

INERTIAL CORIOLIS FORCE PERTURBATIONS OF ARM AND HEAD MOVEMENTS REVEAL COMMON, NON-VESTIBULAR MECHANISMS

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INTRODUCTION

Pitch or roll head movements made during passive rotation tend to be nauseogenic and disorienting. Traditionally these effects have been associated exclusively with the unusual pattern of vestibular stimulation, often termed Coriolis, cross-coupled stimulation (CCS), generated by such movements (Johnson, et al., 1951; Graybiel and Johnson, 1963). Models have been developed to explain the contribution of semicircular canal and otolith activation to disorientation and motion sickness (Guedry and Benson, 1978). In the course of experiments on the etiology of space motion sickness, we found that the nauseogenic and disorienting effects of head movements during rotation were highly gravitoinertial force (GIF) dependent, being greatly lessened in 0 g and greatly heightened in 1.8 g relative to 1 g baseline values (Graybiel et al., 1977; Lackner and Graybiel, 1984). This was the case despite maintaining the patterns of semicircular canal activation constant across different GIF levels.

In other experiments, we made detailed measurements of actual head trajectory and perceived head trajectory, rather than assuming what perceived trajectory would be on the basis of theoretical assumptions as has previously been the case (e.g. Guedry and Benson, 1978). These observations indicated that the apparent path of a pitch head movement during rotation was skewed in a fashion that could not be related to semicircular canal or otolith activity. This skewed path is illustrated in Figure 1. When a subject rotating counterclockwise tilts his head forward he feels it deviate rightward and then return somewhat toward the midline as the movement is completed. The subject also experiences a complex pattern of whole body tumbling. This "scalloping" was force level dependent, paralleling the disorienting and nauseogenic potential of the head movements, being less in 0 g and greater in 1.8 g than in 1 g.

We thought this pattern of apparent path deviation might be due to altered motor control of the head owing to the Coriolis forces present in movements made during rotation.

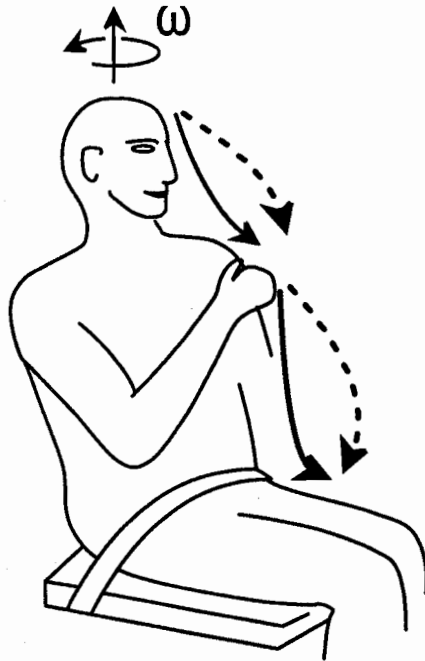


Figure 1. Illustration of a subject attempting to move arm and head straight down (broken arrows) while rotating counterclockwise. The movements are deviated rightward (solid arrows) which is correctly perceived.

Coriolis forces are proportional to the velocity and mass of the head (or other moved body part such as an arm) when the head is moved during body rotation, $F_{\text{cor}} = -2m(\omega \times v)$, where m is the mass of the head, v its linear velocity relative to the torso and ω is the angular velocity of the torso. These Coriolis forces also act on the otolith organs and semicircular canals of the inner ear. It is these latter effects that vestibular theorists have emphasized.

To see whether alterations in sensory-motor control of the musculature was occurring during exposure to Coriolis forces, we had subjects make arm movements during body rotation and indicate the experienced path of the arm. Subjects while rotating counterclockwise made arm movements in a parasagittal plane. When extending the arm outward they felt it deviate rightward and then return toward the intended plane as the movements slowed; flexing the arm resulted in a mirror symmetric apparent deviation. This was precisely the same form of apparent scalloping experienced when head movements rather than arm movements were made. Moreover, the magnitude of illusory curvature of arm movements was also, like that of head movements, proportional to background gravito-inertial force level.

Together these observations signified to us that an understanding of human spatial orientation would require consideration of skeletal musculature control mechanisms as well as vestibular function. As a first step in this direction we wanted to measure precisely the actual and perceived motion of an arm movement perturbed by a Coriolis force. Moreover, we wanted to characterize the time course and form of any adaptive compensations that might develop to correct deviations from the intended movement path or movement terminus. We expected that the understanding of arm movement control and perception so gained would generalize to the control of head movements made in a rotating environment.

PERCEPTION AND CONTROL OF ARM MOVEMENTS DURING CORIOLIS FORCE PERTURBATIONS

A circular rotating room (22 feet in diameter, 7.5 feet in height) that could be completely darkened was the site of the experiment. Subjects sat at the center of the room

in a chair with a contoured headrest and a horizontal, waist-high desktop. The surface of the Plexiglas desktop was smooth, providing no tactile clues about the location of light-emitting diodes (LEDs) embedded in it from underneath. These LEDs served as targets the subject could point to. A low profile button switch was placed on the surface, to the right of the subject's torso. Subjects initiated a pointing trial by pressing the button switch with their right hand, which turned on an LED 35 cm straight ahead. Releasing the button during the onset of the pointing movement extinguished the LED and triggered data collection. The position of the fingertip was monitored with a WATSMART motion analysis system to an accuracy and resolution below 2 mm.

Eleven subjects reached in total darkness to the location of the extinguished LED before the room began to rotate, during 10 rpm counterclockwise rotation, and after the room stopped. The pre-rotation reaches established a baseline performance. During rotation, a transient rightward Coriolis force was generated on the arm when it moved forward; otherwise, there were no differences between pre- and per-rotation conditions. The post-rotation period was included to assess the effects on reaching of adaptation retained from the rotation period.

When reaching, subjects were attempting to make a smooth, continuous movement to the target at a comfortable speed. They were told to correct perceived in-flight errors if they could do so without slowing down, stiffening the arm, or stopping. During the pre-rotation period, the room was dark and subjects made 40 reaches to the target, in five sets of eight. Then, with the lights on they mimicked the last movements they felt they had executed in darkness. The room was darkened again and accelerated to 60°/s counterclockwise at 1°/s². Subjects remained as motionless as possible for one minute after constant velocity was reached and then made 40 more reaching movements. Accelerating at a low rate, delaying reaching onset, and locating the subject on the axis of rotation prevented vestibular signals, postural reflexes, and visual illusions from influencing the reaches. The same procedure was followed for decelerating the room to a stop. Afterwards, the subjects made 40 reaching movements. At the end of the experiment, with the room lights on, subjects mimicked what the initial per-rotation and initial post-rotation movements had felt like. They had been forewarned that this mimic task would be required. It should be emphasized that during testing the only object ever visible was the target LED which extinguished with the onset of a reach. Consequently, subjects never had visual feedback about the accuracy of their reaches.

Pre-rotation, subjects (N=11) pointed in a straight line toward the target LED. The path of the fingertip deviated only 5 mm left of a straight line path between the start button and the movement endpoint. The average movement endpoint was 3 mm left of the target and 30 mm short of it. Movement time was 660 ms and peak velocity 825 mm/s.

On their first reach during rotation, every subject showed significant lateral deviations of movement path and endpoint in the direction of the Coriolis force generated. Throughout, our criteria for significance will be post-hoc Scheffé tests ($p < .05$, at least) following ANOVAs that showed a significant main effect for rotation period. Movements reached an average, peak rightward deviation from a straight line path of 15 mm before turning back toward baseline, but still ended 41 mm right of pre-rotation reaches (Figure 2). With additional reaches subjects rapidly adapted to the Coriolis force perturbations: by the last set of eight per-rotary reaches, the movements were straight, deviating only 2 mm right of a straight line path, and had regained pre-rotation endpoint accuracy. These movements also felt straight and accurate.

Every subject's first post-rotation reach was a mirror-image of his or her initial pre-rotation reach. The paths of the initial movements deviated 25 mm left of a straight line path and ended 36 mm left of the baseline endpoint, both of which are significant differences from pre-rotation. Re-adaptation to normal conditions occurred at the same rate as adaptation to Coriolis force perturbations had. In the mimetic movements made after re-adaptation was complete, subjects matched the actual post-rotation endpoint errors but underestimated the

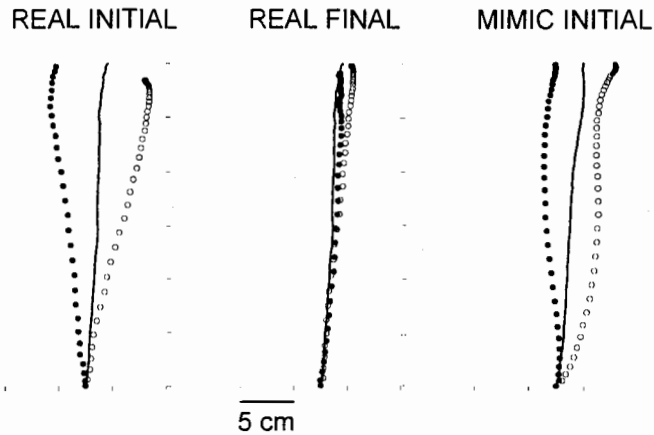


Figure 2. Top view of average ($N=11$) reaching movements made before (solid lines), during (open dots) and after (solid dots) 10 rpm counterclockwise rotation. Represented are the first attempt to reach in darkness for an extinguished visual target (REAL INITIAL) and the fortieth attempt (REAL FINAL), as well as subsequent attempts to mimic what the initial movements had felt like (MIMIC INITIAL).

curvature of the movement paths. The mimetic movements ended 33 mm left of baseline but their maximum deviation from a straight line was only 5 mm leftward. The subjects' mimic of their initial per-rotary movements accurately reproduced the endpoint errors but erred in the shape of the actual movement path. The mimetic movements ended 38 mm right of baseline, which was also their peak deviation from the baseline movement path, and the mimic paths had one more inflection point than the actual movements, first deviating right then bending back toward the center and finally deviating right again.

Thus, our major findings were that transient Coriolis force perturbations initially prevented subjects from reaching the intended endpoint. Additional reaching movements, despite the absence of visual and tactile feedback about reaching accuracy, led to adaptive compensations such that movement paths initially deviated rapidly resumed their original straight-line characteristics and subjects accurately reached to the target position. Moreover, from their mimic movements it was clear that subjects perceived their initial endpoint errors and deviations in movement path. These results indicate that the nervous system must be continuously monitoring and updating movement trajectory control. They also implicate muscle spindle and efferent signals in the process and perhaps joint and tendon afferents, as well.

These results are directly relevant to theories that address how the central nervous system regulates muscle properties responsible for posture and movement. For example, equilibrium-point theories propose that central nervous system commands directly regulate the spring-like characteristics of muscles (Feldman, 1966a,b, 1986; Bizzi et al., 1976, 1984, 1992). These theories avoid the great computational demands placed on the nervous system by theories that propose muscle innervation commands are generated from inverse dynamic calculations. In equilibrium-point theories, a desired posture is achieved by programming a length/tension relationship that results in muscle lengths and tensions and muscle torques around a joint that balance external loads. Movements are planned as a series of length/tension relationships that would bring about a corresponding series of equilibrium postures if sufficient settling time were allowed.

Proponents of equilibrium-point theories predict that transient perturbations of a movement would not affect the programmed endpoint of a movement. Feldman (1980), for example, taught subjects to move their forearms to well-defined positions in a familiar force field. He then instructed them not to voluntarily intervene if he transiently mechanically perturbed their arms during voluntary movements. Perturbed and unperturbed movements reached the same endpoint. Bizzi et al. (1984) trained monkeys to move a manipulandum to visual targets without sight of their arm. He then deafferented their arms by dorsal rhizotomy and studied their performance on the learned task after they were given additional training with visual feedback. When a torque was applied at movement onset that propelled a

monkey's arm beyond its desired endpoint and then removed, the arm went to the desired position, as predicted.

Equilibrium-point theories also predict that transient Coriolis force perturbations such as in our experiments, should not deviate arm movement endpoints because the programmed length/tension relationship and the external load at the end of the movement would remain constant. The significant deviations we observed cannot be accounted for by the idea that movement and posture are the trajectory and equilibrium state of a mass-spring system whose spring-like parameters are set by the nervous system.

The apparent conflict between the endpoint errors caused by Coriolis force perturbations and the endpoint accuracy found by Bizzi, Feldman and others may be explained by the differences between paradigms. In our experiment, inertial Coriolis force perturbations were given without contact, but in the others there were local contact cues from perturbations given by torque motors via a contoured arm rest or manipulandum. Monkeys with arms deafferented by dorsal rhizotomies require significant retraining in the task of moving a manipulandum to a visual target even without perturbations. In the retraining process, they may learn to make use of spatially relevant sensory feedback arising from reaction forces generated in parts of the body with intact sensory innervation. Interestingly, Day and Marsden (1982) found that perturbations delivered via local contact to an unanesthetized thumb do not prevent achievement of learned positions, but with cutaneous anesthesia there are endpoint errors. These considerations show that our new technique for transiently perturbing a limb is ideal for evaluating theories of movement control. The results obtained disconfirm equilibrium-point hypotheses. In fact, methods traditionally used to evaluate equilibrium-point hypotheses are more appropriate for investigation of tool use and object manipulation, e.g. how something in contact with the arm or hand behaves or affects the arm movement.

In our experiment on Coriolis force perturbations of reaching movements, adaptations occurred as additional reaches were made, despite the absence of visual or tactile feedback about reaching accuracy, restoring straight-line trajectories and target accuracy. Post-rotation, when Coriolis forces were first absent there were mirror-image aftereffects to the initial errors made during rotation. Thus, the form of adaptation involved generating a new set of muscle commands that canceled the spatial deviations of the pointing finger from its intended straight-line path.

The pattern of findings indicates that muscle spindle signals during movement are interpreted in relation to motor commands. Under normal conditions, reaching involves generating a set of motoneuronal innervations to accomplish the desired movement. Coriolis forces deviate the arm from the expected path and activate spindle primary and secondary receptors in the unexpectedly stretched muscles of the arm. Spindle primary and secondary outputs code velocity and position, respectively (Matthews, 1972). Unexpectedly, high levels of spindle discharge are interpreted as lengthening of the host muscle and referred to the joint about which the muscle acts (cf. Matthews, 1988). This would largely account for the perceived deviation of an arm exposed to Coriolis force perturbations of its path. How such signals contribute to the adaptive process is an issue we have discussed in detail elsewhere (Lackner and DiZio, 1994; Lackner, 1985).

PERCEPTION AND CONTROL OF HEAD MOVEMENTS AND MOTION SICKNESS DURING CORIOLIS FORCE PERTURBATIONS

Armed with these ideas we returned to our original goal of understanding human perceptual responses to head movements during body rotation. We set out to test whether

the control and appreciation of movement path, and possibly the evocation of motion sickness symptoms would be influenced by factors like the non-vestibular, sensory-motor control and calibration mechanisms we observed in reaching movements. The situation is more complex with head movements because of the vestibular stimulation also generated by Coriolis forces. Therefore, we developed a paradigm that permitted the vestibular stimulus to be held constant and the non-vestibular, sensory-motor control component to be experimentally manipulated. This was achieved by comparing the responses to head movements during rotation when subjects tilted their head with no external load versus for the same attempted movement with extra mass added to the head. Adding mass externally has no effect on vestibular stimulation, but it does affect the magnitude of the Coriolis force applied to the head as a whole (mass is a factor in the equation for Coriolis force).

We expected that Coriolis force perturbations of the head/neck system would affect the control and perception of head trajectory relative to the trunk, whereas the vestibular signal would affect perceived movement of the whole body and reflexive control of gaze. In particular, we predicted that larger Coriolis forces with constant vestibular stimulation would produce larger perceptual deviations of the head from its actual path.

Precise descriptions of the perceptual consequences of CCS are difficult for subjects to make because CCS can be confusing and nauseogenic. CCS is usually generated by having subjects make head movements after they have been rotating at constant velocity for some period. Guedry and Benson (1978) found that relatively little disorientation and motion sickness is elicited by CCS when head movements are made immediately after reaching constant velocity. In pilot experiments, we found that subjects could easily discern the effects of head-loading on perceived head trajectory when head movements were made immediately after acceleration to constant velocity was complete. The following describes an experiment using this paradigm for testing non-vestibular effects of head loading on perceived trajectory of the head relative to the torso.

Eight subjects participated in the experiment which involved making head movements in a rotating chair. There was a lap belt and padded stops to limit the extent of pitch head movements but no other restraints. The head could be moved actively between an upright position and 40° pitched forward. The subjects wore a three-axis rate sensor on a light-weight headband (total mass = 88 grams) which was used in preliminary sessions to give feedback about movement velocity and in experimental sessions to measure actual and perceived head trajectory. In one of the two experimental sessions, a 500 gram mass was added to a biteplate held by the subject, in the other, no mass was added. The added mass required the subjects to activate neck extensor muscles beyond their normal levels for maintenance of a static upright or pitched forward head posture and it increased the effective inertia of the head that had to be controlled during movements. Vestibular stimulation was the same in both sessions because head movements always had comparable amplitudes and velocities, but Coriolis force perturbations of the head/neck system were greater in the session with the added mass. CCS was produced by having the subject make a pitch forward head movement immediately after acceleration at 9°/s² to 90°/s² counterclockwise rotation. The chair was then stopped, the subject released the biteplate and, after a two minute pause, we recorded from the rate sensors while the subject mimicked the perceived path of the head movement that had been made during rotation. Subjects also reported motion sickness severity on a 1 to 10 scale. This procedure was repeated eight times on each test day, with enough rest between trials for any disorientation and motion sickness symptoms to abate completely.

Subjects attempted to pitch their head straight forward in a midsagittal plane but perceived a deviation to the right, the direction of the Coriolis force. The perceived deviation was greater and more severe motion sickness symptoms were elicited in the condition with the mass added to the head. Both differences were highly significant statistically. Impor-

tantly, the perceived and actual pitch amplitude and velocity of head movements did not differ across the head loaded and unloaded conditions.

Interestingly, neither our baseline nor our head loaded observations give patterns of experienced trajectory that are in accord with traditional vestibular models of orientation. For example, Benson and Guedry's model (1978) fails to predict either the perceived scalloping of head movements or the effects of head weighting on motion sickness and disorientation. It also predicts semicircular canal stimulation that codes leftward roll of the head when in fact our results show that subjects perceived rightward roll.

These findings demonstrate that non-vestibular, sensory-motor mechanisms also contribute to the disorientation and motion sickness elicited by head movements made during body rotation. The Coriolis forces generated in this experiment deviated movements to the right and subjects accurately perceived this direction of deviation. Although the synergies among muscles controlling head movements are quite complex, multi-dimensional frames of reference can be identified (Baker et al., 1985). Such complex but systematic relationships establish the conditions necessary for the nervous system to make use of muscle spindle feedback in perception of head movement trajectory and updating of motor control. Spindle error signals that drive the adaptation process by which straight forward pitch head movements are restored may also be implicated in the evocation of motion sickness.

The involvement of mechanisms that process muscle spindle signals during movement may explain why head movements, of matched kinematic properties, made while rotating generate disorientation and motion sickness whose severity is proportional to GIF level. We have already shown that other phenomena that depend on muscle spindle signals, for example vibratory myesthetic illusions (Lackner et al., 1992) and the ability to reproduce practiced arm movements (Fisk et al., 1993), are GIF dependent. Additional experiments are in progress to further discriminate vestibular and non-vestibular influences on motion sickness susceptibility and head movement control. The results are demonstrating that vestibular signals represent only one of the factors influencing body orientation and that skeletomuscular control affects both the control and appreciation of orientation.

In summary, we have utilized the inertial, non-contacting Coriolis forces that can be generated in a rotating environment to study basic mechanisms of arm and head movement control and perception. We have identified sensory-motor components influencing head movement control that explain aspects of performance that have been misattributed to vestibular function. Our overall findings indicate that it is essential to broaden our theoretical perspectives and not rely only on vestibular based models to explain spatial orientation. The reliance on such models is seriously hindering an adequate understanding of posture, movement, and orientation.

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