ADAPTATION TO CORIOLIS FORCE
PERTURBATION OF MOVEMENT TRAJECTORY
Role of proprioceptive and cutaneous somatosensory feedback

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ABSTRACT

Subjects exposed to constant velocity rotation in a large fully-enclosed room that rotates initially make large reaching errors in pointing to targets. The paths and endpoints of their reaches are deviated in the direction of the transient lateral Coriolis forces generated by the forward velocity of their reaches. With additional reaches, subjects soon reach in straighter paths and become more accurate at landing on target even in the absence of visual feedback about their movements. Two factors contribute to this adaptation: first, muscle spindle and Golgi tendon organ feedback interpreted in relation to efferent commands provide information about movement trajectory, and second, somatosensory stimulation of the fingertip at the completion of a reach provides information about the location of the fingertip relative to the torso.

INTRODUCTION

The contribution of muscle spindle afferents to the conscious appreciation of limb position was first shown by Goodwin, McCloskey, and Matthews in 1972. They found that resisting the displacement of a limb moving under the action of a tonic vibration reflex led to illusory motion and displacement of the limb in the direction that would be associated with lengthening of the vibrated muscle. Their study along with subsequent observations was also key in revealing that position sense is computed by interpreting spindle output in relation to motor commands (cf. Matthews, 1988; Gandevia, 1996). In the present paper, we provide evidence that muscle spindle signals also figure prominently in the adaptive control mechanisms underlying limb trajectory formation and

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regulation. We also show that the role of spindle signals in trajectory control and adaptation is complemented by tactile somatosensory afferents that specify limb position in relation to the torso when the hand makes contact at the end of a reaching movement.

CORIOLIS FORCE INFLUENCES ON REACHING MOVEMENTS

The experimental paradigm used in our studies is depicted in Figure 1 (Lackner and DiZio, 1994). A subject is illustrated seated at the center of a large, fully-enclosed, circular room that can be rotated. When the room has been turning at constant velocity for a minute the subject will feel completely stationary because the angular acceleration sensitive semicircular canals of his inner ear will have returned to resting discharge levels and he has no visual or somatosensory cues to indicate that he is rotating. If the subject makes a forward reaching movement to point to a target appearing on the surface in front of him, an inertial Coriolis force will be generated on his arm. This Coriolis force ($F_{cor}$) is proportional to the angular velocity of room rotation, $\omega$, the forward velocity of the arm, $v$, in the plane of rotation, and the mass of the arm, $m$, with $F_{cor} = -2m(\omega \times v)$. For example, if the test room is rotating counterclockwise (CCW), the Coriolis force
Figure 2. Left panel shows overhead view of average initial and final pre-, per-, and post-rotation movements. Right panel shows average movement endpoints and curvatures for all movements.

generated will act to displace the subject's arm rightward. Unlike mechanical forces that are often used to perturb reaching movements, e.g. manipulanda controlled by torque motors, Coriolis forces act without localized contact on the arm. As a consequence, no tactile cues are imposed on the arm that can provide information about the magnitude, direction, and duration of the perturbation.

Because Coriolis forces on the arm are dependent on the arm's linear velocity relative to the test chamber, they will mirror the forward velocity profile of the arm and be absent at the beginning and end of a reach. This also makes Coriolis forces an ideal tool for evaluating equilibrium point theories of movement control, which posit that movement trajectory is generated by an evolving series of commands specifying the length-tension properties of the muscles and that detailed monitoring of ongoing limb position is not necessary (Bizzi et al., 1992; Feldman, 1966, 1986). Such theories hold that transient perturbations of movement trajectory will not affect the pre-programmed endpoint of the movement. The endpoint is thought to be determined by the final length-tension properties of the agonist and antagonist muscles specified and these are thought not to be altered by a temporary perturbation. Experiments using mechanical perturbations delivered by manipulanda to disturb reaching movements have provided support for these theories (Bizzi et al., 1992; Feldman, 1986, Feldman et al., 1998).

Figure 2 shows average data of eleven subjects who made reaching movements to a light emitting diode target embedded in the underside of the smooth Plexiglas work surface (cf. Figure 1). When a subject lifted his finger to point, the target was extinguished and the reach was completed in total darkness. Thus, the subjects never received visual feedback about their movement onset, trajectory, or terminus. As can be seen, pre-rotation the subjects were very accurate. The endpoints of the first per-rotation reaches (made during 10 rpm, constant velocity, CCW rotation) were displaced, however, in the direction of the lateral Coriolis force generated by the forward velocity of the arm. With repeated per-rotation reaches, subjects became progressively more accurate and were back to baseline accuracy within 15 reaches despite the absence of visual feedback.

The trajectory curvature of the reaches (defined as the maximum horizontal distance between a straight line joining the start and endpoint of the movement and the actual movement path) showed the same pattern. The pre-rotation movements were essentially straight; the initial per-rotation movements were deviated in the direction of the Coriolis force but the subsequent per-rotation movements became progressively straighter. The
initial post-rotation movements had a trajectory curvature mirror image to the initial pre-rotation movements. An "overhead view" of the first pre-, per-, and post-rotation movements (averaged across subjects) and the final pre-, per-, and post-rotation movements are also presented in Figure 2. The existence of afferent effects in the post-rotation period indicates that the central nervous system has constructed a "model" of the Coriolis forces associated with the per-rotation movements and is still compensating for them although it is no longer appropriate. These anticipatory compensations are why movement trajectories become straight again during the per-rotation period. Such findings are totally contradictory to equilibrium point theories of movement control because these theories would not predict movement errors, adaptive changes, or afferent effects in our experimental situation.

Figure 3. Movement characteristics when subjects end their movements in the air.

DISSOCIATION OF TRAJECTORY AND ENDPOINT ADAPTATION

If we expose subjects to the same experimental paradigm but have them point just above the location of the target so that their reaches end in the air, they exhibit the same pattern of per-rotation trajectory curvature and adaptation and post-rotation afferent effects. However, they do not show the same pattern of per-rotation endpoint adaptation as subjects who touch down at the end of their movements. Instead, they exhibit only partial endpoint adaptation, indicating that terminal hand contact is important for full adaptation to Coriolis forces (see Fig. 3).

To explore the factors that contribute to endpoint and trajectory adaptation and to determine why they are dissociable, we tested labyrinthine defective and cerebellar subjects using the same pre-, per-, and post-rotation paradigm. The subjects in these experiments always made hand contact with the target board surface at the end of their movements. The rotation rate was always 10 rpm, CCW. We tested the labyrinthine-defective subjects in part because equilibrium point theorists had suggested that subjects in our test situation might sense body rotation during the per-rotation period and "correct" for it, thus changing their reaching pattern. This argument does not cohere conceptually for at least two reasons: (i) it should not be necessary by these theories to "correct" for self-rotation, and (ii) if corrections were made, then our subjects should have been reaching more accurately than they were. Nevertheless, it was of interest to test vestibular loss patients because they have an impaired sense of orientation to the
vertical and possibly of adaptive capacity that could affect their performance. All of them had normal tonic vibration reflexes. We tested the cerebellar patients because of possible degradations in adaptive control of movement owing to alterations in muscle spindle gain and feedback. Each patient group was tested along with age-matched, normal control subjects.

Figure 4. Upper panel shows movement paths, endpoints, and curvature for labyrinthine-defective (LD) subjects. Bottom panel shows movement terminal velocities and peak elevations for LD subjects and controls.

Figure 4 (top panel) presents the experimental findings from the labyrinthine defective subjects. These subjects all showed normal trajectory adaptation during the per-rotation period. Their per-rotation reaches were initially curvilinear but subsequent reaches became progressively straighter just like those of normal subjects. They also showed trajectory curvature aftereffects. However, unlike the normal subjects, they failed
to show movement endpoint adaptation. During the per-rotation period, their reaches remained deviated in the direction of the transient Coriolis forces acting during the reaches. Thus, although their reaches straightened out, they reached straight to the wrong place.

As a consequence of this pattern, we wondered if there was something different about the way labyrinthine-defective subjects ended their reaching movements in darkness compared with normal subjects. We therefore examined the position and velocity profiles of the reaching movements of the two subject groups (Figure 4, lower two panels). Several features stand out from this analysis. Compared with the control subjects, the labyrinthine-defective subjects reached higher in the air, moved slower overall, and approached the target surface both more slowly and more vertically. This reaching strategy minimized shear and normal forces on landing thus avoiding the possibility of jamming the fingertip into the surface. We discuss elsewhere the possible reasons for this strategy which partly relate to the labyrinthine-defective subjects having a less precise knowledge of their torso position relative to the target surface (Dizio and Lackner, 2001).

Figure 5. Experimental set up for studying impact forces on fingertip during reaching movements.

FINGERTIP CONTACT FORCES CODE HAND POSITION

The differences between labyrinthine-defective and intact control subjects in movement endpoint adaptation and in finger touchdown suggested impact patterns as being key to whether adaptation of movement terminus would occur. The landing pattern in normal subjects was clearly providing some form of positional information. To identify the nature of this information, we developed the simple experimental set-up
shown in Figure 5. The experiment is done in a normal stationary environment. A subject stands in front of a force plate at waist level and attempts to reach and touch targets that are laser projected upon it. When the subject's finger lifts off a central start button near the body midline, the target is extinguished and the movement is completed in total darkness. (We have evaluated conditions with visual feedback and have used fast as well as natural speed reaching movements, but the basic pattern of results described below remains the same across all conditions.) Subjects were instructed to reach in a manner that was natural and comfortable for them.

Figure 6 shows a typical trace for the finger landing on a target location positioned to the right of the subject's midline. Several features stand out. On impact, lateral, fore-aft, and normal forces are present and all rapidly rise to a maximum. Within 50 msec, the lateral and fore-aft shear forces rapidly diminish and after ≈ 100 msec only a normal force remains. This is true regardless of target position. When a three-dimensional impact force vector is plotted for each target position, it is oriented toward a point near the midline of the shoulder of the pointing arm. This pattern means that the impact forces on the finger at touch down provide a mapping of finger position relative to the torso. This positional information is absent in the labyrinthine-defective subjects because they end their reaches with the finger landing virtually normal to the surface.
Figure 7. Fingertip reaction force vectors for landing on different targets are oriented to a location on the shoulder of the pointing arm.

Figure 7 shows the impact vector map for reaches to the various target locations. In addition to the impact vectors specifying direction, the precise region of the fingertip stimulated also codes finger position relative to the torso. When the subject reaches to more distal compared with more proximal targets the area of the fingertip in contact with the surface moves more proximal. When the subject reaches to the right of the body midline the area of the index finger stimulated is more medial toward the middle finger because the finger is more supinated, and for reaches to the left more lateral. Thus, the region of the finger contacted also provides a body relative specification of finger position. Recent physiological evidence indicates that different classes of tactile afferents may be biased to code different directions of fingertip stimulation, e.g. SAI for distal tangential force components, SAIi for proximal components (Birznieks et al., 2001). Thus, both the fingertip region and the receptor population activated are providing spatially relevant information about hand position.

**MUSCLE SPINDLES AND TRAJECTORY ADAPTATION**

Both labyrinthine-defective and normal subjects sensed the Coriolis forces acting on their arm during their initial per-rotation reaches. They felt their arm was being deviated from its intended path. However, as their movement trajectories became progressively straighter over the course of subsequent reaches, the Coriolis forces although
undiminished in strength, felt progressively smaller until the subjects no longer perceived them at all. During their initial post-rotation reaches, the subjects felt their arm being deviated from its intended trajectory. Here the self-generated compensation for an expected Coriolis force which was no longer appropriate was sensed as an external force, even though no external force was present.

Four of the five cerebellar patients we tested have damage implicating muscle spindle projection regions of the cerebellum. Although all five could reach without difficulty, none of the five showed normal adaptation of movement trajectory or endpoint during the per-rotation period. Their per-rotation reaches were deviated in the direction of the rightward acting Coriolis forces, had rightward curvature, and ended to the right of the target. This pattern persisted virtually without alteration for the entire per-rotation series of 40 reaches. The fifth subject showed partial trajectory adaptation in that his reaches became somewhat less curved but the endpoint errors remained. None of the cerebellar subjects exhibited post-rotation aftereffects. Notably, none of these subjects sensed the presence of Coriolis forces during their per-rotation reaches and they were totally unaware that their reaches were being deviated in path and endpoint from their intended trajectory and terminus.

The responses of our normal, labyrinthine-defective, and cerebellar subjects to Coriolis force perturbations of their reaching movements reveals the importance both of muscle spindle signals (and potentially Golgi tendon organs as well) in the monitoring and adaptive control of movement trajectory and of terminal somatosensory feedback from the fingertip in the adaptive control of movement endpoint. Normal and labyrinthine-defective subjects all adapted movement curvature in response to Coriolis forces. The normal subjects failed to show endpoint adaptation when they reached above the target location and the labyrinthine-defective subjects all of whom had abnormal patterns of movement termination also failed to adapt movement endpoint. By contrast, cerebellar subjects showed degraded ability to adapt either trajectory or endpoint and did not sense that their per-rotation reaches were deviated by the Coriolis forces generated by the forward velocity of their reaches.

CONCLUSION

The critical role of spindle activity in relation to efferent commands for the computation of position sense has been recognized since the classical observations of Goodwin, McCloskey and Matthews (1972). The present findings indicate that similar computations figure in the adaptive control of limb trajectory and that adaptive accommodations are automatically introduced when the path of the limb deviates from the goal intended. This means that, contrary to equilibrium point theories of movement control, the central nervous system must be continuously monitoring and controlling the path of the limb in relation to the intended goal. In addition, we have found that trajectory and endpoint control are dissociable with endpoint being coded at the end of a reach by the impact forces on the fingertip and the region of the fingertip stimulated. These impact vectors subside to a small vertical force within 100 msec, thus positional information is only transiently present and must be used immediately to update motor control, held in memory, or lost.
REFERENCES


