Short review

Adaptation in a rotating artificial gravity environment

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Abstract

The centripetal force generated by a rotating space vehicle is a potential source of artificial gravity. Minimizing the cost of such a vehicle dictates using the smallest radius and highest rotation rate possible, but head movements made at high rotation rates generate disorienting, nauseogenic cross-coupled semicircular canal stimulation. Early studies suggested 3 or 4 rpm as the highest rate at which humans could adapt to this vestibular stimulus. These studies neglected the concomitant Coriolis force actions on the head/neck system. We assessed non-vestibular Coriolis effects by measuring arm and leg movements made in the center of a rotating room turning at 10 rpm and found that movement endpoints and trajectories are initially deviated; however, subjects readily adapt with 10–20 additional movements, even without seeing their errors. Equilibrium point theories of motor control errantly predict that Coriolis forces will not cause movement endpoint errors so that subjects will not have to adapt their reaching movements during rotation. Adaptation of movement trajectory acquired during Coriolis force perturbations of one arm transfers to the unexposed arm but there is no intermanual transfer of endpoint adaptation indicating that neuromotor representations of movement endpoint and trajectory are separable and can adapt independently, also contradictory to equilibrium point theories. Touching a surface at the end of reaching movements is required for complete endpoint adaptation in darkness but trajectory adapts completely with or without terminal contact. We have also made the first kinematic measurements of unconstrained head movements during rotation, these movements show rapid adaptation to Coriolis force perturbations. Our results point to methods for achieving full compensation for rotation up to 10 rpm. © 1998 Published by Elsevier Science B.V. All rights reserved.

Keywords: Reaching; Movement; Trajectory; Adaptation; Coriolis force; Equilibrium point theory

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1. Introduction

Long duration space flight has adverse effects on bone, muscle and vestibular physiology [1,10,11,21,22,33]. Artificial gravity generated by rotation has frequently been proposed as a way of providing an effective countermeasure for preventing bone demineralization and changes in sensory motor function during prolonged missions, such as a flight to Mars which might last several years round trip. In a rotating space vehicle, the centripetal force provided by the walls of the vehicle against the feet of the astronaut is the source of the artificial gravity. Centripetal force is proportional to the square of the velocity of rotation in radians times the radius of rotation. This means that a particular level of artificial gravity can be generated by many combinations of rotational rates and radii. For example, roughly 1.1 g could be generated with a radius of 1000 m and a rotational velocity of 1 rpm and by a radius of 10 m with a rotational rate of 10 rpm. There is a great advantage to having a vehicle rotating at a higher velocity in terms of much lower construction cost for the smaller required radius [32].

Although rotation is an effective technique in principle for generating artificial gravity, there are several disadvantages associated with a rotating environment [35]. One of these is the unusual patterns of vestibular cross-coupling stimulation that are generated by head movements during body rotation [36]. Head movements made during high rates of rotation, e.g., 10 rpm, can rapidly induce motion sickness and disorientation [13,23,34]. In addition, when objects move linearly Coriolis forces are generated in a rotating environment. The Coriolis force is proportional to the angular velocity of the rotating environment ($[\omega]$) in radians, the mass of the object (m), and the linear velocity (v) of the moving object: $F_c = -2m\,([\omega]\,v)$. Thus, if one makes a forward movement of the arm or head during counterclockwise rotation about the long axis of the body there will be a rightward Coriolis force generated. In other words, a Coriolis force will tend to deviate the path of the movement perpendicular to the intended direction. Thus, it can be anticipated that alterations of motor control might arise in artificial gravity environments.

In the 1960s, Graybiel et al. conducted a number of studies on adaptation to moving about in a slow rotation room. The general conclusion of these studies, some of which involved rotation durations as long as 21 days, was that it would be difficult to adapt individuals to velocities of rotation greater than 3 or 4 rpm because of the disorientation and vestibular side effects elicited by head movements during rotation [12,13,15,24]. In addition, a number of performance effects were noticed, such as reaching errors, ataxia, and difficulties in locomotion because of the Coriolis forces generated by body movements [20]. Graybiel et al. also developed incremental adaptation procedures which make it feasible in terms of vestibular function to adapt to high rates of rotation, as much as 10 rpm,

but this requires making many hundreds of head movements at gradually increased rotational velocities [14,17,18].

Most attempts to understand the side effects of rotation and to augment adaptation have focused on the Coriolis cross-coupled stimulation of the semicircular canals which head movements elicit. However, systematic experiments have shown that the effects of a given pattern of Coriolis cross-coupling stimulation on the vestibular system are highly gravitoinertial force dependent [9,16,31]. Cross-coupling is much less provocative for a given velocity of rotation and pattern of head movement if a subject is in a less than 1 g force background at the time of making the head movements. By contrast, head movements made during rotation in higher than 1 g force levels are much more provocative than under terrestrial conditions. This gravitoinertial dependence is in part due to otolith unloading which alters the overall pattern of vestibular input [19]. Altered sensory–motor control of the head and neck due to the diminished weight of the head is another non-vestibular etiological factor involved in variations of motion sickness severity produced by head movements during rotation in different background force levels [26].

The alterations in control of the head and neck result both from the changed weight of the head and from
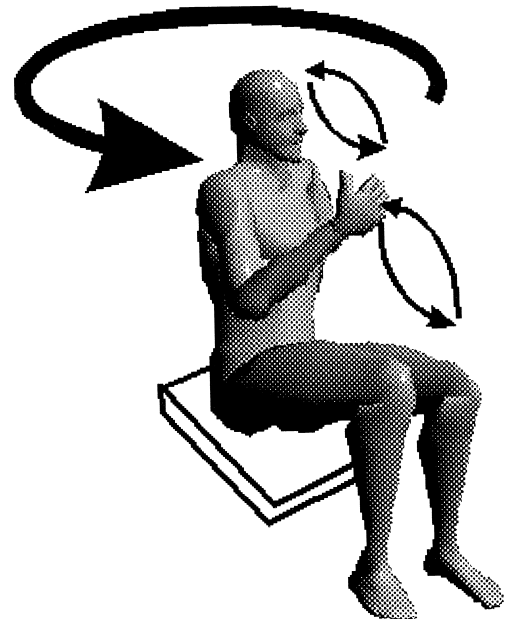

Fig. 1. Illustration of the scalloping motion experienced during voluntary pitch head movements and flexion–extension forearm movements made during body rotation. When subjects are rotating counterclockwise (heavy arrow) and pitch the head forward or extend the forearm they experience a rightward deviation (thin arrows) from the intended path (dotted lines) and the reverse when they raise the head or arm up. The scalloping motion is in the direction of the Coriolis force generated. It is exaggerated when the gravitoinertial force level increases and is almost abolished in microgravity, both for the arm and head.

alterations in muscle spindle gain that occur immediately on transition into free fall or hypergravity. For example, tonic vibration reflexes in the arm muscles are greatly attenuated during exposure to 0 g and heightened during exposure to increased force levels [29]. The disorientation associated with head movements in altered force environments during rotation can be attributed in part to alterations in muscle spindle feedback from the neck because the pattern of misperception of the trajectory of the head during a head movement made during rotation is similar to that experienced when an arm movement is made during rotation [27]. This is illustrated in Fig. 1, which shows a scalloping motion of both arm and head during movements made during rotation.

For the past several years, we have been systematically examining how humans adapt their movement control in a rotating environment. In these studies, we have employed our fully enclosed rotating room with subjects seated at the center of rotation. This positioning has the advantage that the subjects can be brought up to high rates of rotation, 10 rpm in our studies, and still not be exposed to a significant centrifugal force because they are seated at the center of rotation. Consequently, we have a situation in which the subject feels perfectly normal and the overall pattern of forces acting on his or her body are the same as when not

rotating. Yet, if the subject makes an arm or head movement, he or she will be exposed to a transient Coriolis force, the same as in a rotating space vehicle. This force is absent prior to the movement and at the end of the movement because it is a velocity-dependent force. We began with the study of arm movements to assess effects of transient Coriolis forces loads without abnormal vestibular stimuli.

2. Rapid adaptation to Coriolis forces perturbations of arm movements

Interestingly, one of the most prominent theories of motor control, the alpha equilibrium point hypothesis [2,3], would predict that arm movements made during rotation should show deviations of movement path but be accurate in terms of reaching the desired target position. According to this theory, the nervous systems codes for a movement permits a transient Coriolis perturbation to deviate the path of a movement but ensures that a temporary perturbation will not affect final position. Since the Coriolis force is a transient force and is gone at the end of the movement, the pre-programmed final hold position should not be affected by the transient disturbance. Thus, alpha equilibrium point theories predict that one does not need to adapt to a
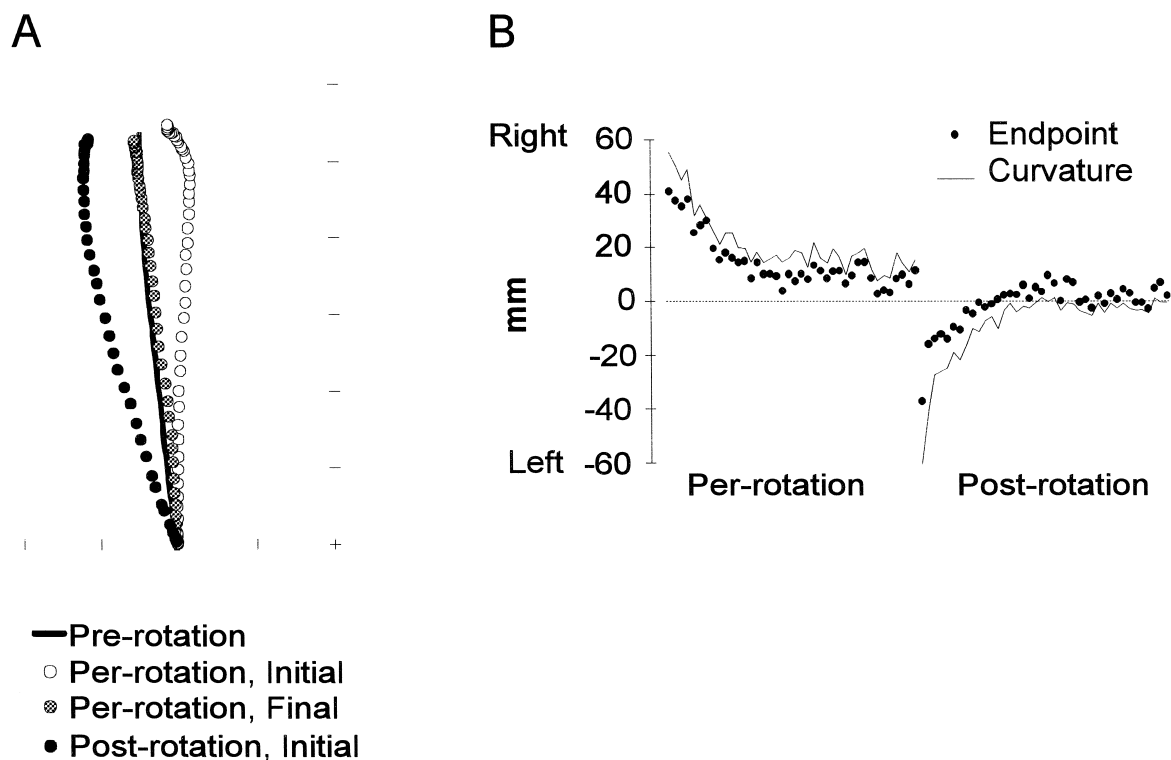

Fig. 2. (A) Top view of reaching movements (averaged for 11 subjects) in the rotating room. The task requires extending the right hand forward to the location of a just extinguished visual target in darkness. Fingertip position is sampled at 100 Hz. The room was turning counterclockwise per-rotation, so forward reaching movements generated rightward Coriolis forces. Movement endpoints and trajectories are initially deviated in the direction of the Coriolis forces per-rotation and in mirror-image fashion post-rotation. (B) Plots of endpoint and curvature with repeated movements per- and post-rotation. The horizontal axes represent average pre-rotation baseline performance.

rotating environment, because ones limb position at the end of the movement will be accurate. If true, this would be a great advantage because individuals would be able to perform accurately, at least with regard to the end point position of their movements, in a rotating environment and not have to adapt. The systematic series of studies that we have conducted shows unfortunately that this is not the case.

In our initial studies, we looked at subjects' accuracy in pointing to targets [28]. The important feature of these studies was that the experiments were conducted in a totally dark rotating room, and that when the subject lifted his/her finger from a start button to point the target was extinguished, thus the subject reached without receiving any visual feedback about movement accuracy. The targets were light emitting diodes embedded in a Plexiglas panel with a smooth top so that when the subjects finger touched the panel at the end of a movement there were no direct tactile cues about whether the goal of touching the target position had been met. The subjects made reaching movements pre-rotation, per-rotation, and post-rotation. By comparing the pre-rotation baseline movements with the first movements made during rotation, we could see what the initial effects of Coriolis forces were on both movement trajectory and endpoint. By comparing the first per-rotation movements with the last per-rotation movements we could determine whether any adaptive changes occurred during the course of pointing movements made during rotation. And finally, by comparing the pre-rotation baseline movements with the first movements made during post-rotation we could see if there were any aftereffects as a consequence of the movements made during rotation.

The patterns of fingertip motion we observed were exceedingly interesting. First, the initial movements made during rotation showed large deviations of movement path and endpoint in the direction of the transient Coriolis force generated during the movement. The subjects reached in a curved path and missed the target position. By contrast, pre-rotation they pointed in a straight path accurately to the target position. The final movements made per-rotation showed a complete return to the pre-rotation baseline pattern. In other words, full adaptation had occurred despite the absence of visual or direct tactile feedback about reaching accuracy. In fact, in about 15 per-rotation movements, baseline accuracy had been regained. Post-rotation all of the subjects showed a mirror image pattern to that initially exhibited during rotation. Now movements were curved in the opposite direction and ended on the opposite side of the target. These results are shown in Fig. 2.

The pattern of aftereffects means that the nervous system had programmed a compensation for the Coriolis force, a compensation that was no longer appropriate because the subjects were no longer rotating. In this context, a key feature of our experiment is that even though it involved periods of rotation the subjects always felt stationary because the room was accelerated up to constant velocity at a very slow rate, below threshold for detection of motion, and at the end of the per-rotation period decelerated to rest in a similar fashion.

3. Independent adaptation of movement endpoint and trajectory

In other experiments, we used the same basic experimental paradigm except that subjects attempted to point above the position of the target as seen just before it was extinguished. Our goal was to see what influence terminal contact of the hand with the target board surface had in the first experiments even though the contact did not give the subject direct feel of whether they had hit the target position. The results were clear cut. Subjects were able to adapt but the adaptation was primarily of movement path. During the rotation period, subjects initially showed a deviation of movement path and endpoint in the direction of the Coriolis force that had acted during the movement but, with repeated reaches, the subjects reached in straighter and straighter paths. Within about 15 movements, subjects again reached as straight as they had pre-rotation. However, the endpoints of the movements showed only partial adaptation and remained deviated per-rotation in the direction of the transient Coriolis forces. Thus, there was complete adaptation of movement path with it becoming straight like the pre-rotation reaches but only partial adaptation of movement endpoint. Post-rotation the subjects reaches showed curvature to the opposite direction to that exhibited initially per-rotation and only missed the endpoint slightly. This pattern indicates that there was full retention of trajectory adaptation and of the partial endpoint adaptation that occurred during rotation. With additional post-rotation movements, subjects quickly returned to pre-rotation baseline values. The movement path adaptation during rotation must be contingent on the abnormal patterns of proprioceptive feedback resulting when a movement is perturbed by the Coriolis force. By contrast, the absence of restoration of accurate movement endpoint indicates that contact with the smooth target surface is important in providing spatial information about the location of hand contact. The fingertip is stimulated slightly differently for different locations on the surface.

In ongoing experiments, we are finding that the pattern of contact force, the orientation of the force vector, on the fingertip differs according to where on a horizontal surface the fingertip lands. These cues allow the nervous system to detect whether the finger has landed in the desired location or not. Even though the differences are not perceptually salient the nervous system nevertheless is able to resolve them and initiate corrective compensations in reaching behavior.

The primary feature of this experiment is that it shows there can be independent adaptation of movement endpoint and movement path. This is counter to the primary as-

sumption of equilibrium point models that the control of movement and posture, i.e. trajectory and endpoint, are unified in the execution of movement. Thus, these data are further evidence against the usefulness of the equilibrium point models of motor control.

4. Intermanual transfer of adaptation to Coriolis force perturbations

In another experimental series, we looked at the issue of whether adaptation achieved during rotation by making reaching movements with one arm would transfer to the other arm [8]. The basic paradigm was to make alternating sets of pointing movements with the right and then the left arm pre-rotation to get measures of baseline performance. During rotation, reaching movements were made only with the right arm to targets. As in our earlier experiments, when the subject began to point the target light went out and the movement was completed in total darkness. The subjects made contact with the surface at the end of the movement. Eighty movements were made with the right arm per-rotation. Post-rotation, like pre-rotation, the subject initially reached with the left arm eight times, then with the right arm eight times, and alternated in this

fashion until a total of 24 movements had been made with each hand.

The results were highly interesting. Complete adaptation was achieved during rotation with the right arm so that by the end of the rotation period the right arm was making straight reaches accurately to the target location. Post-rotation the initial reaches made with the left arm went in a straight line but missed the target position to the side. The direction of miss was opposite to the direction of endpoint error during initial exposure to rotation. In other words, this finding means that there was transfer of endpoint adaptation but not trajectory adaptation to the left arm. The first movements made with the right arm showed a curved path to the correct target location. This means that the endpoint adaptation originally achieved with the right arm during rotation had been dissipated by the post-rotation movements made with the left arm. In other words, the transfer of endpoint control occurs in both directions. The curved path of the initial post-rotation reaches with the right arm means that trajectory adaptation had been achieved during rotation with the right arm and had not been dissipated by the first eight post-rotation movements made with the left arm. Thus, trajectory adaptation does not show intermanual transfer. These results are also counter to equilibrium point theory predictions
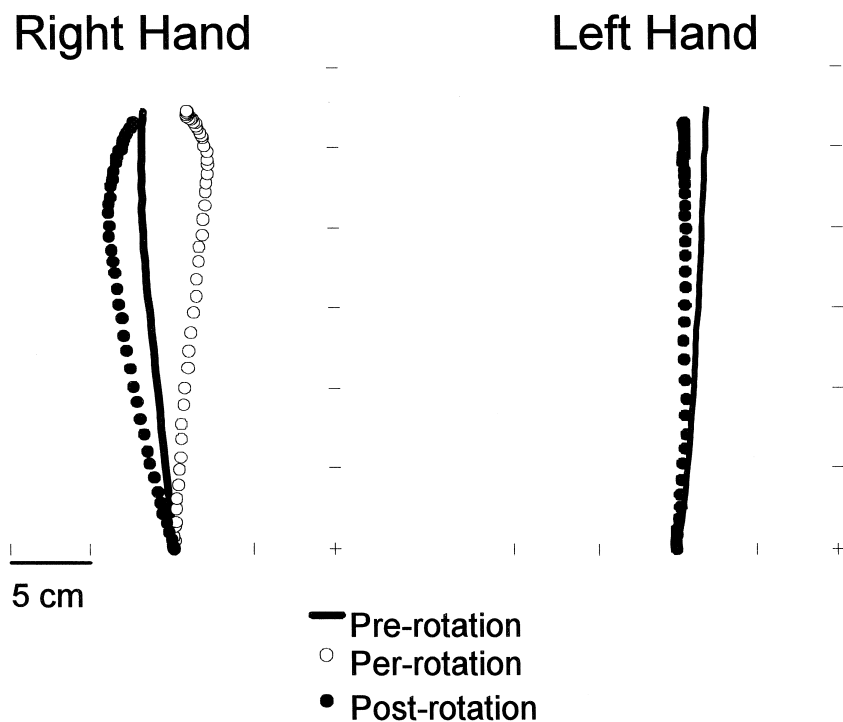

Fig. 3. Reaching movements made (averaged across eight subjects) in a study of intermanual transfer of adaptation to Coriolis forces in the rotating (counterclockwise) room. Same view, scale and sampling as in Fig. 2A. Baselines were established for both hands pre-rotation, 80 reaches were made per-rotation with the right hand to adapt it fully (not shown) to counterclockwise rotation. The initial post-rotation movements with the left hand went straight to a deviated endpoint. These movements mirrored the endpoint error but not the curvature of the initial per-rotation movements that had been made with the right hand. With subsequent left handed reaches (not shown) endpoint error rapidly diminished. When subjects first reached with the right hand after eight post-rotation movements of the left hand, their movements ended on target but arched symmetrically to the initial per-rotation reaches with the right hand.

and show that not only is there independent representation of movement path and endpoint but there is intermanual transfer only of endpoint adaptation. Fig. 3 illustrates the experimental findings.

5. Rapid adaptation to Coriolis forces perturbations of leg movements

We are also concerned with how well locomotion will adapt to a rotating environment in which Coriolis forces are generated when the legs are in motion. In an initial series of experiments, we have had subjects while standing make kicking movements at visual targets before, during and after 10 rpm rotation [7]. One interesting feature of leg movements during rotation is that because the leg has a

5 cm

— Pre-rotation
○ Per-rotation, Initial
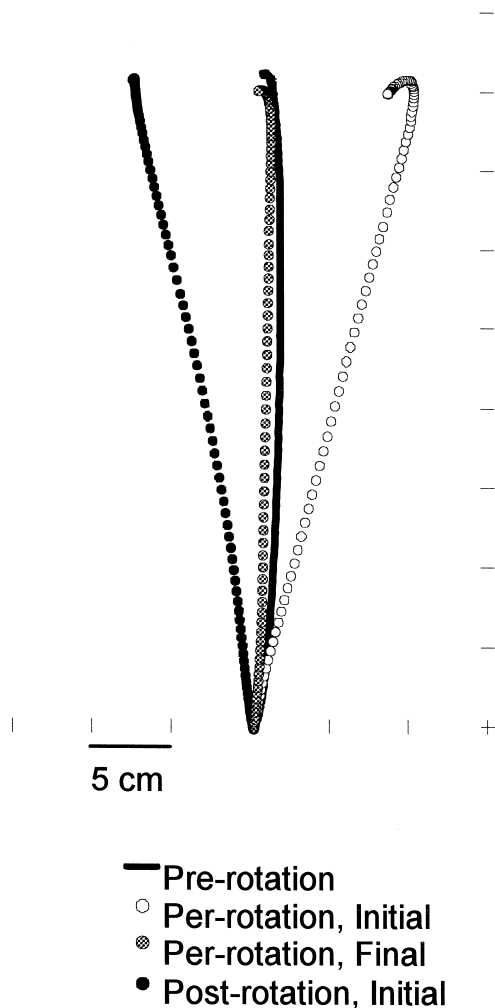⊗ Per-rotation, Final
● Post-rotation, Initial

Fig. 4. Pointing movements of the leg (averaged across eight subjects) to a recently extinguished visual target on the floor of the rotating room. Same view, scale and sampling as Fig. 2A. Subjects stood and used their right leg, their head and waist were stabilized. Movement endpoints were initially deviated in the direction of the rightward Coriolis forces generated per-rotation (counterclockwise) and were deviated in mirror-image fashion post-rotation.

considerably greater mass than the arm, the Coriolis force acting on the leg is much larger than the Coriolis force acting on the arm for a movement of comparable velocity. Fig. 4 shows the path of the toe during a leg movement viewed from above. There is a large deviation of the foot in the direction of the Coriolis force. Moreover, unlike with the arm movements, there is no tendency for the first per-rotation leg movement to curve back toward the intended path as the forward velocity of the leg diminishes and the Coriolis force abates.

This pattern means that equilibrium point theory also does not hold for movement of the legs. As subsequent leg movements are made subjects rapidly regain straight movement paths. By the time they have completed 15–20 leg movements their movements are again straight and accurate. This happens despite the absence of visual feedback. It should be noted that the movements that were made are simple movements of the leg. They do not involve transport of the head or body. Nevertheless, the rapidity with which adaptation occurs and with which aftereffects of adaptation are dissipated during return to a stationary environment lends great hope that locomotory adaptation to rotation can be relatively simple to attain.

6. Rapid adaptation to Coriolis forces perturbations of head movements

We are currently studying the control and adaptation of head movements in a rotating environment and have made the first ever kinematic measurements of free, unconstrained head movements during rotation [6]. The path of the head during exposure to Coriolis cross-coupling stimulation turns out to be surprisingly complex and cannot be predicted from the pattern of vestibular stimulation alone. Fig. 5 presents the actual motion of the head during attempts to make voluntary pitch forward movements before and during 10 rpm counterclockwise rotation. As can be seen, there is displacement of the head in pitch, in yaw, and in roll with regard to the torso. In addition, there is a lateral displacement of the head in the direction of the Coriolis force and the head does not end in the sagittal plane of the body as it does with head movements made pre-rotation.

With subsequent head movements during rotation, adaptation occurs so that the path of the head movement becomes straighter and there is less deviation of the head about the other axes. Near complete adaptation about some axes is achieved within 10–15 head movements. However, substantial deviation in roll still remains. This pattern suggests that there are two factors in adaptation. One factor is changes in head trajectory that are related to altered sensory motor control of the head. These changes are analogous to the adaptive changes that occur with the arm movements as illustrated earlier in Fig. 2A. This
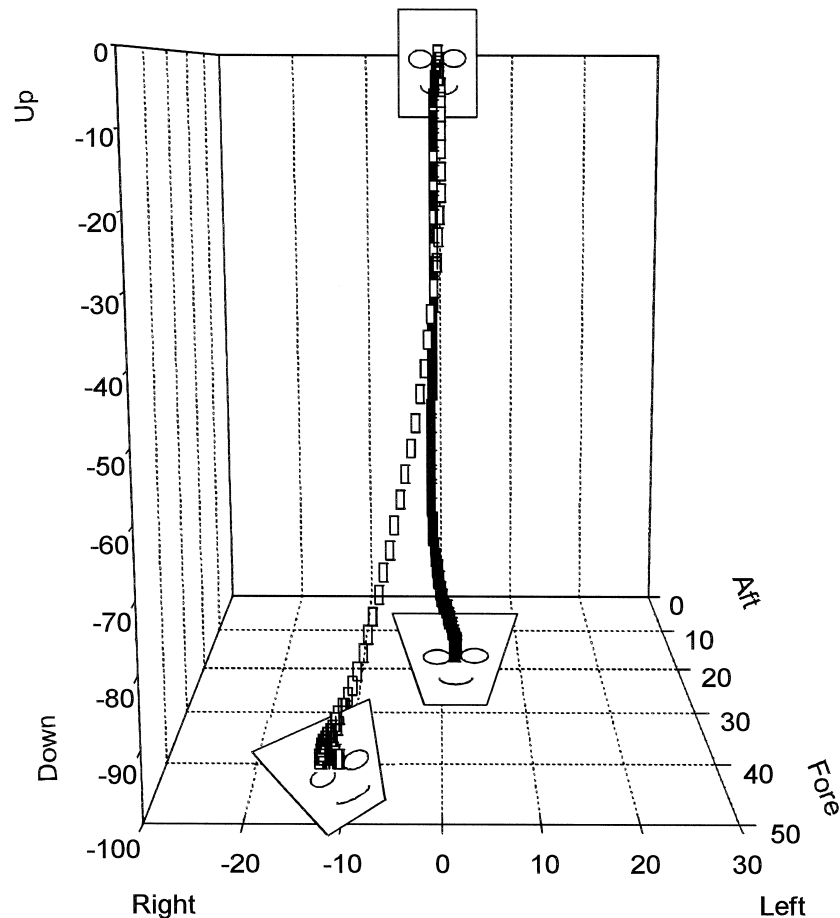
Fig. 5. Three-dimensional paths of typical pitch head movements made at 10 rpm counterclockwise in the rotating room. A point between the eyes was tracked at 100 Hz. The view is looking toward and slightly down on the subject, and the coordinate system is fixed relative to the subject's torso. The icons indicating head orientation are drawn smaller than the plotting scale. The solid rectangles are pre-rotation and the open rectangles per-rotation. Pre-rotation the path of the head is essentially straight with no lateral deviation and no rotation in yaw or roll. Per-rotation the head is initially deviated in the direction of the Coriolis forces generated and there is also rotation in yaw and roll. There is a rapid return to the median plane with additional per-rotation movements (not shown) but the roll orientation of the head does not adapt as quickly.

means that the altered sensory motor control of the head can be adapted or compensated for quite readily. However, adaptation to rotation about the roll axis seems to have a longer time course and this may well reflect a longer time constant for adaptation of the vestibular system. In this case, the responsible factor is probably the altered patterns of canal stimulation associated with head tilts during rotation. Thus, adaptation of head movement control would appear to be a dual process rather than a single process as in the case of arm movement regulation. It may be possible to develop 2-step adaptation procedures for faster overall sensory–motor compensation than simultaneously engaging both adaptive processes.

7. Conclusions

In summary, we have now obtained the first quantitative measurements of the effects of Coriolis forces on the execution of arm, leg, and head movements. The trajectories of all three types of appendages are initially deviated by exposure to Coriolis forces. The pattern of deviation and subsequent adaptation with additional movements is totally counter to the predictions of alpha equilibrium point theories of movement control. Adaptation occurs quite readily, even in the absence of visual feedback, but is only complete if tactile contact is provided at the end of the movement. The pattern of touch input specifies where on the surface finger contact is made. Adaptation to rotation speeds up to 10 rpm can be achieved quite readily. This finding is totally counter to early theoretical views that it would not be possible to adapt to rates of rotation greater than 3 or 4 rpm. Following exposure there are aftereffects and the pattern of these aftereffects shows that the nervous system has anticipated the Coriolis forces associated with movements and planned compensatory motor innervations that precisely counter and eliminate the consequences of

the Coriolis force perturbations, thus restoring movement accuracy.

An important feature of our experiments is that after motor adaptation to the Coriolis forces associated with movement has taken place the subject no longer perceives the Coriolis forces. Movements again seem normal despite the continuing presence of Coriolis forces during a movement. This means that individuals who live and work in a fully enclosed rotating environment will likely come to feel as if they are in a normal non-rotating environment. This should not be too surprising because under every day circumstances we also do not accurately perceive the forces that act on our bodies. For example, if we lift one foot while standing on two, the force on the sole of the stance foot doubles but we perceive little if any change in force level [25,30]. By contrast, if while recumbent, the same force increase were passively applied to the sole of one foot it would seem like an enormous force that might do damage to the limb. The point is that those forces that are associated with voluntary stance, locomotion, and movement are perceived as being negligible when we are just controlling our bodies per se and not manipulating or moving external objects. Another important feature of our experiments is that they show that movement trajectory is quite accurately monitored and controlled by the nervous system. Equilibrium point theories of motor control are inadequate to handle such complexity and rapid adaptability. Such theories necessitate tight coupling of endpoint and trajectory control, but our results demonstrate independent mechanisms for adaptation of endpoint and trajectory. Equilibrium point theories don't rely on prediction or sensing of transient perturbations in order to update motor calibration, but our results prove that internal models of transient Coriolis force perturbations as well as proprioceptive and tactile feedback, even in the absence of vision, are fully adequate to allow rapid and complete adaptation. Further evidence for the importance of internal models comes from our ongoing experiments [4,5]. We are finding that stationary subjects experiencing illusory self-rotation show curvilinear movement paths in pointing to targets. The pattern of their errors indicates that their nervous systems are automatically compensating for the Coriolis forces that would be generated by their reaches if they were actually rotating. The compensations result in reaching errors because they are in fact stationary. The study of rotating environments, both real and illusory, thus gives us insights as well into the ways in which our bodies are calibrated to the static force environment of Earth.

Our results are very hopeful with regard to the use of artificial gravity in long duration space missions. They indicate that the maximum rotation rate to which individuals can adapt may be as high as 10 rpm or more. Adaptation of arm and leg movement control can be surprisingly rapid. Head movement control clearly takes longer, but with appropriate adaptation procedures also seems quite straight forward. This means that rotating space vehicles of relatively small diameters, about 20–40 m, would in fact be feasible for providing 1 g of artificial gravity on long duration missions.

Acknowledgements

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