Gravitoinertial Force Background Level Affects Adaptation to Coriolis Force Perturbations of Reaching Movements

JAMES R. LACKNER AND PAUL DIZIO
Ashton Graybiel Spatial Orientation Laboratory, Brandeis University, Waltham, Massachusetts 02254-9110

Lackner, James R. and Paul DiZio. Gravitoinertial force background level affects adaptation to Coriolis force perturbations of reaching movements. J. Neurophysiol. 80: 546–553, 1998. We evaluated the combined effects on reaching movements of the transient, movement-dependent Coriolis forces and the static centrifugal forces generated in a rotating environment. Specifically, we assessed the effects of comparable Coriolis force perturbations in different static force backgrounds. Two groups of subjects made reaching movements toward a just-extinguished visual target before rotation began, during 10 rpm counterclockwise rotation, and after rotation ceased. One group was seated on the axis of rotation, the other 2.23 m away. The resultant of gravity and centrifugal force on the hand was 1.0 g for the on-center group during 10 rpm rotation, and 1.031 g for the off-center group because of the 0.25 g centrifugal force present. For both groups, rightward Coriolis forces, ≈0.2 g peak, were generated during voluntary arm movements. The endpoints and paths of the initial per-rotation movements were deviated rightward for both groups by comparable amounts. Within 10 subsequent reaches, the on-center group regained baseline accuracy and straight-line paths; however, even after 40 movements the off-center group had not resumed baseline endpoint accuracy. Mirror-image aftereffects occurred when rotation stopped. These findings demonstrate that manual control is disrupted by transient Coriolis force perturbations and that adaptation can occur even in the absence of visual feedback. An increase, even a small one, in background force level above normal gravity does not affect the size of the reaching errors induced by Coriolis forces nor does it affect the rate of reacquiring straight reaching paths; however, it does hinder restoration of reaching accuracy.

INTRODUCTION
Rotating a space craft to generate artificial gravity is a potential way of preventing cardiac deconditioning, muscle atrophy, skeletal structural changes, and of enhancing hygiene and livability during interplanetary missions. In a rotating space vehicle, artificial gravity is actually the centrifugal force \( F_{\text{cent}} \) associated with rotation and is proportional to \( \omega^2 r \) where \( \omega \) is the rate of rotation and \( r \) the radius. \(^1\) Analyses of centrifugal and other forces in a rotating environment and predictions of their potential consequences for movement and object manipulation have been presented by several authors (Loret 1961; Nicogossian and McCormack 1987; Stone 1970). Most adverse side effects of rotating environments reach their asymptotic minima at radii of ~40 m, which at 5 rpm would generate a 1-g artificial gravity level (Stone 1970). Head movements made in a rotating environment, especially at high velocities of rotation, can be disorienting and nauseogenic (Graybiel et al. 1960; Johnson et al. 1951; Schubert 1932). The reason for this is that making head movements about an axis other than that of rotation elicits a complex pattern of stimulation of the vestibular system known as Coriolis, cross-coupled stimulation. Graybiel and colleagues demonstrated that humans could adapt their head movement control relatively rapidly to rotation rates up to 5 rpm (Graybiel 1973; Graybiel and Knepton 1972; Graybiel and Wood 1969). After adaptation, head movements again felt normal and no longer were disorienting or provocative.

Other studies have shown that the nauseogenic and disorienting effects of Coriolis, cross-coupled stimulation depend on gravito-inertial force \( (G)^2 \) background level, being enhanced at >1-g levels and diminished at <1-g acceleration (DiZio et al. 1987; Graybiel et al. 1977; Lackner and Graybiel 1984).

Manual control in rotating environments has received relatively scant attention. The effect of centrifugal force on reaching movements has been evaluated (Bock et al. 1992, 1996a,b; Cohen 1970, 1997; Welch et al. 1996), and recently the influence of transient Coriolis forces on pointing movements has been studied (DiZio and Lackner 1995; Lackner and DiZio 1994). The present study investigates the combined influences of centrifugal and Coriolis forces on reaching.

Coriolis \( (F_{\text{Cor}}) \) and centrifugal forces \( (F_{\text{cent}}) \) are physically independent and have different influences on reaching. Reaching movements in a rotating room generate transitory Coriolis forces that do not exist before the reach begins or after it ends. Coriolis forces are always orthogonal to movement direction and at any moment are proportional to the arm’s mass \( (m) \), linear velocity \( (v) \) in relation to the room, and the angular velocity \( (\omega) \) of the room: \( F_{\text{Cor}} = -2m(\omega \times v) \). The placement of subjects in the room thus affects the magnitude and direction (relative to the body) of \( F_{\text{Cor}} \) but not \( F_{\text{cent}} \), as illustrated in Fig. 1. As a consequence, identical transient Coriolis force perturbations of the arm can be achieved while the body is exposed to different, static G force backgrounds by relocating the subject within the room and keeping \( \omega \) constant.

Certain prominent theories of motor control, the \( \alpha \) equilibrium point model (Bizzi et al. 1992), and the \( \lambda \) equilibrium

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\(^1\) An analysis of artificial gravity can also be made without reference to centrifugal forces that are inferred inertial reaction forces in a rotating framework. The alternative approach is in terms of centripetal forces contributed by the “floor” of the rotating vehicle providing forces directed toward the spin axis. Centripet al forces are analogous to terrestrial ground reaction forces on objects that oppose the gravitational pull.

\(^2\) G refers to the gravito-inertial resultant vector. This is the vector sum of the gravitational force, \( g \), and the inertial forces present. It is conveniently expressed in multiples of \( g \) units with \( g \) being 9.8 m/s\(^2\).
The subjects rapidly returned to accurate straight force perturbations they would encounter in a rotating space (DiZio and Lackner 1995; Lackner and DiZio 1994). The equally well seated in the center of a rotating room and pointing to targets vehicle with less than a 1-g point accuracy should not be affected by Coriolis force influences on proprioceptive function raise the issue of whether our observations concerning initial reactions and modulations of mechanical perturbations, when adaptation to Coriolis perturbations is complete, the disturbing Coriolis force is no longer perceived as being present even though it is. After the subjects were brought to rest, their first reaching movements were mirror images to those first made during rotation. In other words, they exhibited a persistence of recalibration and had to readapt to the stationary environment.

These experimental results established the possibility of rapidly adapting limb movement control to the Coriolis perturbations generated during voluntary movement in a rotating environment. Coupled with other experimental observations we made (DiZio and Lackner 1995), the findings demonstrated that adaptation occurs because the proprioceptive and somatosensory feedback during the movements did not correspond to that which would normally accompany the intended movements. New motor commands became associated with the intended movements that had the consequence of precisely compensating for the Coriolis forces and restoring reaching accuracy.

Such findings point to an important role of proprioceptive and somatosensory feedback in the control and calibration of limb movements. From experiments we have carried out in parabolic flight, we know that the proprioceptive representation of forearm position is influenced by background force level. For example, subjects who have been trained in 1 g to make specific repetitive patterns of forearm movement will systematically deviate from this pattern when tested in the 0-g and 1.8-g force phases of parabolic flight (Fisk et al. 1973). In 0 g there is an underdamping of movements with undershoots of intended position, and in 1.8 g the opposite pattern occurs. The magnitude of vibratory myesthetic illusions elicited by tendon vibration is also influenced by background force level (Lackner et al. 1992), indicating that muscle spindle output or its central processing is modulated by G. We have also found that when the unseen arm is deviated by Coriolis forces in parabolic flight, its felt deviation is larger than normal in 1.8 g and almost abolished in 0 g (Lackner and DiZio 1989, 1992). These modulations of proprioceptive function are probably due in part to descending signals stemming from otolith stimulation or propriospinal influences resulting from the altered effective weight of the body.

G influences on proprioceptive function raise the issue of whether our observations concerning initial reactions and adaptive compensations to Coriolis forces in a 1-g rotating environment will predict performance in a rotating space vehicle with less than a 1-g level of artificial gravity. Will, for example, adaptation to Coriolis force perturbations occur equally well in 1-g and non-1-g resultant force backgrounds if proprioceptive function at the start of exposure is adapted for a 1-g background? This question speaks directly to the feasibility of preadapting astronauts on Earth to the Coriolis force perturbations they would encounter in a rotating space craft with a resultant force level different from 1 g, or if they began exposure to Coriolis forces in a non-1-g background field. The same question bears also on the basic

![Diagram](https://example.com/diagram.png)

**FIG. 1.** Illustration of Coriolis ($F_{\text{Cor}}$) and centrifugal forces ($F_{\text{cen}}$) during reaching movements made in the on-center and off-center experimental conditions in the rotating room. Coriolis forces exist on mobile body parts (just the arm in the illustration), they always act orthogonally to movement direction, and their magnitudes are proportional to the rotational velocity of the room ($\omega$), and the arm’s mass ($m$) and linear velocity ($v$) within the room; $F_{\text{cor}} = -2m(\omega \times v)$. During rotation, centrifugal forces act on both the moving arm and the immobile body parts of the subject, in a fixed direction relative to the room and with a magnitude proportional to the distance from the center ($r$) and the square of the rotation rate, $F_{\text{cen}} = \omega^2 r$. In this experiment, each subject reached forward parallel to his or her midline 40 times pre-, per, and postrotation. Ten pointed radially outward from the center (cross), and ten sat near the wall and pointed toward the center. When the room was rotating 10 rpm counterclockwise, a rightward Coriolis force was generated in both conditions, ~0.2 g peak. In the on-center condition, the start position for each reach was exactly on the axis of rotation, so the centrifugal force was 0 on the hand and <0.04 g on the rest of the body. In the off-center condition, the subject reached 35 cm toward the center from a start position at a radius of 2.23 m. Centrifugal force on the hand was 0.25 g (resultant equal 1.031 g) at the start position and 0.21 g with the arm extended forward, resisting the direction of movement.

Point model (Feldman 1986) predict that movement endpoint accuracy should not be affected by Coriolis force perturbations of movement trajectories because the perturbing force vanishes as the velocity of the arm approaches zero. We found, however, that the reaching movements of subjects seated in the center of a rotating room and pointing to targets are deviated in the direction of the Coriolis forces generated (DiZio and Lackner 1995; Lackner and DiZio 1994). The movements ended to the side of the targets in the direction that the Coriolis force acted when the arm was in motion, and the trajectories were more curved than usual. With repeated movements, the subjects rapidly returned to accurate straight line reaches. Full accuracy was regained within ~15 reaches when subjects were denied visual feedback about the position of their hand in relation to the target during their movement; with visual feedback, adaptation to the Coriolis perturbations was more rapid and occurred within ~8–10 reaches. This adaptation is much more rapid than that which occurs for mechanical perturbations of limb movements (cf. Shadmehr and Mussa-Ivaldi 1994) to targets. Unlike the case of mechanical perturbations, when adaptation to Coriolis perturbations is complete, the disturbing Coriolis force is no longer perceived as being present even though it is.
issue of whether G modulates proprioceptive function. If proprioceptive feedback is altered in non-1-g static force backgrounds, then adaptive compensations to transient Coriolis force perturbations in subjects denied visual feedback should be affected as well.

To begin exploration of these issues, we studied how well subjects were able to adapt to comparable Coriolis force perturbations of reaching movements under two different static force conditions. The study was conducted in the Graybiel Laboratory’s slow rotation room (SRR) facility, a fully enclosed, 3.3-m radius rotating environment. A rotational velocity of 10 rpm counterclockwise was employed for both conditions. At or below this velocity when the subject is within 50 cm of the center, brief, rightward Coriolis force perturbations are generated on the moving arm without any significant centrifugal force on the arm or other parts of the body, including the vestibular system. The Coriolis force on the hand will be ~0.2 g at a reaching velocity of 1 m/s. At larger distances from the center, reaching movements made toward the center at the same rate generate rightward Coriolis forces of the same magnitude on the arm; in addition, significant centrifugal forces are present. These centrifugal forces resist the motion of reaching movements made toward the center of the room; they also increase the effective weight of the body, load the otolith organs, and alter the pattern of touch and pressure cues on the body’s support surfaces, e.g., feet and buttocks. In our experiment, one group of subjects was tested on-center where there was virtually zero centrifugal force present at 10 rpm so that the resultant gravitoinertial force was 1 g. The other group was tested 2.23 m off-center where a 0.25-g centrifugal force was present so that the resultant gravitoinertial force was 1.031 g. Figure 1 illustrates these conditions.

METHODS

Subjects

Twenty individuals participated. They were without vestibular or sensory-motor impairments that could have influenced their performance and had normal or corrected to normal vision.

Apparatus

A test chair that could be relocated in the rotating room was used for both test conditions. The chair had a head holder that was adjusted for individual subjects to comfortably support the head and prevent significant movements. A horizontal Plexiglas surface was fixed to the chair at waist level with a light-emitting diode (LED) embedded in its surface from below serving as a target. During testing, the LED was the only object ever visible because the room lights were turned off. The LED remained illuminated only so long as the subject depressed a microswitch that marked the start position; when the finger was lifted to point to the LED it went out. The LED was located 35 cm in front of the microswitch, and both were ~25 cm right of the subject’s midline. The surface of the Plexiglas was perfectly smooth so that the subject could not receive tactile cues about the LED’s position. Reaching movements to the target were recorded by a WATSMART motion monitoring system that tracked an infrared emitter taped to the subject’s right index finger.

Procedure

Ten subjects were tested seated at the center of rotation; the chair was located so that the start button was directly on the rotation axis of the SRR (see Fig. 1). The other 10 were tested 2.23 m away facing the center of rotation. The centrifugal force generated by rotation and thus the resultant force on the hand depended on arm position. On center, with the arm in the start position, the centrifugal force on the hand was zero (resultant gravitoinertial force equal to 1.0 g), with the arm extended 35 cm to place the finger on the target it was 0.04 g; this small force was directed forward assisting the movement. At 2.23 m from the center, with the arm in the start position, the centrifugal force on the hand was 0.25 g (resultant equal to 1.031 g), and with the finger on the target, it was 0.21 g, resisting the forward motion of the arm. In both conditions, a rightward, relative to the subject, Coriolis force was generated while the arm was moving.

A session was begun with several practice reaches to the target while the room was stationary and the room lights were on. The subject attempted to reach in a simple, natural, normally paced movement, not to go abnormally slowly or rapidly. The subject was told to complete the pointing movement without stopping while attempting to hit the target location. After the practice period, the SRR lights were extinguished and remained off until the completion of the experiment.

The test sessions were divided into three components, prerotation, per-rotation, and postrotation, each of which involved 40 reaching movements. Subjects were given a 30-s rest period after every eight reaches to prevent fatigue. After the 40 prerotation reaches, the SRR was accelerated at 1°/s² to a constant angular velocity of 10 rpm. At least 1 min was allowed to elapse for the horizontal semicircular canals to return to equilibrium and for any potential oculargyral illusion to abate (Graybiel and Hupp 1946). After the subject had completed the 40 per-rotation reaches, the SRR was decelerated to rest at 1°/s². After at least 1 min at 0 rpm, during which no voluntary movements of the head or arms were made, the subject made the postrotation reaches. These movements completed the subject’s task.

Data analysis

Computer algorithms were used to identify the endpoint, duration, and peak forward velocity of each reaching movement. The endpoint and duration were defined as the position and time, respectively, at which the velocity of the finger first dropped to 5 mm/s. In addition, binary search algorithms were used to find the maximum leftward and rightward deviations of the finger from a straight line path between the start and endpoint, as a measure of trajectory curvature. Each subject’s final 8 prerotation movements were averaged to obtain stable baseline performance measures. A test chair that could be relocated in the rotating room was used for both test conditions. The chair had a head holder that was adjusted for individual subjects to comfortably support the head and prevent significant movements. A horizontal Plexiglas surface was fixed to the chair at waist level with a light-emitting diode (LED) embedded in its surface from below serving as a target. During testing, the LED was the only object ever visible because the room lights were turned off. The LED remained illuminated only so long as the subject depressed a microswitch that marked the start position; when the finger was lifted to point to the LED it went out. The LED was located 35 cm in front of the microswitch, and both were ~25 cm right of the subject’s midline. The surface of the Plexiglas was perfectly smooth so that the subject could not receive tactile cues about the LED’s position. Reaching movements to the target were recorded by a WATSMART motion monitoring system that tracked an infrared emitter taped to the subject’s right index finger.

RESULTS

Prerotation, baseline reaches

Subjects in both force level groups made nearly straight reaches. The average endpoints fell 15 mm to the left of and 7 mm beyond the target for the on-center group, and 7 mm...
to the right and 6 mm beyond for the off-center group. The average movement trajectories were curved only 1 mm to the left for the on-center group and 1 mm to the right for the off-center group. These prerotation values of movement endpoint and trajectory curvature were statistically indistinguishable from the values for the final postrotation reaches, indicating that they represent a stable baseline for assessment of changes due to Coriolis forces, adaptation, and G level.

Reaching errors relative to baseline

A multivariate analysis of variance (Statistical Package for the Social Sciences MANOVA procedure) assessed whether reaching movements were affected by G level (1 g, on-center group and 1.031 g, off-center group; between subjects) and by the rotation exposure (initial per-rotation, final per-rotation, initial postrotation; within subjects). Lateral endpoints were affected by rotation \( [F(2,17) = 10.093, P = 0.001] \) and an interaction of rotation and G level \( [F(2,17) = 3.603, P = 0.049] \). For curvature of movement trajectory there was only an effect of rotation \( [F(2,17) = 25.167, P < 0.0001] \). Fore-aft endpoints showed no significant changes in the MANOVA. Figure 2 illustrates the average lateral and fore-aft endpoints and trajectory curvatures for the initial per-rotation, final per-rotation, and initial post-rotation movements. The sections below describe the patterns observed during and after rotation and the results of our planned comparisons.

Per-rotation reaching errors

Subjects in both force backgrounds made large lateral errors but reached the correct distance in their first per-rotation movements. The movement trajectories were deflected rightward, in the direction of the Coriolis force \((\approx 0.2 \, \text{g}, \text{peak})\) that developed as the peak movement velocity was approached. As the reaching movements slowed and the Coriolis forces diminished, the hand tended to return toward the target but stopped considerably off to the right side. The average lateral endpoint error (difference from baseline) was 40 mm for the on-center group and 37 mm for the off-center group, the average error in curvature was 23 mm rightward for the 1-g group and 18 mm rightward for the off-center group. These lateral endpoint and trajectory errors were significantly larger than zero \( [\text{correlated } t\text{-tests}; t(9) > 3.140, P < 0.012] \) for both groups, but were not significantly different between the groups. The movement trajectories are illustrated in Fig. 3. The distance of per-rotation reaches was slightly but not significantly shortened relative to baseline for both groups, and the extent of this shortening was not different between groups.

Every subject showed increased accuracy and a straighter trajectory after making several additional movements. This is shown in Fig. 4, which presents sequentially the lateral movement endpoints and curvatures for all 120 reaches, averaged across subjects for each group separately. By the end of the per-rotation period, the trajectories and endpoints of the on-center test group were statistically indistinguishable from their prerotation baselines. That is, they had fully adapted to the Coriolis forces generated by their movements and were again reaching in straight lines to the target position. By contrast, the off-center test group only showed partial adaptation of their movement endpoints. Approximately 60% of the initial lateral endpoint deviation was eliminated in the 40th per-rotation movement, leaving a significant error \( [t(9) = 2.562, P = 0.030] \). Although the movements never ended in the right location, they became as straight as baseline reaches. The lateral endpoint errors of the last (40th) per-rotation reaches were significantly different \( [\text{uncorrelated } t\text{-tests}; t(18) = 2.91, P = 0.009] \) between the on-center and off-center test groups, in fact they were nonoverlapping sets. The trajectory curvatures and fore-aft endpoint errors were not different for the two groups.
FIG. 3. Top views of the initial and final (40th) pre-, per-, and postrotation reaching movements sampled at 100 Hz and averaged for the 10 subjects in the 1-g and 1.031-g test conditions. Prerotation movements are straight and accurate. In both 1 g and 1.031 g, initial per-rotation movements are deviated to the right and end to the right, the direction of the Coriolis force generated. In 1 g, the final per-rotation movements are identical to prerotation, but in 1.031 g the endpoints remain deviated rightward although the path becomes straight again. Postrotation movement patterns mirror the initial per-rotation ones with the important difference that the initial endpoint errors are smaller in 1.031 g than 1 g. There are no changes in reaching distance.

Postrotation reaching errors

In their first postrotation reach, every subject in the on-center group showed lateral endpoint errors and trajectory deviations. These aftereffects were of equivalent magnitude but of opposite sign (i.e., they were mirror images) to their first per-rotation reaches. Lateral endpoint and trajectory values were significantly different both from prerotation baseline values and initial per-rotation values. With additional reaching movements, straight line trajectories and prerotation endpoints were regained within about a dozen movements.

The trajectories and lateral endpoints of the first postrotation reaches of the off-center group also deviated in the direction opposite their initial per-rotation reaches, but only by ~60% of the per-rotation deviation. Within 8 or 10 additional postrotation reaches, their movement endpoints and curvatures were back to prerotation baseline values. The trajectory deviations and endpoints of the initial postrotation reaches were significantly different from both the prerotation baselines and the initial per-rotation values. In addition, the deviations of the off-center group’s initial postrotation endpoints were significantly smaller \[ t(18) = 2.98, P = 0.01 \] than those of the 1-g group’s movements. There were no initial postrotation mirror-image deviations of reaching distance in either group nor any change during the subsequent 40 postrotation movements.

Analyses of variance showed that both groups of subjects maintained a near constant, movement velocity and movement duration for the pre-, per-, and postrotation reaches. Peak movement speed averaged 986 mm/s and movement duration 660 ms for the 1-g group and 1,095 mm/s and 611 ms for the 1.031-g group. This means that 1) subjects did not alter their reaching movement strategy in response to the Coriolis and centrifugal forces generated during their per-rotation reaches, and 2) the peak magnitude of the Coriolis forces acting on the arm during the per-rotation reaches remained virtually constant throughout the experiment for both test groups.

Discussion

Subjects tested in the rotating room at both force levels showed large lateral trajectory and endpoint deviations in their first reaching movements made at constant velocity rotation. The deviations were in the direction of the transient Coriolis forces generated by voluntary reaching movements. The initial trajectory and endpoint deviations are sufficiently
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FIG. 4. Plots of lateral endpoint and trajectory curvature for all 120 reaches of an experimental session, averaged across subjects for the 1 g (top plots) and 1.031 g (bottom plots) test groups. Endpoints are deviated right of baseline by the introduction of Coriolis forces and return all the way to baseline within ~15 per-rotation reaches for the 1-g force group. Improvement stops after the 1st 8 per-rotation reaches without full return to baseline for the 1.031-g group. By contrast, trajectory curvature shows return to baseline values for both groups.

large to be functionally significant in operating control panels and manipulating objects in a typical vehicle environment in space or on earth. These results are in accord with our earlier observations and constitute powerful evidence against equilibrium position theories of motor control, both the α (Bizzi 1980; Bizzi et al. 1976, 1992) and λ models (Feldman 1966a,b, 1974, 1986). These theories are of direct relevance to motor control in artificial gravity environments because they have to predict that the trajectories of movements should be deviated by the transient Coriolis forces but that the endpoints should not. From the equilibrium point perspective, movement is controlled by an evolving set of motor commands that specify changing length-tension relations of the relevant muscles. Transient perturbations (e.g., such as the Coriolis forces in our experiment) are predicted to deflect the trajectory only temporarily because the programmed endpoint of the movement is achieved by agonist-antagonist activation patterns that create a static equilibrium position determined by the controlled, elastic properties of the muscles. The highly significant endpoint errors initially exhibited by all of our subjects exposed to Coriolis forces (forces that vanish at the end of the movement) indicate that equilibrium point theories are incorrect in their basic prediction. In fact, errors are initially present, and one does have to adapt limb movement control in an artificial gravity environment to attain prescribed target configurations of the limb.

Our results further show that adaptation of arm movement control to the Coriolis forces associated with artificial gravity environments is remarkably rapid in a 1-g gravito inertial background. For the simple type of movements studied, trajectories and baseline endpoint accuracy were back to normal in ~10 movements even though the subjects never received visual or direct tactile feedback about their reaching errors relative to the target. Instead, they had to make use of proprioceptive feedback derived from spindle primary and secondary receptors in relation to efferent commands, and tactile contact with the smooth Plexiglas panel to determine that the movement executed did not correspond to the one they had intended. We have shown in other contexts that such forms of motor-proprioceptive monitoring are a common feature of limb motor control (Lackner and DiZio 1993, 1994; Lackner and Graybiel 1981, 1982). Such reprogramming is automatic and persists when rotation stops, which is why the initial per-rotation and initial postrotation reaches are mirror images of each other (see Fig. 4).

A key aspect of the present findings is that the subjects tested off-center, only adapted partially to Coriolis force perturbations that were comparable in magnitude to those experienced by the on-center test subjects who adapted fully. This finding has important implications for the practical employment of artificial gravity environments in space flight. A resultant background force level of just 1.031 g off-center was associated with only about one-half as much adaptive compensation of endpoint errors as a normal 1-g level so that movements remained inaccurate during rotation. An examination of the left side of Fig. 4 shows that endpoint adaptation in the off-center group asymptoted by the eighth per-rotation reaching movement, showing no additional
change after that. This means that the factors triggering or leading to endpoint adaptation were no longer being expressed for the off-center group although the movement endpoints were still deviated.

The difference in completeness of endpoint adaptation is probably not caused by direct physical effects of centrifugal force on the arm. The centrifugal force acts in a direction to oppose forward motion of the arm in the off-center condition, yet there are no changes in reaching distance or velocity when it is introduced so it is unlikely to affect adaptation in the orthogonal direction, in which Coriolis forces act. The lack of fore-aft kinematic changes in the off-center group even for the first per-repetition reach means that motor compensations were planned for the background centrifugal force of 0.25 g on the arm that was present before the movement started. The magnitude of the background centrifugal force could be detected by otolith input and by altered touch and pressure patterns on the subject’s body.

A possible reason for the difference in endpoint adaptation to Coriolis force in the two conditions relates to observations that we have made concerning the influence of gravitoinertial force level on the perception of limb position. As mentioned in the introduction, we found that subjects attempting to set their forearm to particular prepracticed positions (without sight of their limbs) showed systematic errors when tested under parabolic flight conditions during periods of “steady-state” 0-g and 1.8-g background force level. The errors were opposite in direction for 0 g and 1.8 g and pointed to force-dependent alterations in limb proprioception (Fisk et al. 1993). These results, along with other observations we have made studying tonic vibration reflexes in parabolic flight (Lackner et al. 1992), strongly suggest that alterations in muscle spindle activity occur as a function of background force level. Spindle sensitivity seems diminished in 0 g and enhanced in 1.8 g; such changes can be understood on the basis of otolith-spinal modulation of spindle gain (cf. Watt et al. 1986). They are also consistent with recent observations on pointing movements during prolonged exposure to microgravity (Watt 1997). Golgi tendon organ activity must also be altered in different gravitoinertial force backgrounds because of the alteration in effective body weight and different muscle forces necessary to maintain postural configuration.

These findings translate directly to the current observations. The only basis for adaptation in the present experiment was the discrepancy between the expected and received proprioceptive feedback for the movement attempted, and tactile contact at the end of the movement. When a subject’s arm is deflected by a Coriolis force, spindle activity and Golgi tendon organ activity will be increased in the muscles that are stretched or prevented from shortening at the expected pace. If spindle background activity level is unusually high, as would be expected in our 1.031-g test condition for the reasons just described, the relative change in spindle activity triggered by a Coriolis force perturbation would be less than in the 1-g condition for the same perturbation. Accordingly, less adaptive compensation would be necessary before the change in spindle activity caused by a Coriolis force perturbation would be above the signal-to-noise detection range. By contrast, if a subject were fully adapted in terms of sensory-motor control of posture and movement to a static 1.031-g force field, then we would expect that person to show the same degree and rate of adaptation to Coriolis forces as subjects in our 1-g test condition. Otolith-spinal reflexes have proven to be a useful measure of posture and movement adaptation during prolonged exposure to an altered static force background (Watt et al. 1986).

Both the on-center and off-center groups showed complete, rapid adaptation of movement curvature, as seen in the right side of Fig. 4. When rotation commenced, movements became curved in the direction of the Coriolis forces; with continued reaches during rotation, the movements became as straight as prerotation, and when rotation stopped, they initially curved in the other direction. The same was true for both groups, in contrast to the G-dependent patterns of endpoint adaptation. We have observed independent adaptation of movement endpoint and movement shape in several other studies (DiZio and Lackner 1995, 1996) including one involving vestibular loss patients (DiZio and Lackner 1996).

The labyrinthine-defective subjects showed normal trajectory adaptation but incomplete endpoint adaptation. Interestingly, the muscle spindle primary and secondary systems are normally modulated by vestibular signals. Spindle primaries contribute signals related to muscle velocity and length and spindle secondaries to muscle length. In terms of adaptation of movement control, it is likely that the spindle primaries are involved in adaptation of movement endpoint (the length signal) and shape (the velocity signal) and spindle secondaries in movement endpoint (the length signal). With alteration of spindle gain owing to labyrinthectomy or to changed background force level, the dynamic response seems to be better preserved than the static allowing trajectory path adaptation but diminished movement endpoint adaptation. Our evidence of independent adaptation of movement trajectory curvature and endpoint shows that CNS mechanisms monitor and represent them distinctly, although in actual execution they are normally implemented synergistically.

In summary, we have shown that the ability to adapt to Coriolis force perturbations of limb trajectory and endpoint is highly dependent on gravitoinertial force level and is significantly degraded even by as small a 0.031-g change in background resultant force. It is likely, however, that full adaptation could be achieved if visual or tactile feedback about reaching accuracy were provided. Our results indicate that one should not underestimate the importance of small differences in gravitoinertial force backgrounds for the sensory-motor control of whole-body and limb movement control. Interestingly, during every day activities when we simultaneously turn and reach for objects, our self-movements can generate large Coriolis forces on our reaching limb. Nevertheless, our movements are accurate, indicating that the CNS must compensate for the Coriolis forces that will be generated. In other experiments (Cohn et al. 1997, 1998), we have shown that subjects experiencing illusory, rotary self-displacement show reaching errors to targets. These errors reflect automatic compensations that are being made for the Coriolis forces that would be present during the reaches if the subjects were actually rotating. These observations indicate that virtual reality systems inducing apparent self-displacement will affect sensory-motor control. We are currently exploring how adaption acquired to virtual rotation transfers to real rotation and vice versa. These are
issues of fundamental importance both for theories of motor control as well as the possible use of artificial gravity in long-duration space missions.

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Address reprint requests to J. R. Lackner.

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