Coriolis-Force-Induced Trajectory and Endpoint Deviations in the Reaching Movements of Labyrinthine-Defective Subjects

PAUL DIZIO AND JAMES R. LACKNER
Ashton Graybiel Spatial Orientation Laboratory and Volen Center for Complex Systems, Brandeis University, Waltham, Massachusetts 02454

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DIZIO, Paul and James R. Lackner. Coriolis-force-induced trajectory and endpoint deviations in the reaching movements of labyrinthine-defective subjects. J Neurophysiol 85: 784–789, 2001. When reaching movements are made during passive constant velocity body rotation, inertial Coriolis accelerations are generated that displace both movement paths and endpoints in their direction. These findings directly contradict equilibrium point theories of movement control. However, it has been argued that these movement errors relate to subjects sensing their body rotation through continuing vestibular activity and making corrective movements. In the present study, we evaluated the reaching movements of five labyrinthine-defective subjects (lacking both semicircular canal and otolith function) who cannot sense body rotation in the dark and five age-matched, normal control subjects. Each pointed 40 times in complete darkness to the location of a just extinguished visual target before, during, and after constant velocity rotation at 10 rpm in the center of a fully enclosed slow rotation room. All subjects, including the normal controls, always felt completely stationary when making their movements. During rotation, both groups initially showed large deviations of their movement paths and endpoints in the direction of the transient Coriolis forces generated by their movements. With additional per-rotation movements, both groups showed complete adaptation of movement curvature (restoration of straight-line reaches) during rotation. The labyrinthine-defective subjects, however, failed to regain fully accurate movement endpoints after 40 reaches, unlike the control subjects who did so within 11 reaches. Postrotation, both groups’ movements initially had mirror image curvatures to their initial per-rotation reaches; the endpoint aftereffects were significantly different from prerotation baseline for the control subjects but not for the labyrinthine-defective subjects reflecting the smaller amount of endpoint adaptation they achieved during rotation. The labyrinthine-defective subjects’ movements had significantly lower peak velocity, higher peak elevation, lower terminal velocity, and a more vertical touchdown than those of the control subjects. Thus the way their reaches terminated denied them the somatosensory contact cues necessary for full endpoint adaptation. These findings fully contradict equilibrium point theories of movement control. They emphasize the importance of contact cues in adaptive movement control and indicate that movement errors generated by Coriolis perturbations of limb movements reveal characteristics of motor planning and adaptation in both healthy and clinical populations.

INTRODUCTION

Mechanically perturbing movements during their course has been a useful tool for studying motor control. We have introduced an alternative technique to perturb movement trajectories using inertial accelerations that act without mechanical contact (Lackner and Dizio 1989, 1992, 1994). Subjects make reaching movements to targets while seated at the center of a fully enclosed room that can be rotated. At constant velocity rotation, the sensory information they receive is consistent with being stationary and they feel stationary. When they reach during rotation, their arms are deflected by the inertial Coriolis forces generated by their arm movements. As illustrated in Fig. 1, the Coriolis force \( F_c \) evoked by an arm movement is dependent on the cross product of the linear velocity of the arm \( v \), the velocity of rotation of the room \( \omega \), and the mass of the arm \( m \):

\[
F_c = -2m(\omega \times v)
\]

This dependence on arm velocity means there is no unusual force acting on the arm before the movement starts nor when it is over. Because \( F_c \) is an inertial force, there is no mechanical contact with the surface of the arm to activate somatosensory receptors that could provide information about the direction and magnitude of the perturbation as is the case in most load-compensation experiments. Thus, Coriolis accelerations provide a unique way of transiently perturbing free-limb movements without requiring the subject to grasp a manipulandum or to be constrained by an external mechanical apparatus or an inertial load attached to the arm.

Subjects exposed to Coriolis force perturbations of their reaching movements initially exhibit large trajectory deviations and endpoint errors in the direction of action of the transient Coriolis forces. It has been argued that these errors result because the subjects are still experiencing rotation or are experiencing some form of visual mislocalization of the targets to which they are pointing (Feldman et al. 1998). Such experienced body rotation or visual mislocalization could result from continuing semicircular canal activity associated with acceleration of the test chamber to constant velocity. We considered this unlikely because visual mislocalizations owing to angular acceleration (i.e., “oculogyral illusions”) (cf. Graybiel and Hupp 1946) would be in the direction opposite the reaching errors we observed, because we always let at least 2 min elapse after constant velocity was attained to allow canal activity to decay back to resting level, and because our subjects always reported feeling stationary at the time of testing. Nevertheless...
subject was seated in a chair at the center of rotation. A smooth, horizontal, acrylic plastic (Plexiglas) surface at waist level served as the work space for making movements. Light-emitting diodes (LEDs) embedded in the underside of this surface could be activated to serve as targets. Reaches began from a start button about 12 cm anterior to the right shoulder. When depressed the button lit an LED target 35 cm straight ahead.\(^1\) When the subject lifted his or her right index finger to point, the LED was extinguished, and the subject pointed in complete darkness because the room lights were out during the experiment. The only object visible to the subject at any time during the experiment was the LED. The subject’s finger touched the smooth surface at the completion of a movement, and there was no direct tactile feedback available about whether the target was hit or not because the target was embedded in the underside of the surface. A WATSMART motion-recording system was used to monitor the position of an infrared emitter attached to the tip of the finger. Sampling was at 100 Hz. The subject’s left hand rested in his or her lap throughout testing. Figure 1 illustrates the experimental situation.

**Procedure**

Each experimental session included 120 reaching movements equally divided among pre-, per-, and postrotation periods. Movements were made in groups of eight followed by brief rest periods to minimize fatigue. The subjects attempted to reach in a natural fashion, raising their finger and reaching forward to touch the position of the target (which went out as they lifted their finger) in a single uninterrupted movement without stopping in mid-air. The subjects practiced for three or four reaches before data collection began for the prerotation movements. After completion of the 40 prerotation movements, the room was accelerated at \(1^{1/3}\) \(s^{-2}\) to a constant velocity of 10 rpm, counterclockwise. After 2 min at constant velocity, the 40 per-rotation movements were made. The room was then decelerated to rest at \(1^{1/3}\) \(s^{-2}\), and 2 min later the 40 postrotation movements were made. The 2-min periods following accelerations were to allow semicircular canal activity in the control subjects to decay back to baseline. In the rest periods between sets of eight movements, subjects were asked whether they had sensed any body rotation.

**Data analysis**

A computer algorithm was used to identify the duration and endpoint of each movement as where tangential finger velocity fell to 3% of peak level. Binary search algorithms were used to compute the peak forward velocity of the movement and the maximum leftward or rightward deviation of the movement path from a straight line connecting the start and endpoint of the movement. The last eight prerotation movements were averaged for each of these dimensions to provide prerotation baselines, and the last eight per-rotation movements were averaged to provide stable estimates of the adaptation to Coriolis forces achieved. Statistical planned comparisons were carried out to evaluate changes from baseline of initial and final per- and postrotation reaches and changes from initial per-rotation to final per-rotation reaches. These comparisons provided, respectively, assessments of the disrupting effects of Coriolis forces on reaching

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\(^1\) When a subject is positioned at the center of rotation and the slow rotation room is turning at 10 rpm, the centrifugal acceleration associated with rotation is negligible. It amounts to 0.039 g when the subject’s arm is positioned 35 cm from the center of rotation at the target goal position. The biologically effective force acting on the subject is the gravitoinertial acceleration, which is the resultant of the inertial and gravitational accelerations; with the subject’s hand at the target position, this acceleration is 1.00076 \(g\) compared with 1 \(g\) under nonrotating conditions. For comparison, in mile-high Denver, Colorado, the force of earth gravity is about 0.9992 \(g\); in Boston, MA, at sea level it is about 1.00 \(g\).
movements, whether adaptation to the Coriolis forces occurred, and whether aftereffects were present postrotation.

**RESULTS**

We present first a general description of the pattern of results and then a detailed statistical treatment.

**Prerotation reaches**

Both groups reached in essentially straight lines toward the target position. There were no intergroup differences in endpoint accuracy or path curvature. Figure 2 shows averaged raw traces of key movements, and Fig. 3 shows the average endpoint and curvature deviations of all reaches from baseline (average of last 8 prerotation reaches).

**Per-rotation reaches**

The initial per-rotary reaches of both subject groups were displaced in movement path and endpoint (relative to baseline) in the direction of the transient Coriolis accelerations generated during the reaches, as shown in Fig. 2. The path deviations (28 mm right for LD and 25 mm for controls) and endpoint errors (32 mm right for LD and 39 mm for controls) were highly significant and of statistically equal size for the two groups. The final per-rotation reaches of the control subjects were not significantly different in curvature or endpoint from the prerotation baseline reaches, indicating full adaptation or compensation to the Coriolis forces so that these subjects were again reaching in straight paths to the baseline position. The LD subjects exhibited a different pattern. Their final per-rotation reaches had significantly smaller endpoint errors (13 mm) than their initial per-rotation reaches but still differed from their prerotation baseline reaches. This means the LD subjects only achieved partial endpoint adaptation. However, their final per-rotation reaches were significantly less curved than their initial per-rotation reaches and were not different from their prerotation baseline. Thus at the end of the per-rotation period, they were again reaching in straight paths but still missing the target position. The control subjects achieved a 90% reduction of their initial endpoint errors within their first 11 per-rotation reaches and returned 90% toward straight movements paths within 5 reaches. The LD subjects achieved 90% of their asymptotic, partial adaptation of movement endpoints within about 10 reaches and 90% of their return to straight line movement paths within 5 reaches, see Fig. 3.

**Postrotation reaches**

The control subjects showed aftereffects in their initial postrotation reaches that were mirror image to the initial per-rotation movement paths that were displaced by Coriolis forces. Average trajectory (30 mm left) and endpoint (30 mm left) were both significantly deviated leftward, which is opposite in direction to the Coriolis forces that had been generated during the per-rotary reaching movements. These postrotation deviations represent persistence of the adaptation acquired during rotation. The initial postrotation reaches of the LD group also showed significant mirror image curvature deviation (44 mm left). However, movement endpoints were not significantly different from the prerotation baseline (1 mm right). This pattern indicates persistence of the full trajectory adaptation that was achieved and of the partial endpoint adaptation.
Statistical analysis

All statistical differences referred to in the preceding text were obtained with Bonferroni corrected t-tests following the appropriate ANOVAs. The initial analysis was a multivariate ANOVA (SPSS GLM repeated-measures procedure) of movement endpoint and curvature that showed significant effects of subject group (LD, control), \( F[2,7] = 56.45, P < 0.001 \), and exposure period (prerotation, initial per-rotation, final per-rotation, and initial postrotation), \( F[6,48] = 14.45, P < 0.001 \), and an interaction of group and rotation period, \( F[6,48] = 4.23, P = 0.001 \). Univariate ANOVA of movement endpoint showed main effects of group (\( F[1,8] = 5.87, P = 0.042 \)) and exposure period (\( F[3,24] = 169.9, P < 0.001 \)) and an interaction of exposure period and subject group (\( F[3,24] = 14.48, P < 0.001 \)). The source of the interaction was the difference between groups in extent of endpoint adaptation at the end of the per-rotation period (full adaptation only for the control subjects) and in the size of the postrotation aftereffect (larger for the control subjects), see Table 1. Univariate ANOVA of curvature showed only an effect of exposure period (\( F[3,24] = 258.9, P < 0.001 \)). t-tests showed significant changes from prerotation baseline curvature in the initial per- and postrotation reaches and no difference from baseline in final per-rotation movements for either group.

The finding that LD subjects showed complete trajectory curvature adaptation but incomplete endpoint adaptation, whereas the control subjects showed full adaptation of both raised the possibility that other aspects of the movements of the two groups might be different as well. Consequently, we examined additional movement features including movement distance, duration, and peak velocity; variability of peak trajectory curvature and of endpoints; peak elevation, the highest vertical position attained during a reach; and terminal velocity, the velocity of the finger just before contact with the surface.

Movement distance, duration, and peak velocity

The LD subjects did not reach quite as far forward or as fast as the controls. A multivariate ANOVA of all variables showed that the two groups differed from each other, but neither group varied across its pre-, per-, and postrotation periods. Table 2 summarizes these movement characteristics. The shorter and slower movements of the LD subjects means that the peak Coriolis force they experienced during rotation was somewhat smaller than that of the control subjects.

Movement variability

We calculated the standard deviation of trajectory curvature and endpoint for each subject’s 40 baseline (prerotation) reaches and compared the averages of the LD and control groups. The groups did not differ significantly on either measure, with endpoint variabilities of 13.87 ± 4.79 and 12.9 ± 3.69 (SD) mm and curvature variabilities of 6.2 ± 2.39 and 5.0 ± 1.5 mm for LDs and controls, respectively.

### Table 1. Comparison of Coriolis perturbations, adaptation, and aftereffects of movement endpoint and curvature averaged across LD (n = 5) and control subjects (n = 5)

<table>
<thead>
<tr>
<th>Group</th>
<th>Coriolis-Induced Deviation</th>
<th>Magnitude of Adaptive Compensation</th>
<th>Uncompensated Deviation</th>
<th>Aftereffect</th>
</tr>
</thead>
<tbody>
<tr>
<td>LD</td>
<td>Endpoint 31.6* (4.11)</td>
<td>−18.2* (3.33)</td>
<td>13.4* (4.44)</td>
<td>−0.7 (4.86)</td>
</tr>
<tr>
<td></td>
<td>Curvature 27.9* (6.84)</td>
<td>−31.6* (5.09)</td>
<td>−3.7 (7.30)</td>
<td>−43.6* (6.51)</td>
</tr>
<tr>
<td>Control</td>
<td>Endpoint 38.8* (3.68)</td>
<td>35.7* (3.30)</td>
<td>3.1 (4.21)</td>
<td>−29.6* (4.06)</td>
</tr>
<tr>
<td></td>
<td>Curvature 25.2* (6.13)</td>
<td>−28.1* (5.55)</td>
<td>−2.9 (6.34)</td>
<td>−29.8* (6.74)</td>
</tr>
</tbody>
</table>

All entries are in millimeters. Coriolis-Induced Deviation, initial per-rotation minus pre-rotation baseline; Magnitude of Adaptive Compensation, final per-rotation minus initial per-rotation values; Uncompensated Deviation, final per-rotation minus pre-rotation baseline; Aftereffect, initial post-rotation minus pre-rotation baseline. Standard deviations are given in parentheses. * Significant differences, \( \alpha < 0.05 \), Bonferroni corrected, paired t-tests.

### Table 2. Average movement distance, duration, and peak velocity in LD (n = 5) and control subjects (n = 5)

<table>
<thead>
<tr>
<th>Group</th>
<th>Distance, mm</th>
<th>Duration, ms</th>
<th>Peak Velocity, mm/s</th>
</tr>
</thead>
<tbody>
<tr>
<td>LD</td>
<td>322 (26)</td>
<td>666 (63)</td>
<td>682 (110)</td>
</tr>
<tr>
<td>Control</td>
<td>368 (29)</td>
<td>719 (51)</td>
<td>958 (102)</td>
</tr>
</tbody>
</table>

Standard deviations are in parentheses.

### Table 2

![Image](https://via.placeholder.com/150)

**FIG. 4.** Peak vertical elevation of the finger and terminal velocity (0.03 s prior to movement end) averaged separately for every reaching trial of the 2 subject groups. Error bars (1 SD) are shown for every other trial.
Terminal velocity

The terminal velocity of the finger in each reach was measured by averaging the velocity (3 point central difference) for three samples preceding the endpoint. Inspection of Fig. 4A shows that just before contact with the target board the control subjects were moving faster than LDs, especially in the first 10 per-rotation reaches and first 3 postrotation reaches, where the primary adaptation and re-adaptation of reaching endpoint and trajectory occurred. An ANOVA including subject group, exposure period, and repetition (40 movements per period) indicated significant group differences \((F[1, 8] = 7.13, P = 0.036)\). A second ANOVA including only the last 20 repetitions in each exposure period showed no difference between groups. \(t\)-tests showed that terminal velocity was faster in the control than LD group on the first eight per- and the first two postrotation reaches.

Peak elevation

The LD subjects lifted their finger higher above the target surface than the control subjects in the prerotation period, but they progressively reduced their peak elevation until in the postexposure period it ultimately matched that of the control subjects, see Fig. 4B. An ANOVA including group, exposure period, and repetition showed that the intergroup difference was significant \((F[1, 8] = 10.78, P = 0.019)\). Simple effects contrasts across all repetitions and subjects showed that the per-rotation \((F[1, 4] = 64.58, P = 0.001)\) and postrotation \((F[1, 4] = 13.55, P = 0.009)\) terminal velocities differed from prerotation for the LD group but not for the controls.

Discussion

The LD and normal subject groups both showed large movement path and endpoint deviations during their initial per-rotation movements relative to prerotation baseline values. These errors were in the direction of the transient Coriolis forces generated by their movements. The individuals in both groups had no prior experience making reaching movements during passive rotation and had no inkling of how their movements would be affected. Both groups reported that they always felt completely stationary during testing. The LD group also did not experience any sensation of movement during the acceleration to constant velocity rotation nor during deceleration to rest. Consequently, the motor commands they issued prerotation and in the first per-rotation trials to point to the same target position should have been the same, and we can conclude that the deviations of movement path and endpoint that occurred were caused by the Coriolis force perturbations rather than vestibular signals indicating body rotation. These findings quantitatively replicate our earlier studies (Lackner and DiZio 1994, 1998) and violate the equifinality prediction of equilibrium point theories (Bizzi et al. 1992; Feldman 1966, 1986).

With additional movements during rotation, both the LD subjects and the controls showed adaptive changes despite not receiving visual feedback about the path or accuracy of their movements. The normal control subjects were back to prerotation baseline, again reaching in straight paths to the target in less than a dozen additional reaches. The LD subjects showed rapid adaptation of movement paths as well, also being back to straight line reaches in less than a dozen movements. However, their movement endpoints only partially returned toward baseline and ultimately remained significantly deviated. The initial postrotation movements of each group reflected the character of the adaptation they acquired. The normal control subjects showed movement paths and endpoints mirror symmetric to their initial per-rotation patterns. The LD subjects showed mirror symmetric path curvature but much less endpoint deviation.

In several other studies, we have also seen dissociations of trajectory and endpoint adaptation (DiZio and Lackner 1995; Lackner and DiZio 1994, 1998). For example, if subjects are exposed to the same experimental regimen as used here but with the single exception that they point in the air above the location of the just extinguished target, then they will show full trajectory curvature adaptation but greatly reduced endpoint adaptation. Put simply, they show the same dissociated adaptation pattern as our LD subjects. This dissociation is attributable to the absence of finger contact at the end of reaching movements for the control subjects and an abnormal pattern of finger contact for the LD subjects. We have found that when normal subjects in a stationary environment touch a smooth surface with their fingertip at the end of a movement, unique patterns of shear forces are generated during the initial 30 ms of contact. These patterns provide a spatial mapping of finger position in relation to the subject’s body with the origin about midway between the subject’s head and shoulder (DiZio et al. 1999; Lackner and DiZio 2000a). Soechting and Flanders (1989), who studied whether reaching movements are represented in a visual or body centered reference frame, earlier had identified this same location as the origin for planning pointing movements to visual targets. Our observations thus complement theirs and identify a mechanism for updating calibration.

The LD subjects who participated in the present study ended their movements differently than the control subjects. The simplest way to characterize the difference is that they terminated their movements more tentatively. Their movement elevations were higher, their peak velocities were lower, their terminal velocities were slower, and they came more straight down onto the surface. The LD subjects may adopt this strategy because they do not have otolith-derived information about their head orientation relative to gravity and, consequently, in the dark they may have a less accurate representation of trunk orientation to the target surface. The consequences of this strategy are to diminish the magnitude and directional variation of the shear forces at the fingertip making the landing primarily the generation of a normal force at the fingertip. It avoids jamming the finger into the surface but it also diminishes the spatial cues about finger terminal position that are necessary in order for the CNS to detect and correct endpoint errors.

Daghestani et al. (2000) have found that when normal and LD subjects simultaneously step forward and point to real or virtual target positions their hand paths differ and their reaches are terminated differently. The LD subjects in their study reached higher and tended to come down more normally to the target location, just like our LD subjects. Our LD subjects showed normal adaptation of movement curvature because such adaptation is not dependent on terminal contact forces. Curvature can be determined from the pattern of muscle spindle signals actually occurring in relation to those expected for the intended movement. We have described elsewhere the different roles of terminal cutaneous and continuous muscle spindle signals in movement adaptation (Cohn et al. 2000; Lackner and DiZio 1994,
These models also show the importance for accurate motor control of central registration of ongoing self-motion and internal models of expected loads.

In summary, the present results eliminate vestibular artifacts as being the origin of the limb movement trajectory and endpoint deviations induced by Coriolis perturbations during constant velocity rotation. They are in accord with other studies indicating a failure of equilibrium point models of movement control (e.g., DiZio and Lackner 1995; Gomi and Kawato 1996; Lackner and DiZio 1994). They also emphasize the value of using inertial Coriolis forces as a tool for studying adaptive motor control without the contaminating somatosensory cues induced by mechanical perturbations of limb movements.

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