perrotary movements the onset of the lateral deviation (relative to the initial prerotation trajectory) had begun as the increasing forward velocity of the arm produced a rapidly increasing rightward Coriolis force; the (oppositely directed) lateral deviations from baseline in the initial postrotary movements appeared slightly earlier in the movement trajectories, as can be seen in the first few samples plotted in Fig. 3. The lateral inflections back toward the target occurred at similar distances into the movements as in the first perrotation movements and were of a comparable magnitude.

The first postrotary movements tended to overshoot target distance, whereas the initial perrotary movements had tended to undershoot. With repeated postrotary pointing movements, accuracy was rapidly regained quasiexponen-

tially, as with the perrotary movements, and the subjects again made straight reaches to the target.

Fast movements with terminal contact

PREROTARY REACHES. All subjects made nearly straight reaches toward the target but ended on average 23 mm to the left of the target. Reaching distance was 20 mm short of the target at the beginning of the period but only 8 mm at the end. The prerotation movement duration was 373 ms and the peak velocity was 1,382 mm/s.

PERROTATION REACHES. Subjects showed large deviations of movement trajectory relative to prerotation reaches in the direction of the Coriolis forces generated by the movements. Across subjects for the initial reach the peak trajectory deviation was 53 mm rightward relative to prerotation reaches. Unlike the slow perrotary movements described above, there was little tendency for the hand to curve back toward the target near the end of the trajectory. The lateral endpoint averaged 51 mm to the left of the prerotation baseline. The distance of the reach was also shortened relative to baseline.

As they made additional reaches, the subjects' arm movement trajectories rapidly regained endpoint accuracy while maintaining straightness. Baseline accuracy was nearly regained in eight movements, but then after the 30-s rest pe-

riod that separated sets of eight movements the next movement was again deviated in the direction of the Coriolis force. This pattern was present to varying extents in all five sets of eight movements and can be seen in Fig. 4. The return of errors after each rest period indicates some loss of adaptation during the 30 s separating movement sets. By the fifth set of eight movements, stable adaptation was largely achieved. The average endpoint error of the subjects' final perrotary reaches was only 9 mm and the average trajectory error was 16 mm.

POSTROTATION REACHES. The first postrotation reaches were deviated leftward—the direction opposite that of the initial perrotation reaches. The average leftward change from baseline was 39 mm for endpoint and 53 mm for peak trajectory position. The return inflection toward the target position occurred near the end of the movement. As with the initial postrotation slow movements, the lateral deviation began very shortly after movement onset. After about eight movements the postrotary movements were again nearly as accurate as the prerotation movements, the endpoints deviating only 4 mm and the trajectories 5 mm.

MIMETIC REACHES. These movements showed that subjects were aware of their lateral endpoint errors in all conditions tested. At both speeds they correctly reproduced the shape of their prerotation and initial postrotation movement trajectories, but their reproductions of the initial perrotation reaches had one more inflection point than the actual reaches.

INDIVIDUAL DIFFERENCES. Every subject in both movement speed conditions showed the following pattern evident in the average data: rightward trajectory and endpoint deviations during initial perrotation reaches, return to prerotation accuracy by the last perrotation reach, leftward deviation of trajectory and endpoint on the first postrotation reach, and return to baseline performance within 40 reaches. The size of the rightward and leftward deviations of per- and postrotation reaches varied from subject to subject. Figure 5 shows that subjects who moved faster, generating larger Coriolis forces, had larger endpoint and trajectory errors on the initial per- and postrotation reaches (note that Fig. 5 also presents data from our 2nd experiment, described above). Subjects also differed in two ways that are not evident from the average data: *1*) baseline endpoint consistency (SD) and *2*) drift of the endpoint baseline (a monotonic change of endpoint throughout the prerotation period, also evident at the ends of the per- and postrotation periods). The direction of drift varied and the right-left deviations due to onset and offset of rotation were superimposed on the drift.

STATISTICAL ANALYSIS. Changes from baseline in lateral movement endpoint and trajectory for the initial perrotation, final perrotation, and initial postrotation trials are summarized in the *top panels* of Fig. 6. A multivariate analysis of variance (ANOVA) (SPSS MANOVA procedure) was performed on endpoint and trajectory changes with movement speed (fast-slow) as a between-subjects factor and rotation exposure (initial per-, final per-, and initial postrotation) as a within-subject factor. It showed only a highly significant effect of rotation exposure [Pillai's Trace $F(4,88) = 19.3, P < 0.001$]. Our primary concern was

whether reaching errors were significantly >0 on the initial per- and postrotation reaches at both movement speeds. Having these predefined questions justifies performing multiple *t* tests, but instead we used post hoc Scheffé 95% confidence intervals, which make it harder to find significant differences. The estimates of variance used for these tests were the within-group mean squared error values from the movement speed × rotation exposure effect from separate univariate ANOVAs performed on the change from baseline scores for endpoint and trajectory. We found identical patterns for endpoint and trajectory: changes from baseline were significantly different from 0 for the initial per- and postrotation trials but were indistinguishable from 0 at the end of the perrotation period for both slow and fast movements.

To determine whether the tendency for trajectories to curve back toward the target was significant we performed an ANOVA on the differences between endpoints and peak trajectory positions. Here there were effects of movement speed [$F(1,22) = 9.66, P = 0.005$] and rotation exposure [$F(2,44) = 15.93, P < 0.001$]. The inflections toward the target were larger for slow movements than fast and for the initial per- and postrotation reaches than the well-adapted final perrotation reaches.

Slow movements without terminal contact cues

Initial perrotation movements showed significant trajectory and endpoint deviations relative to the prerotation movements in the direction of the Coriolis forces generated by the movements. As can be seen in Fig. 7, as a movement neared completion and the Coriolis force diminished, there was an inflection of the finger toward the target position. The finger ended up closer to the target than it had in experiment 1, where contact had been involved, with the average error being 16 mm relative to prerotation. The peak trajectory deviation relative to baseline was 42 mm, also somewhat less than in experiment 1. With repeated movements the subjects made no improvement in endpoint accuracy but the difference between the endpoint and the peak trajectory deviation became as small as in the baseline (see Fig. 8). That is, subjects made straight movements to errant endpoints. The aftereffects also revealed that trajectories had adapted but endpoints had not. The initial postrotation movement trajectories showed significant trajectory deviations in the direction opposite those of the initial perrotation movements, 39 mm leftward. The endpoints of the same reaches were on average 12 mm to the left of baseline. The postrotation movement trajectories were virtually mirror images of those of the initial perrotary movements. After 15–20 postrotary movements, accuracy was restored to prerotation level and movement trajectories were again straight.

Fast movements without terminal contact cues

The initial perrotary movements showed large, 51 mm trajectory deviations relative to prerotation movements. Toward the end of a movement the finger hooked slightly back laterally toward the target location but stopped well short of it, 46 mm rightward. Significant adaptation took place with additional perrotary movements, but endpoints were still 19 mm right of prerotation values after 40 points.

Lateral endpoint error vs. peak velocity

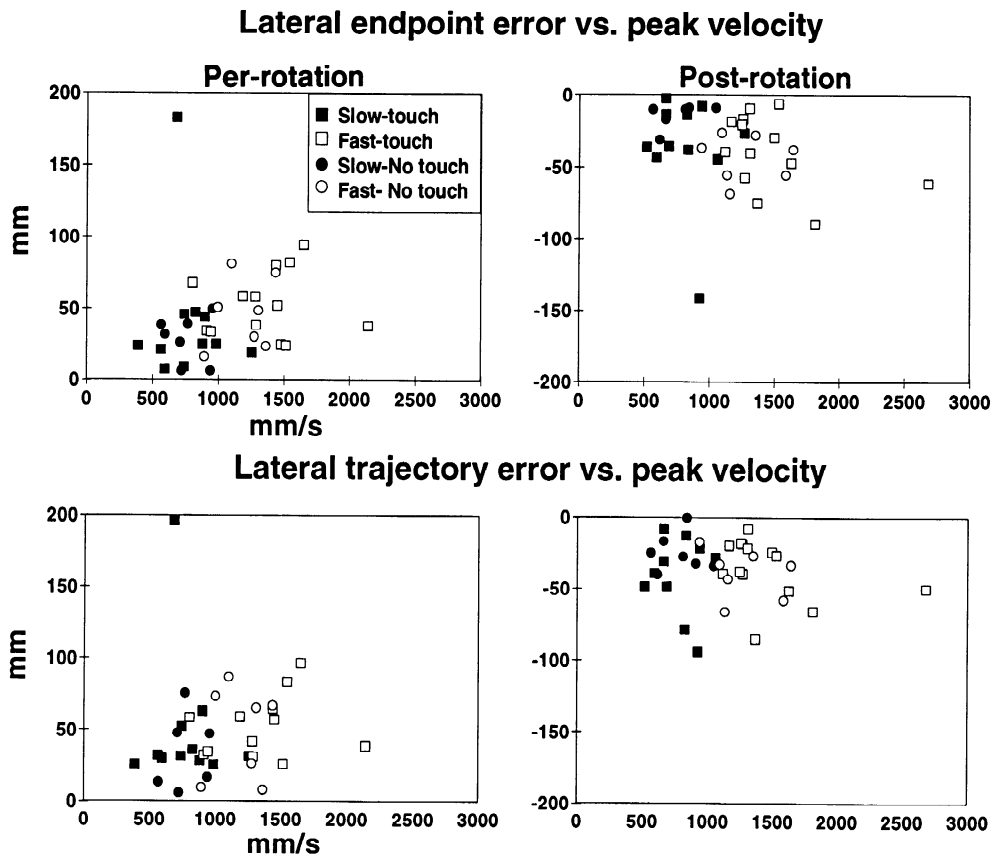## Lateral trajectory error vs. peak velocity

FIG. 5. Plots of lateral endpoint and peak lateral trajectory errors vs. peak velocity for individuals making slow and fast movements where contact was made with the work surface at the end (touch) and where the finger was held in the air above the target at the end (No touch). Error values (change from baseline, prerotation values) are presented for the subjects' 1st perrotation and 1st postrotation reaches in a normal stationary environment after adaptation to Coriolis forces had occurred.

Peak trajectory deviations that had been to the right of the initial perrotary movement endpoints shifted over the course of 40 movements until they exactly equaled endpoints. That is, the movements to the deviated endpoints became straight. The initial postrotation movements were mirror reflections of the perrotary movements; the endpoints deviated 46 mm leftward and the trajectories 58 mm. Within 25 movements, accuracy was back to prerotation levels.

Mimetic reaches

The subjects in the slow and fast noncontact movement conditions made mimetic reaches that accurately reflected the trajectory deviation direction of their initial perrotary and postrotary movements. They were also aware of their endpoint errors except for the slow perrotary reaches, which actually ended to the right of baseline but were reproduced as ending slightly to the left. The reproductions of fast perrotary reaches had one more lateral inflection point than the actual reaches, as was the case for movements with terminal contact, described above.

Statistical analysis

Our first analysis examined the changes from baseline in endpoint and trajectory of movements. A MANOVA revealed a main effect of rotation exposure [Pillai's Trace $F(4,48) = 10.31, P < 0.001$] and an interaction of rotation

and movement speed [Pillai's Trace $F(4,48) = 5.16, P = 0.002$]. Followup univariate analyses showed that the main effect was present for both endpoint and trajectory errors, but the interaction only for endpoints. Post hoc Scheffé tests (0.05 confidence level) showed that the pattern of trajectory errors was the same for fast and slow movements: there were significant deviations from baseline in opposite directions for initial per- and postrotation movements. The trajectory errors of the final perrotation reaches were significantly smaller than the initial perrotary trajectory errors but significantly >0. That is, there was significant but not complete adaptation. The pattern of endpoint errors differed for slow and fast movements. Both had initial perrotation changes from baseline that were significantly >0 but the postrotation aftereffect was significant only for fast movements. The magnitudes of the endpoint errors in these conditions were larger for fast than slow movements. The source of the interaction between movement speed and rotation exposure was identified in comparisons involving the endpoints of final perrotation reaches. Final perrotary endpoints were significantly less deviated than initial perrotary endpoints for fast movements but not for slow. Nevertheless, the absolute sizes of the final perrotary endpoint errors were the same at both speeds and were significantly different from 0 for both. Put differently, for the fast movements without terminal contact, the endpoint errors induced by rotation diminished incompletely, but for slow movements their size remained unchanged.
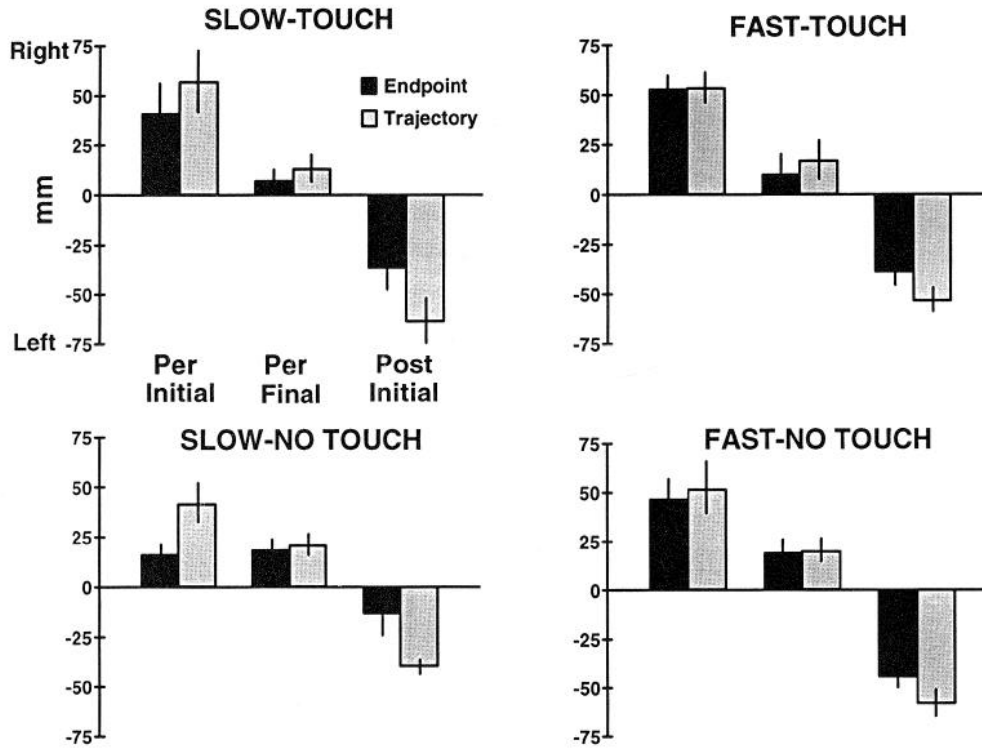
Lateral endpoint and trajectory errors

FIG. 6. Bar graphs of mean errors (changes from baseline, prerotation values) in lateral endpoint and peak lateral trajectory positions. *Top*: averages for subjects who made slow ($n = 11$) and fast ($n = 13$) reaches with terminal contact (TOUCH). *Bottom*: averages for subjects who made slow ($n = 7$) and fast ($n = 7$) reaches with the hand held in the air at the endpoint (NO TOUCH). The graphs show the average for the initial perrotation reaches, where Coriolis forces were 1st generated by a movement, the final perrotation reaches, and the 1st postrotation reaches. Error bars: SE.

The next set of analyses examined differences between lateral endpoints and peak trajectory positions, an index of the amount of corrective curvature occurring within single movements. ANOVA revealed main effects of movement speed [$F(1,12) = 5.56$, $P = 0.036$] and room rotation [$F(2,24) = 8.5$, $P = 0.006$]. Post hoc Scheffé tests ($\alpha = 0.05$) showed that there was corrective curvature in initial per- and postrotary slow movements, but not in fast movements.
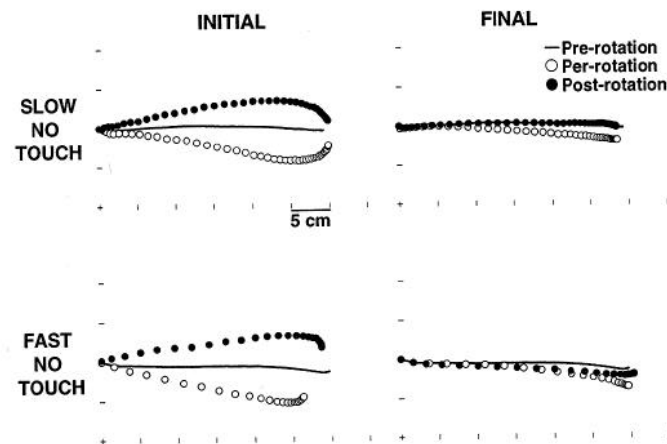

FIG. 7. Top view of the average trajectories for slow ($n = 7$) and fast ($n = 7$) reaches where subjects did not touch the work surface but held the finger in the air above the target. Data treatment is as indicated in Fig. 3.

Our final set of analyses was designed to compare endpoint and trajectory errors across the two experiments to see how movements with and without terminal contact differed. Univariate ANOVAs were performed on endpoint and trajectory errors, with movement speed and contact condition (terminal touch of the finger vs. no touch) as between-subjects factors and rotation exposure as a within-subject factor. The within-group mean squared error value from the movement speed × touch × rotation interaction was used to compute Scheffé 95% confidence intervals to make individual comparisons. No differences in trajectory errors were present between the touch and nontouch conditions for comparable movement speeds and rotation exposure conditions. The only endpoint differences that appeared were for slow movements; the movements without terminal contact had smaller endpoint errors in the initial per- and postrotation reaches. Excluding the one subject who had very large endpoint errors in the slow touch condition (see Fig. 5) did not alter the significance of the difference between the endpoints for the touch and nontouch groups.

DISCUSSION

Movements with terminal contact

The first reaching movements made during rotation show errors of two sorts: large and highly significant trajec-
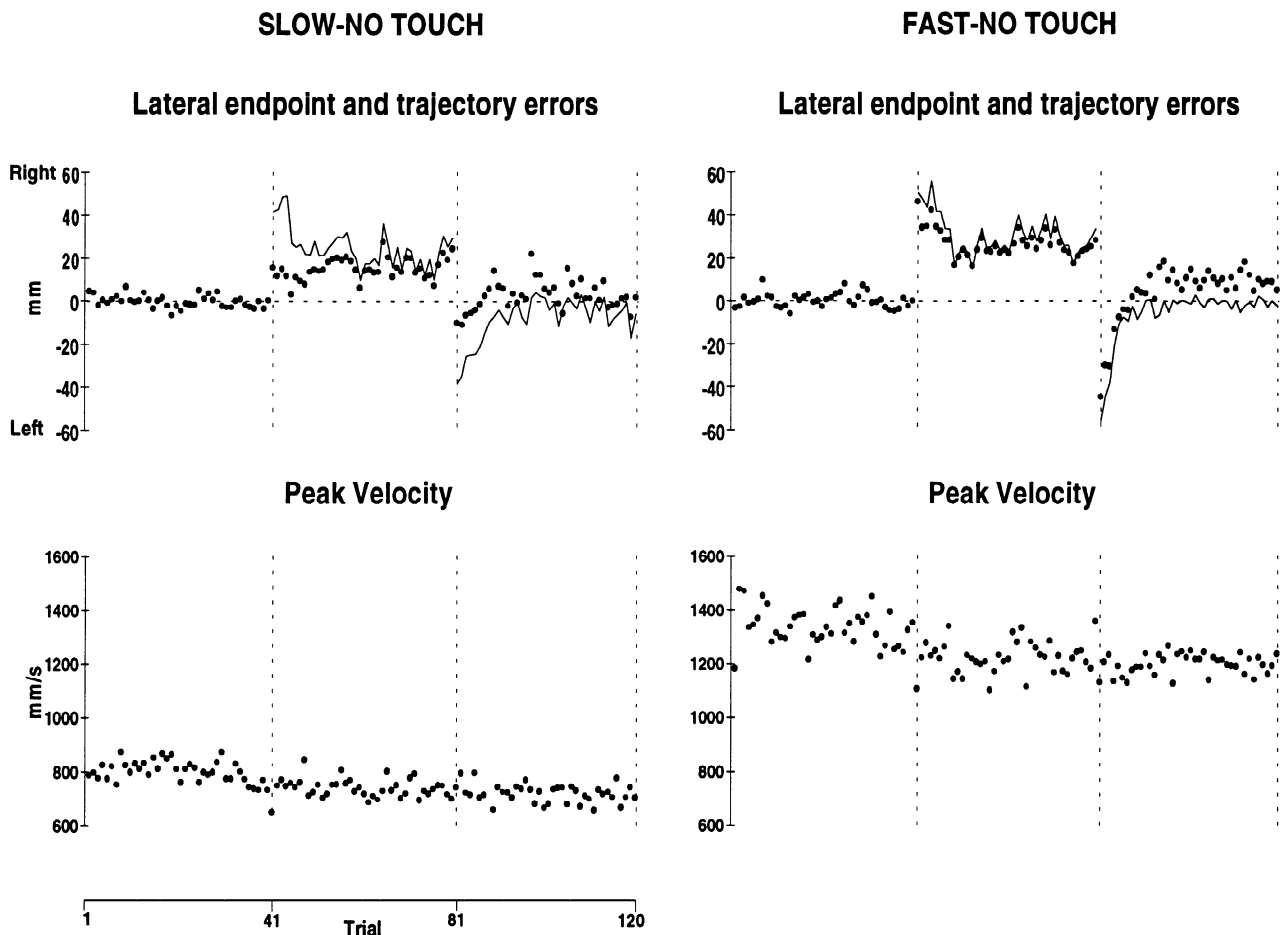
FIG. 8. Plots of movement parameters for all 120 reaches in the experiment, averaged across the subjects who made slow ($n = 7$) and fast ($n = 7$) movements that ended with the finger in the air above the target surface. *Top plots*: dots represent lateral endpoints; lines represent peak lateral trajectory positions. *Bottom plots*: peak velocity in the horizontal plane.

tory deviations in the direction of the rightward Coriolis forces generated by the arm movements, and endpoint errors in the same direction. The initial movement trajectories of every subject were displaced by the Coriolis forces both for slow and fast movements. Endpoint errors were also made by all subjects.[1,2] Despite the absence of visual or

tactile feedback about movement accuracy, subjects rapidly adjusted their pointing movements, doing so more quickly for fast than slow movements. Considering the reduction of endpoint errors as a single exponential process, the "time constant" of return to baseline was 13 reaches for slow movements and 8 for fast movements. For both slow and fast movements, the adaptation was virtually perfect in the sense that the endpoints and trajectories of the final perrotary movements were statistically indistinguishable from baseline. Moreover, on cessation of rotation large errors of opposite sign were made in pointing to the target, indicating the persistence of the adaptation achieved during rotation, i.e., compensation for expected Coriolis forces was still being made although it was no longer appropriate. The aftereffects also suggest complete compensation because their absolute magnitudes were statistically identical to the initial errors during rotation.

These findings fail to support the notion that natural pointing movements to targets are planned and executed as evolving virtual trajectories consisting of a series of equilibrium positions. The Coriolis force generated by a movement during rotation is a temporary, noncontact perturbation dependent on the velocity of the arm. Equilibrium

---

[1] During angular acceleration an observer may see a target light that is physically stationary in relation to the observer to be displacing in the direction of acceleration. This phenomenon, known as the oculogyral illusion, can persist beyond the period of angular acceleration until the semicircular canals return to their equilibrium state (Graybiel and Hupp 1946). Because of this we purposely waited ≥ 1 min after constant velocity was attained and after deceleration to rest before subjects began their pointing movements. For the low acceleration rate used, this was ample time for any oculogyral illusions to dissipate (Evanoff and Lackner 1986). Moreover, our subjects' initial perrotation reaching movements were displaced in the direction of the Coriolis force generated (rightward). If they had mislocalized the visual target because of an oculogyral illusion and pointed to its apparent location, then they would have pointed leftward in the direction of rotation. After completion of the experiments reported here we had the opportunity to test labyrinthine-defective subjects without detectible horizontal semicircular canal or otolith function. They showed the same initial trajectory and endpoint errors as our normal subjects.

[2] Centrifugal force cannot be responsible for the lateral endpoint errors observed in the present experiments. In other experiments we have changed the direction of room rotation. Reversal of direction reverses the direction of the Coriolis forces during reaching but keeps the centrifugal force the same. Subjects show mirror-symmetric endpoint errors for opposite directions of rotation, showing that the errors are attributable to the transient Coriolis forces.

point specification requires that as the Coriolis force diminished toward the end of a movement, the finger should have been brought to the target position by the programmed length-tension relations (or evolving virtual trajectory) of the involved arm muscles.

Movements without terminal contact cues

Initial slow and fast perrotary movements were deviated in their trajectories by the Coriolis forces and remained partially deviated at their termination despite the absence of terminal contact with the target board. Adaptive shifts in movement endpoints did not occur with additional reaches for the slow movement speed and only incompletely for the fast. However, for both movement speeds, the trajectories adapted completely in the sense that perrotary movements to altered endpoints became straight reaches to the wrong place. The persistence of trajectory adaptation resulted in curvature of initial postrotary trajectories in the direction opposite the Coriolis forces that had been present during rotation. The lack of perrotation endpoint adaptation for slow movements led to an immediate return to baseline endpoints for the initial postrotary reaches. By contrast, the perrotary endpoint adaptation for fast movements led to leftward postrotary endpoint errors.

Implications for equilibrium point hypotheses

There are four facts relevant to equilibrium point hypotheses that emerge from our results: *1*) the trajectories and endpoints of natural reaching movements were deviated in the direction of unexpected Coriolis forces, *2*) the size of the endpoint errors was smallest for slow movements that did not involve final contact with a surface, *3*) with repeated exposure to Coriolis forces the endpoint accuracy and straight-line trajectories characteristic of unperturbed movements were restored for movements with terminal contact despite denial of visual and tactile feedback about target position, and *4*) adaptation of endpoint and trajectory occurred independently in movements made without terminal contact.

Failure of the equifinality prediction is a serious disconfirmation of all current equilibrium point hypotheses of movement control. This prediction is that the position of a limb, given time to come to rest, should be the same when the external loads and programmed length-tension relationships are the same. In our experiment the arm came to rest at different positions when transient Coriolis forces were present even though the external loads were identical at the endpoint of every reach. The Coriolis force perturbations in our experiment had magnitudes of 3–13 N, assuming a 4.5-kg mass of the arm. This corresponds with the ranges used in other perturbation experiments that have reported equifinality (Bizzi et al. 1982, 1984; Feldman 1974; Mussa-Ivaldi et al. 1985).

Several differences between our approach and other paradigms may explain the contrasting outcomes. First, others have studied planar single or dual joint movements in terms of joint angles (Bizzi et al. 1984; Feldman 1974); we have measured the position of a natural multijoint movement in terms of extrinsic spatial coordinates of the end effector. The ~45-mm lateral endpoint errors we found at

the finger translate into an error of ~4.5° about the shoulder. In terms of reaching movement accuracy, this represents a highly significant functional error.

Second, there were no touch cues concurrent with perturbations of the arm in our experiment; but in other tests of equilibrium point hypotheses, perturbations have been delivered through a handle or arm holder. Interestingly, when the skin is anesthetized, subjects attempting goal-directed thumb movements make endpoints errors if perturbed by a contact force (Day and Marsden 1982). This finding suggests that unanesthetized subjects given a "do not intervene" instruction may unintentionally make use of spatially relevant touch cues to alter ongoing movements or to correct subsequent ones that are made. In experiments where the individual is attempting to position an external manipulandum to a target or goal position during simulated inertial (e.g., Shadmehr and Mussa-Ivaldi 1993) or viscous (Sanes 1986) loads, the results show what happens when an environmental object being held behaves differently than expected. These studies are perhaps best considered analyses of adaptive tool use or tool manipulation. By contrast, our study represents an analysis of adaptive limb movement control per se.[3]

Third, we observed rapid adaptation to Coriolis force perturbations. We took great care to test naive subjects and to measure their very first responses in a rotating environment, and observed nearly normal behavior after only 8–10 reaches in conditions with terminal contact. Other experiments may not have analyzed these first few critical movements and thereby missed the involvement of adaptive mechanisms. Fourth, we tested multiple movement speeds with and without terminal contact. The smaller endpoint errors we found in the nontouch slow movement condition may be considered more consistent with equilibrium point hypotheses; however, the large errors for fast movements without terminal contact are inconsistent. The fast movements are in fact a more critical test of the hypothesis because they better reflect central planning, being performed in a more open-loop fashion. The absence of behavior predicted by equilibrium point models, except in the case of a slowly moving limb not contacting anything, suggests that the springlike behavior of muscle systems is more functionally relevant for control of posture than movement.

The presence and character of adaptation in our experiment are also problematic for equilibrium point hypothesis. All forms of the hypothesis have stressed that central commands that tune the springlike qualities of muscles unify theoretically the description of posture and movement (cf. Bizzi et al. 1992 and Feldman 1986 for reviews). We have observed complete adaptation of movement trajectories with incomplete or no adaptation of endpoints. In the slow movements without terminal contact the deviation of the endpoint of the arm by Coriolis forces never

---

[3] In experiments involving head movements during body rotation we have found that subjects show different responses depending on whether mechanical contact on the head is involved. Subjects who receive mechanical stimulation that deviates the head trajectory adapt over time so that their head movements again become normal. When they are tested without the mechanical contact present they show little evidence of the adaptive compensation, indicating that it is specific to the apparatus (the tool) used and the presence of contact cues.

diminished in 40 reaches, but the trajectories of movements to the altered endpoint became just as straight as prerotation. For fast movements with no contact there was partial reduction of endpoint errors induced by Coriolis forces but the initially curved trajectories became as straight as in normal conditions. The symmetrical curvature of initial per- and postrotation trajectories for both slow and fast (no contact) movements and the greatly reduced or nonexistent endpoint errors in the postrotation period confirm the independence of endpoint and trajectory adaptation and control. This is inconsistent with the idea of unified control of posture and movement.

That subsequent movements disrupted by Coriolis forces gradually resume straight-line trajectories means that a straight-line kinematic plan is formulated independent of dynamic conditions before the execution stage (see also Morasso 1981). The achievement of such adaptation without visual or tactile feedback indicates that proprioceptive feedback from the arm in relation to efferent signals is sufficient. Our subjects' ability to mimic reasonably accurately their initial perrotation movements in terms of trajectory deviations means that such information is continuously monitored.[4] That is, information about muscle force, length, rate of change in length, and joint angle during movement is used to plan forces for the next movement that will incrementally cancel the Coriolis force loads anticipated. Adaptive mechanisms (e.g., Bullock and Grossberg 1988; Jordan and Rumelhart 1992; Lackner 1981) must be monitoring and adjusting movement dynamics. Equilibrium point models claim to relieve the CNS of this complex computational burden. Our results show that any model of execution must deal with it, so equilibrium point models have no advantage over ones that explicitly purport to solve the inverse dynamics and inverse kinematics problems (Hollerbach 1981; Hollerbach and Atkeson 1987). Hasan and Stuart (1988) have expressed the same view.

Role of spindle signals in adaptation to Coriolis perturbations of arm trajectory

Our subjects' initial postrotation reaches were always mirror-symmetric to their initial prerotation reaches. This means that compensation for the Coriolis forces was programmed in the form of a trajectory compensation so that after adaptation was complete the perrotation reaches (viewed from above) had straight-line trajectories like the prerotation reaches (see Figs. 3 and 7).

Trajectory adaptation occurred in all four of our experimental conditions regardless of movement speed and whether the hand made contact with the target board surface at the end of the movement. The subjects never received visual or tactile feedback about hand position, movement trajectory, or movement endpoint in relation to the target. Consequently, the adaptive replanning of move-

ment trajectory had to be based on "detecting" that the actual movement path did not correspond to that intended.[4] Spatial information about limb position is known to be contributed in substantial part by muscle spindle primary and secondary endings. Primaries are thought to provide a velocity and position signal and secondaries a position signal (Matthews 1972). Matthews (1964, 1988) has shown that to be functionally useful these signals have to be interpreted in relation to information about ongoing motor commands, i.e., efference copies.

The contribution of spindle input to the appreciation of limb position can be seen when a skeletal muscle is mechanically vibrated at ∼100–120 Hz. Such vibration elicits a tonic vibration reflex, causing the muscle to contract (Hagbarth and Eklund 1966). If the muscle is prevented from shortening by restraining the limb that it controls, then apparent motion of the limb will be experienced in the direction that would be associated with physical lengthening of the vibrated muscle (Goodwin et al. 1972). For example, vibration of biceps brachii causes illusory extension of the restrained forearm. Lackner and Levine (1979) demonstrated that by vibrating the appropriate postural muscles of the restrained body, apparent rotation or tilt of the body could be elicited about virtually any desired axis.

The normal relationship between muscle innervation and trajectory is also affected by exposure to nonearth gravity background force levels. Lowering and raising the body in a deep knee bend is achieved by trajectory control of the legs. When a person first lowers the body in a deep knee bend during exposure to a twice-earth gravity background force level (2 g), the person misperceives the movement trajectory. The person feels that the downward motion is too rapid and that the supporting surface has simultaneously moved upward under the feet (Lackner and Graybiel 1981). By contrast, during exposure to half-earth gravity, a person feels that the downward motion is too slow and that the support surface has also moved downward. When subjects make repeated deep knee bends at the altered force level their movements rapidly begin to seem normal again (Lackner 1990). However, on reexposure to the usual 1 g background force level of earth, their movements again feel abnormal and the surroundings seem to move as they do; but, in a fashion, that is consistent with a persistence of adaptation to the altered force level. Lackner (1985, 1990) has shown how misapprehensions of movement trajectory in altered background force levels can be related to mismatches between expected and actual patterns of spindle feedback in relation to movement commands. In fact, the effects can be predicted on the basis of the muscle vibration illusions.

These observations are synergistic with the present pointing results. In both situations mismatches are present between expected and occurring patterns of spindle feedback in relation to efferent commands, misperceptions of movement trajectories occur, and adaptation takes place rapidly with additional movements. There is also evidence from a variety of other sources that one can monitor efferent commands and relate them to associated afferent signals. For example, most models to explain the perceptual stability of the visual world during voluntary eye movements include relating representations of efferent signals (corollary dis-

---

[4] We have recently repeated the fast and slow arm movement conditions of experiment 1 with one variation (Lackner and DiZio 1993). After each pointing response subjects were allowed to correct their endpoints if they thought they had missed the target. Subjects always detected accurately the direction of the trajectory deviation induced by the Coriolis force. Paradoxically, their pattern of endpoint correction movements shows that they often made endpoint "corrections" by moving in the wrong direction.

charge) to the extraocular muscles and signals specifying changing retinal stimulation (cf. Grüsser 1987 for a review).

The production of speech is a quintessential example of trajectory control and the muscles involved have dense spindle representations. Lackner and Tuller (1979) have shown that during speech production several types of efference monitoring and sensory feedback evaluation take place and that subjects can monitor and compare the efferent commands issued to the musculature with those intended. This allows the detection of self-produced speech errors at far shorter latencies than those for acting on the basis of auditory or proprioceptive feedback. Command errors involving very small timing differences are more difficult to detect than those involving distortions of the intended trajectory. For example, an important difference in the production of [pi] versus [bi] is that vocal band vibration begins ~90 ms earlier for the voiced [bi], all other production details being the same, whereas for [di] versus [gi], the tongue tip makes contact with the alveolar ridge as opposed to the velum so that a different spatial trajectory and endpoint are involved. Trajectory errors such as producing [di] instead of [gi] can be readily detected with reaction times <100 ms, i.e., before the speech sound is even completed. These observations mean that a representation of the desired trajectory is available for comparison with the trajectory actually initiated or to be initiated.

If as we talk our voice is fed back to us over headphones but delayed by ~200 ms, this tends to disrupt our speech and speech sounds will be omitted or repeated and the pace of speaking will be affected. In studies of adaptation to delayed auditory feedback, Katz and Lackner (1977) found that subjects are able to improve their performance by the development of particular production strategies. To account for their observations they introduced the concept of "confirmatory feedback," feedback that cannot be used during the production of a particular series of speech trajectories because of the rapidity with which they are executed but that is of key importance in indicating whether or not the produced sequence corresponded to the intended one. It provides the basis for determining what compensatory changes are necessary for subsequent movements. Adults who become deaf show progressive degradation of their speech production, losing precise control of timing, pitch, and intensity in the absence of confirmatory feedback.

Recently, in a paper directly relevant to the present pointing experiments, Ghez and colleagues have reported on movement control in a patient with large fiber sensory neuropathy (Ghez et al. 1990). This disorder eliminates position sense, so that this patient is only aware of the position of her limbs when she can see them. She is quite accurate in pointing to visual targets when allowed ongoing visual feedback about her movements, but rapidly becomes inaccurate when denied visual feedback. Ghez et al. (1990) suggest that the proprioceptive feedback that normally accompanies limb movements may be used to update control parameters to maintain accurate sensorimotor control, that is, it functions as confirmatory feedback. Their observations demonstrate the importance of being able to monitor movement trajectory for maintaining movement accuracy for subsequent movements.

The present results complement those of Ghez and colleagues by showing that subjects can monitor both movement position and velocity and after a disturbance is introduced and can begin updating control on the next movement on the basis of proprioceptive and motor signals. The ability to detect both position and velocity is demonstrated by the ability of our subjects to reinstate straight-line movement trajectories during exposure to Coriolis forces. The adaptive compensation is a "mirror image" innervational pattern that cancels the position and velocity deviation of the trajectory due to the Coriolis forces.

Physiological mechanisms for recalibrating movement trajectory

What physiological mechanisms might account for the adaptive modifications of trajectory that our subjects exhibited with continued exposure to Coriolis perturbations? On what bases can it be determined that intended and actual movement trajectories do not correspond and a direction for compensatory action be calculated? Studies by Asanuma et al. (1979), Evarts (1968), and Fetz and Cheney (1980) have shown that individual corticospinal tract neurons encode the direction of force and magnitude of force exerted. In early work, Evarts showed that rate of change of force seems to be especially salient, thus allowing a limited discharge frequency range to be associated with a wide range of force generation, much as sensory neurons can encode broad intensity domains. Georgopoulos and colleagues (1982, 1983) have demonstrated that the trajectory direction of a limb movement can be coded by a population vector that represents the resultant activity of many neurons, each with relatively broad individual directional tuning. Recently, Georgopoulos has also described population vectors related to force generation that code dynamic force, net force, and bias force owing to gravity. Because the direction of net or total force exerted and that of dynamic force can be represented independently, the dynamic force can be dissociated from the static force. This distinction is important for the model presented below.

Physiological (Asanuma et al. 1979) and anatomic (Strick and Preston 1978) studies have shown that many neurons in primary motor cortex receive both proprioceptive signals from the muscles that they innervate and tactile signals from the skin of the appendage they control. As Asanuma has pointed out, this arrangement reflects an organization parallel to that present at the spinal cord level and serving to mediate a variety of segmental and intersegmental reflexes including the stretch reflex. Asanuma suggests that the cortical organization might function in long-loop reflexes that can complement and augment the gain of the functional stretch reflex.

We propose that a comparator function could also be provided by this cortical motor connectivity. Motor command cells and population vector ensembles may receive sensory feedback about muscle action in terms of length and change in length as well as whether tactile contact has been made on the limb surface. If a movement is mechanically perturbed, the proprioceptive feedback from the muscles will not correspond to that which normally would occur for the motor commands issued and there would be
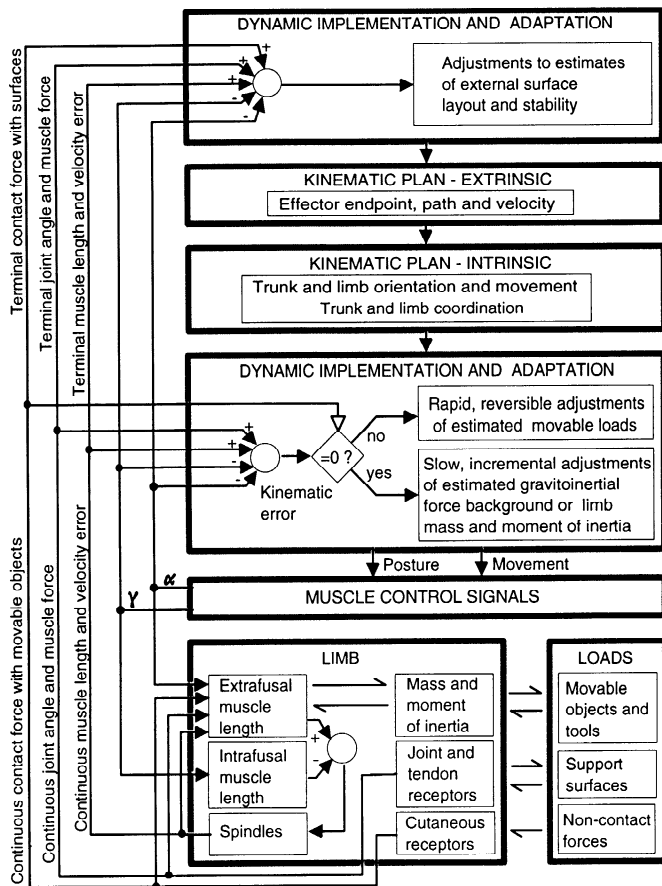
FIG. 9. Model of movement control and adaptation to contact and noncontact forces. See text for explanation.

tactile feedback indicating obstruction and locus of obstruction; depending on voluntary set, such a pattern could lead to load compensation responses to complete the movement. By contrast, if the proprioceptive feedback were inappropriate and tactile cues were absent, such as with Coriolis perturbations, this would mean that the control of limb trajectory per se was inaccurate, in other words, that an adaptive recalibration of limb movement control was immediately in order. This distinction thus provides within population vector modules in the motor cortex a way of distinguishing on the basis of proprioceptive, tactile, and motor signals between perturbations in the environment for which accommodation needs to be made and changes in limb dynamics and inertia for which adaptive modifications need to be made.

Figure 9 presents a model embodying these distinctions showing how movement trajectory could be monitored so that deviations from expected trajectory could be detected and used to update later movements, much as Katz and Lackner (1977) found confirmatory feedback to be used in speech production control. Visual feedback could be incorporated in this model as well to provide the distal teacher function proposed by Jordan and Rumelhart (1992). In the figure, the *top boxes* outlined by heavy lines represent separate processes and planning; the *bottom two boxes* represent a limb and its loads. Lines with arrows represent sensory and motor information flow and direction; lines with half-arrows represent mechanical and inertial forces and their

direction of action. At summation points (O) the sign of each input (+ or −) is indicated. At decision points (◇), the open arrows indicate the signal being evaluated and the filled arrows the information transmitted. The effects of contact and noncontact forces on muscles are distinguished. Sensory information about loads comes from joint, tendon, cutaneous, and spindle receptors. Information from the muscle spindles depends on the level of both α and γ motor signals. Sensory signals are monitored throughout a movement and at the end. The terminal sensory signals together with the efferent commands are used in dynamic implementation and adaptation to generate an updated representation of surface layout. The kinematic plan stages use this "layout" to constrain movement endpoint and trajectory. This allows adaptive remapping of endpoint with maintenance of a straight-line trajectory. The other dynamic implementation and adaptation process monitors the sensorimotor signals throughout a movement to determine whether there is a trajectory error and whether the error is due to an external perturbation. If an error is present and cutaneous cues indicate contact, an estimate of the object being contacted can be rapidly made, such as when one learns to move an unexpected weight. If local contact cues are absent, alterations are made in estimates of the limb's inertia, moment of inertia, or the gravitoinertial force; this is a quasiexponential process. Separate representations of external objects, limb inertia, and gravitoinertial force are included because our experimental findings indicate that muscle control signals cannot generate accurate limb trajectories or endpoints without taking into account factors that affect limb dynamics. Separate motor commands for movement and posture are included to indicate the possibility that equilibrium point control may be approximately adequate for slow movements without terminal contact; such movements are like assuming an unloaded posture.

Presumably the adaptive changes that are instituted when limb or muscle dynamics are altered would also involve the participation of cerebellar mechanisms that are known to be implicated in a wide range of adaptive, plastic changes (Ito 1971; Marr 1969). In fact, the cerebellum also receives the appropriate signal combinations to make the computations that are exemplified in the model. Consequently, cerebellum and motor cortex, separately and in synergy, could make the distinctions described.

REFERENCES

AGARWAL, G. C. AND GOTTLIEB, G. L. Compliance of the human ankle joint. *J. Biomech. Eng.* 99: 166–170, 1977.
ASANUMA, H., LARSEN, K. D., AND YUMIYA, H. Direct sensory pathways

to the motor cortex in the monkey: a basis of cortical reflexes. In: *Integration in the Nervous System,* edited by H. Asanuma and V. J. Wilson. Tokyo: Igaku Shoin, 1979, p. 223–238.

BIZZI, E. Central and peripheral mechanisms in motor control. In: *Tutorials in Motor Behavior,* edited by G. E. Stelmach and J. Requin. Amsterdam: North-Holland, 1980, p. 131–143.

BIZZI, E., ACCORNERO, N., CHAPPLE, W., AND HOGAN, N. Arm trajectory formation in monkeys. *Exp. Brain Res.* 46: 139–143, 1982.

BIZZI, E., ACCORNERO, N., CHAPPLE, W., AND HOGAN, N. Posture control and trajectory formation during arm movement. *J. Neurosci.* 4: 2738–2744, 1984.

BIZZI, E., DEV, P., MORASSO, P., AND POLIT, A. Effect of load disturbances during centrally initiated movements. *J. Neurophysiol.* 41: 542–556, 1978.

BIZZI, E., HOGAN, N., MUSSA-IVALDI, F. A., AND GISZTER, S. Does the nervous sytem use equilibrium point control to guide single and multiple joint movements? *Behav. Brain Sci.* 15: 603–613, 1992.

BIZZI, E., MUSSA-IVALDI, F. A., AND GISZTER, S. Computations underlying the execution of movement: a biological perspective. *Science Wash. DC* 253: 287–291, 1991.

BIZZI, E., POLIT, A., AND MORASSO, P. Mechanisms underlying achievement of final head position. *J. Neurophysiol.* 39: 435–444, 1976.

BOCK, O., HOWARD, I. P., MONEY, K. E., AND ARNOLD, K. E. Accuracy of aimed arm movements in changed gravity. *Aviat. Space Environ. Med.* 63: 994–998, 1992.

BULLOCK, D. AND GROSSBERG, S. Neural dynamics of planned arm movements: emergent invariants and speed-accuracy properties during trajectory formation. *Psychol. Rev.* 95: 49–90, 1988.

COHEN, M. M. Hand-eye coordination in altered gravitational fields. *Aerosp. Med.* 41: 647–469, 1970.

COOKE, J. D. Dependence of human arm movements on limb mechanical properties. *Brain Res.* 165: 366–369, 1979.

DAY, B. L. AND MARSDEN, C. D. Accurate repositioning of the human thumb against unpredictable dynamic loads is dependent upon peripheral feedback. *J. Physiol. Lond.* 327: 393–407, 1982.

DIZIO, P. AND LACKNER, J. R. Arm movement endpoint errors induced by Coriolis stimulation. *Soc. Neurosci. Abstr.* 18: 516, 1992.

DIZIO, P. AND LACKNER, J. R. Transfer of adaptation to Coriolis force perturbations from the exposed to the non-exposed arm. *Soc. Neurosci Abstr.* 19: 1595, 1993.

EVANOFF, J. N. AND LACKNER, J. R. Influence of voluntary ocular deviation on vestibular nystagmus. *Acta Oto-laryngol.* 102: 450–456, 1986.

EVARTS, E. V. Relation of pyramidal tract activity to force exerted during voluntary movement. *J. Neurophysiol.* 31: 14–27, 1968.

FELDMAN, A. G. Functional tuning of the nervous system during control of movement or maintenance of a steady posture. II. Controllable parameters of the muscle. *Biophysics* 11: 498–508, 1966a.

FELDMAN, A. G. Functional tuning of the nervous system during control of movement or maintenance of a steady posture. III. Mechanographic analysis of the execution by man of the simplest motor task. *Biophysics* 11: 766–775, 1966b.

FELDMAN, A. G. Change of muscle length as a consequence of a shift in equilibrium of a muscle-load system. *Biophysics* 19: 534–538, 1974.

FELDMAN, A. G. Superposition of motor programs. I. Rhythmic forearm movements in man. *Neuroscience* 5: 81–90, 1980.

FELDMAN, A. G. Once more for the equilibrium point hypothesis (λ model). *J. Mot. Behav.* 18: 17–54, 1986.

FETZ, E. E. AND CHENEY, P. O. Postspike facilitation of forelimb muscle activity by primate corticomotoneuronal cells. *J. Neurophysiol.* 44: 751–772, 1980.

FISK, J., LACKNER, J. R., AND DIZIO, P. Gravitoinertial force level influences arm movement control. *J. Neurophysiol.* 69: 504–511, 1993.

GEORGOPOULOS, A. P., CAMINITI, R., KALASKA, J. F., AND MASSEY, J. T. Spatial coding of movement: a hypothesis concerning the coding of movement direction by motor cortical populations. *Exp. Brain Res. Suppl.* 7: 327–336, 1983.

GEORGOPOULOS, A. P., KALASKA, J. F., CAMINITI, R., AND MASSEY, J. T. On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *J. Neurosci.* 2: 1527–1537, 1982.

GHEZ, C., GORDON, J., GHILARDI, M. F., CHRISTAKOS, C. N., AND

COOPER, S. E. Roles of proprioceptive input in the programming of arm trajectory. *Cold Spring Harbor Symp. Quant. Biol.* 55: 837–847, 1990.

GOODWIN, G. M., McCLOSKEY, D. I., AND MATTHEWS, P. B. C. The contribution of muscle efferents to kinesthesia shown by vibration induced illusions of movement and by paralysing joint afferents. *Brain* 95: 705–748, 1972.

GRAYBIEL, A. AND HUPP, D. I. The oculogyral illusion: a form of apparent motion which may be observed following stimulation of the semicircular canals. *J. Aviat. Med.* 3: 1–12, 1946.

GRÜSSER, O. J. Interaction of efferent and afferent signals in visual perception. A history of ideas and experimental paradigms. In: *Sensorimotor Interactions in Perception and Action,* edited by D. G. Bouwhuis, B. Bridgeman, D. A. Owens, W. L. Shebilske, and P. Wolf. Amsterdam: North-Holland, 1987, p. 3–22.

HAGBARTH, K.-E. AND EKLUND, G. Motor effects of vibrating muscle sitmuli in man. In: *Muscular Afferents and Motor Control,* edited by R. Granit. Stockholm: Almqvist & Wiksell, 1966, p. 177–186.

HALLETT, M., SHAHANI, B. T., AND YOUNG, R. R. EMG analysis of stereotyped voluntary movements in man. *J. Neurol. Neurosurg. Psychiatry* 38: 1154–1162, 1975.

HASAN, Z. AND STUART, D. G. Animal solutions to problems of movement control: the role of proprioceptors. *Annu. Rev. Neurosci.* 11: 199–223, 1988.

HOFFER, J. A. AND ANDREASSEN, S. Regulation of soleus muscle stiffness in premammillary cats: intrinsic and reflex components. *J. Neurophysiol.* 45: 267–285, 1981.

HOGAN, N. An organizing principle for a class of voluntary movements. *J. Neurosci.* 4: 2745–2754, 1984.

HOLLERBACH, J. M. Computers, brain, and control of movements. *Trends Neurosci.* 5: 189–192, 1981.

HOLLERBACH, J. M. AND ATKESON, C. G. Deducing planning variables from experimental arm trajectories: pitfalls and possibilities. *Biol. Cybern.* 56: 279–292, 1987.

HOUK, J. C. AND RYMER, W. Z. Neural control of muscle length and tension. In: *Handbook of Physiology. The Nervous System. Motor Control.* Bethesda, MD: Am. Physiol. Soc., 1981, sect. 1, vol. II, p. 257–324.

ITO, M. Neural design of the cerebellar motor control system. *Brain Res.* 40: 81–85, 1971.

JORDAN, M. I. AND RUMELHART, D. E. Forward models: supervised learning with a distal teacher. *Cognit. Sci.* 16: 307–354, 1992.

JOYCE, G. C., RACK, P. M. H., AND WESTBURY, D. R. The mechanical properties of cat soleus muscle during controlled lengthening and shortening movements. *J. Physiol. Lond.* 204: 461–474, 1969.

KATZ, D. AND LACKNER, J. R. Adaptation to delayed auditory feedback. *Percept. Psychophys.* 22: 476–486, 1977.

KELSO, J. A. S. Motor control mechanisms underlying human movement reproduction. *J. Exp. Psychol.* 3: 529–543, 1977.

LACKNER, J. R. Some aspects of sensory-motor control and adaptation in man. In: *Intersensory Perception and Sensory Integration,* edited by R. D. Walk and H. L. Pick. New York: Plenum, 1981, p. 143–173.

LACKNER, J. R. Human sensory-motor adaptation to the terrestrial force environment. In: *Brain Mechanisms and Spatial Vision,* edited by D. Ingle, M. Jeannerod, and D. Lee. Amsterdam: Nijhoff, 1985, p. 175–210.

LACKNER, J. R. Sensory-motor adaptation to high force levels in parabolic flight manuevers. In: *Attention and Performance,* edited by M. Jeannerod. Hillsdale, NJ: Erlbaum, 1990, vol. 13, p. 527–548.

LACKNER, J. R. AND DIZIO, P. Rapid adaptation of arm movement endpoint and trajectory to Coriolis force perturbations. *Soc. Neurosci. Abstr.* 18: 515, 1992.

LACKNER, J. R. AND DIZIO, P. Factors contributing to initial reaching errors and adaptation to Coriolis force perturbations. *Soc. Neurosci. Abstr.* 19: 1595, 1993.

LACKNER, J. R. AND GRAYBIEL, A. Illusions of postural, visual, and substrate motion elicited by deep knee bends in the increased gravitoinertial force phase of parabolic flight. *Exp. Brain Res.* 44: 312–316, 1981.

LACKNER, J. R. AND LEVINE, M. S. Changes in apparent body orientation and sensory localization induced by vibration of postural muscles: vibratory myesthetic illusions. *Aviat. Space Environ. Med.* 50: 346–354, 1979.

LACKNER, J. R. AND TULLER, B. Role of efference monitoring in the detection of self-produced speech errors. In: *Sentence Processing,* edited by

E. C. T. Walker and W. E. Cooper. Cambridge, MA: MIT Press, 1979, p. 281–294.

MARR, D. A theory for cerebellar cortex. *J. Physiol. Lond.* 202: 437–470, 1969.

MATTHEWS, P. B. C. The dependence of tension upon extension in the stretch reflex of the soleus of the decerebrate cat. *J. Physiol. Lond.* 47: 521–546, 1959.

MATTHEWS, P. B. C. Muscle spindles and their motor control. *Physiol. Rev.* 44: 219–288, 1964.

MATTHEWS, P. B. C. *Mammalian Muscle Receptors and Their Central Actions.* London: Arnold, 1972.

MATTHEWS, P. B. C. Proprioceptors and their contribution to somatosensory mapping: complex messages require complex processing. *Can. J. Physiol. Pharmacol.* 66: 430–438, 1988.

MORASSO, P. Spatial control of arm movements. *Exp. Brain Res.* 42: 223–227, 1981.

MUSSA-IVALDI, F. A., HOGAN, N., AND BIZZI, E. Neural, mechanical and geometric factors subserving arm posture in humans. *J. Neurosci.* 5: 2732–2743, 1985.

MUSSA-IVALDI, F. A., MORASSO, P., AND ZACCARIA, R. Kinematic networks. A distributed model for representing and regularizing motor redundancy. *Biol. Cybern.* 60: 1–6, 1989.

NICHOLS, T. R. AND HOUK, J. C. Improvement in linearity and regulation of stiffness that results from actions of stretch reflex. *J. Neurophysiol.* 39: 119–142, 1976.

RACK, P. M. H. Limitations of somatosensory feedback in control of posture and movements. In: *Handbook of Physiology. The Nervous System. Motor Control.* Bethesda, MD: Am. Physiol. Soc., 1981, sect. 1, vol. II, p. 229–256.

RACK, P. M. H. AND WESTBURY, D. R. The effects of length and stimulus rate on tension in the isometric cat soleus muscle. *J. Physiol. Lond.* 204: 443–460, 1969.

RACK, P. M. H. AND WESTBURY, D. R. The short range stiffness of active mammalian muscle and its effect on mechanical properties. *J. Physiol. Lond.* 240: 331–350, 1974.

SANES, J. N. Kinematic and endpoint control of arm movements is modified by unexpected changes in viscous loading. *J. Neurosci.* 6: 3120–3127, 1986.

SHADMEHR, R. AND MUSSA-IVALDI, F. A. Geometric structure of the adaptive controller of the human arm. Artificial Intelligence Laboratory memo no. 1437 and Center for Biological and Computational Learning memo no. 82. Cambridge, MA: MIT, 1993.

STRICK, P. L. AND PRESTON, J. B. Multiple representation in the primate motor cortex. *Brain Res.* 154: 336–370, 1978.