THE ROLE OF REAFFERENCE IN RECALIBRATION OF LIMB MOVEMENT CONTROL AND LOCOMOTION

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Abstract—The reafference model has frequently been used to explain spatial constancy during eye and head movements. We have found that its basic concepts also form part of the information processing necessary for the control and recalibration of reaching movements. Reaching was studied in a novel force environment—a rotating room that creates centripetal forces of the type that could someday substitute for gravity in space flight, and Coriolis forces which are side effects of rotation. We found that inertial, noncontacting Coriolis forces deviate the path and endpoint of reaching movements, a finding that shows the inadequacy of equilibrium position models of movement control. Repeated movements in the rotating room quickly lead to normal movement patterns and to a failure to perceive the perturbing forces. The first movements made after rotation stops, without Coriolis forces present, show mirror-image deviations and evoke perception of a perturbing force even though none is present. These patterns of sensorimotor control and adaptation, can largely be explained on the basis of comparisons of efference copy, reafferent muscle spindle, and cutaneous mechanoreceptor signals. We also describe experiments on human locomotion using an apparatus similar to that which Mittelstaedt used to study the optomotor response of the Eristalis Fig. These results show that the reafference principle relates as well to the perception of the forces acting on and exerted by the body during voluntary locomotion. © 1997 Elsevier Science Inc.

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The reafference principle of Mittelstaedt and von Holst is a fundamentally important concept for understanding motor control and spatial orientation. The original paper introducing the theory was published almost 50 years ago (1), but its basic ideas remain relevant and there is a richness of example and insight in the paper that is yet to be fully appreciated and explored. We will show here that the reafference concept is also relevant for understanding mechanisms underlying position sense and motor re-calibration of the limbs. In the human, the reafference model has primarily been related to the control of eye movements. The basic notion is that during a voluntary eye movement a copy of the signal to the extracocular muscles, an efference copy or corollary discharge signal, is sent to brain areas that also receive the changing afferent signals from the retina resulting from the voluntary eye movement. These afferent signals contingent on the eye movement are known as the reafferent signals. If the reafferent signals have a magnitude, direction, and time course appropriate for the intended eye movement as specified by the efference copy signal, then perceptual stationarity of the visual world is preserved during the eye movement, despite the changing retinal signal. That is, the experience is one of voluntarily shifting gaze in a stable visual world.

This type of control and monitoring of eye movements is possible in principle because the eyes are a nearly constant load. The center of mass and the center of rotation of the eye are
nearly coincident. Consequently, torques on the
eye related to its orientation, vis à vis gravity
are relatively minor. Much recognized as early
as 1875 that this permitted the eyes to be con-
trolled more simply than other moveable parts
of the body because virtually the same motor
commands to the extracocular muscles would
produce the same end positions of the eyes in
their orbits, despite different orientations of the
head to gravity (2). This physical property of
the eyes allowed Robinson to develop his math-
ematically characterization of the oculomotor
neural discharge patterns necessary to pro-
duce different classes of eye movements (3).
Presumably, visual feedback is used to maintain
calibration of the relationship between effor-
tence copy and reafferent signals, and to "tune"
the oculomotor afferent signals as necessary
(for example, in the case of muscle spasm) to
produce particular movement patterns.

The situation is more complex with regard to
the control of arm movements and other types
of body movements because the load demands
on the muscles of the arm are highly dependent
on body orientation with respect to gravity. This
means that identical motor commands to the
muscles of a limb cannot provide the same
body-relative configuration of the limb for dif-
f erent orientations of the limb to gravity be-
cause the gravity torques differ for different ori-
entation. Interest ing ly, it was long assumed
that appreciation of limb position is determined
by "joint receptors", the unmyelinated Ruffini
type endings in the joint capsules. These recep-
tors were thought to provide the equivalent of
accurate potentiometer indication of joint an-
gle, thus subserving position sense and allowing
judgment of body configuration to gravity.
However, in joint replacement surgery position
sense remains virtually undiminished although
these endings are destroyed.

In what follows we will show that a variation
in Mittelstaedt's concepts of reafference and
efference copy correlations provides insight
into position sense and mechanisms of self-cal-
bration of limb position and movement control.
The solution to the riddle of limb position sense
lies in the demonstration that the spindle recep-
tors of skeletal muscles are a key component in
the appreciation of limb position. Matthews and
his colleagues demonstrated this role in an inge-
nious way (4-6). Mechanical vibration of a
skeletal muscle achieved by holding a physio-
therapy vibrator against the tendons or body of
the muscle excites its primary and secondary
muscle spindle receptors; these in turn activate
the alpha motorneurons of the vibrated muscle
caus ing it to reflexively shorten (7). Matthews
and colleagues discovered that resisting the ac-
tion of such a tonic vibration reflex causes ap-
parent motion of the controlled limb. For exam-
ple, vibration of the biceps brachii of the upper
arm leads to flexion of the forearm if it is unre-
strained; but, if the forearm is not in view and
mechanically prevented from moving under the
action of the tonic vibration re fle x, it will be ex-
perienced as moving into extension although it
is physically stationary. The illusory motion is
in the direction that would be associated with
lengthening of the vibrated muscle. In darkness,
vibration of the appropriate postural muscles
can evoke illusions of head tilt or of tilt and mo-
tion of the entire body. Such illusion head and
body motion is accompanied by apparent visual
motion of a stationary, stably fixated visual tar-
get (in an otherwise dark field); or if a target is
absent, by nystagmoid-like eye movements com-
pensatory for the direction of apparent body mo-
tion (8,9).

These observations and others (6) indicate
that position sense of the limbs is dependent on
patterns of muscle spindle activity interpreted in
relation to patterns of alpha and gamma moto-
n euronal innervation of the skeletal muscles.
Presumably, body configuration relative to the
gravity vector must also be taken into account
in order for gravity dependent torques to be an-
ticipated. In analogy with control of the eyes, it
is tempting to speculate that visual feedback as-
associated with position and movement is impor-
tant in calibration updating. In recent "forward
models" of movement control, visual feedback
serves as the "distal teacher" to provide move-
ment-contingent feedback for updating the in-
ternal model of body dynamics (10,11).

We have obtained some insights into how
arm movement control is calibrated through
studies of sensory-motor adaptation in a rotat-
ing environment (12,13). The impetus for these
studies was our concern whether people would
be able to move and function accurately in an artificial gravity environment such as would be present in a rotating space craft. Rotation has long been proposed as a way of providing a force that could substitute for the role gravity plays in our activities on Earth. Figure 1A provides a simplified illustration of the forces in a rotating environment—the force of gravity is not illustrated. Artificial "gravity" is the centripetal acceleration associated with rotation. In a rotating, cylindrical space craft, the wall or perimeter functions as the "floor" on which to-cemotions takes place. Centripetal force is proportional to the cross product of the radius of rotation and the square of the angular velocity (in radians) of rotation. In general, the shorter the radius of rotation of a space craft the less expensive it will be to achieve a particular level of artificial gravity. Consequently, it is very desirable to see if humans can adapt to relatively high angular velocities of rotation because the cost savings could be immense. A major undesirable side effect of rotation is the Coriolis forces that are generated by movements nonparallel to the axis of rotation of the vehicle. As shown in Figures 1A these forces are proportional not only to the mass of the moved object, but also to the cross product of its linear velocity of movement and the velocity of vehicle rotation \( F_{cor} = -2m(\omega \times v) \). Coriolis forces are inertial forces acting without mechanical contact. The practical consequence of these forces in a rotating environment is that they disrupt body movements and object handling. For example, if one makes a reaching movement directed radially outward in a leftward rotating room, one's arm will be subjected to a rightward Coriolis force. The magnitude of the Coriolis force will be larger if one is reaching while holding a mass.

We have been studying whether people can adapt to Coriolis perturbations of their reaching movements when the centripetal forces associated with rotation are negligible. These observations turn out to provide key insights into how position sense is calibrated and made use of during movement control (12, 13). One simple experimental paradigm we have used is ill-
Illustrated in Figure 1B. Subjects are seated at the center of rotation of a large fully enclosed, rotating room. A horizontal Plexiglas surface extends forward in front of them at waist level. Light-emitting diodes (LEDs) are embedded in the surface from underneath and when lit serve as targets to which the subjects point with their right hand. The surface overlaying the LEDs is smooth and provides no tactile cues about their position. Subjects are kept in total darkness except for a single visible LED target. As they lift their finger off a microswitch that serves as the start position of their hand, the target goes off so that the entire movement is made and completed with neither visual nor tactile feedback about movement trajectory or movement endpoint in relation to the target position. During the pointing movements, the position of an infrared emitting diode taped to the index finger is continuously monitored using a video recording system.

A subject makes a number of reaches pre-rotation to provide a measure of baseline performance. The room is then accelerated to a constant velocity of 10 rpm counter-clockwise (leftward). After 2 min have elapsed (to allow the semicircular canals to return to resting discharge levels), the subject makes additional reaching movements. Because the subject is seated at the center of rotation, the centripetal force on his or her hand is negligible throughout the range of positions it occupies during the reach (less than 0.0906 g). This means that, except for the transient rightward Coriolis force generated when the hand is being voluntarily moved, the resultant force on the hand is the same as in a non-rotating environment. The room is then stopped, and after a 2-min pause the subject makes additional reaches to the target. The disrupting effects of the Coriolis forces on reaching movements and any adaptive accommodations that occur can be seen by comparing initial pre-rotation and final per-rotation reaches with the pre-rotation baseline reaches. Any aftereffects of reaching during rotation can be seen by comparing initial post-rotation and pre-rotation baseline reaches.

Figure 2 shows the average endpoints of reaching movements made pre-, per- and post-rotation for a group of 11 subjects. As can be seen, the endpoints of the first per-rotation movements show large deviations in the direction of the transient Coriolis force generated by the movements. However, with subsequent movements, the endpoints rapidly become more accurate and are nearly back to pre-rotation baseline within 10 to 20 movements, despite the absence of visual or tactile feedback about reaching accuracy. Interestingly, during their first per-rotation reaches, subjects feel their arms being physically deviated from the intended trajectory by some intangible force. This "force" seems to get smaller as they continue to reach until it is no longer felt. The endpoints of the initial post-rotation reaches are displaced in the direction opposite to the initial per-rotation reaches, indicating a persistence of the adaptive compensation achieved during rotation.

With further post-rotation reaches, subjects return to pre-rotation baseline with the same time course as they had acquired adaptation during rotation. During their initial post-rotation reaches, the subjects report a "force" deviating their arms in the direction opposite to that of the Coriolis force that had been present during the per-rotation reaches, despite there being no force present. This "force" diminishes in magnitude as reaching accuracy returns to pre-rotation level.

The average paths of movements, viewed from above, are presented in Figure 3A for the final pre-rotation baseline reaches, the initial and final per-rotation reaches, and the initial and final post-rotation reaches. These paths give a clear perspective on how recalibration is achieved. The initial per-rotation reach is deviated progressively rightward as the forward ve-

![Figure 2. Average movement endpoints for '10 reaching movements (per subject) made in the center of the rotation room before, during, and after 10 rpm, counterclockwise rotation, N = 11.](image-url)
locity of the arm increases and the Coriolis force increases in magnitude, pari passu. Arm velocity is indicated in the figure by the relative spacing of the symbols in the movement paths; the further apart the symbols, the higher the velocity. The movement path then curves back somewhat toward the target position as the hand slows down and the Coriolis force (which is dependent on arm velocity) goes to zero; but it ends to the right of the target position. By contrast, the final per-rotation reach is straight and ends at the target position, just like the pre-rotation reach. The initial post-rotation reach is a mirror image of the initial per-rotation reach. This pattern means that regaining straight line reaching paths and accurate endpoints during rotation involved generating a temporal sequence of muscle innervation that precisely canceled the effects of the Coriolis force. In their first several post-rotation reaches, subjects actually perceived these self-generated compensations as an external force deviating their arm from its intended path! Adaptation to Coriolis force deflections of the arm took place even though visual and tactile feedback about movement path and endpoint in relation to the target was absent.

A great deal of recent evidence has indicated that visual imagery can influence motor control. Athletes and musicians often mentally imagine themselves to be going through the movements associated with particular activities or performances and report that this later enhances their actual performance. Such claims raise the possibility that our subjects who reached in total darkness may have been visually imagining the motion of their arm in relation to the remembered target position. To evaluate this possibility, we tested a group of congenitally blind subjects who had never experienced light sensations. We used exactly the same pre-, per-, and post-rotation reaching movement paradigm with the exception that the blind subjects reached forward to a position on the target board that was in the median plane of their body. The position they were to use as a target was demonstrated to them by placing their finger in that location. Sightless control subjects also performed the task in total darkness with the target position similarly demonstrated to them.

The sighted subjects behaved exactly as those described above. Pre-rotation they reached in straight lines to the remembered target position; per-rotation their reaches were initially deviated in path and endpoint by the Coriolis forces, and with additional reaches movement path became progressively straighter and endpoints more accurate; post-rotation the reaching pattern was mirror image to pre-rotation. By contrast, the pre-rotation reaches of the blind subjects to the target position were curved rather than straight.
lines like those of the normal subjects. The blind subjects' initial per-rotation reaches were deviated in path and endpoint from their pre-rotation reaches in the direction of the Coriolis forces present during the reaches. With additional reaches, adaption occurred such that the final per-rotation reaches had the same curved path and endpoint accuracy as the pre-rotation reaches. The initial post-rotation reaches showed a mirror image compensation persisting for the Coriolis forces that had been present during rotation. The findings are summarized in Figure 3B.

These findings indicate that no form of visual feedback, either real or imagined, is necessary to adapt to Coriolis force perturbations of arm movement trajectory. This raises the issue of why adaptation occurs? What triggers adaptation? In all of our conditions, a subject's hand started and ended with contact on a surface. Even though the contact at the end of the reach did not provide direct tactile feedback about whether the hand reached the target position, we thought it might be functionally significant. Consequently, we repeated our initial experimental paradigm with additional sighted subjects, but with one difference. The LED target went out as before when the subject lifted his or her finger to point, but this time the task was to point just above the target position, keeping the finger in the air above the target without making terminal contact with the smooth Plexiglas surface.

Figure 3C shows the pattern of results. As can be seen the pre-rotation path deviation from a straight line is very small—subjects reach straight to a position above the target. During the initial per-rotation reaches, there is a large path deviation caused by the Coriolis forces. However, subjects soon reach in straighter and straighter paths until the movements become as straight as pre-rotation. Post-rotation, there is a mirror image deviation that decays with subsequent reaches until subjects again reach in straight paths. This pattern of trajectory deviation and adaption corresponds to that which took place when subjects were permitted terminal contact of their hand with the target surface board.

By contrast, the per-rotation endpoint deviations caused by the Coriolis forces show little evidence of adaptation for the reaching movements without terminal contact, remaining largely unchanged from the initial per-rotation reaches. Moreover, although the initial post-rotation reaches are curved, the endpoints are nearly at pre-rotation values. These findings indicate 1) that movement path and endpoint are independently representable in central nervous system programming, 2) that in the absence of vision, contact of the hand at the end of a movement is necessary for correction of movement endpoint to occur during exposure to Coriolis force perturbations of trajectory, and 3) that neither vision nor hand contact is necessary for adaptation of movement path curvature.

We believe several factors are relevant for this dissociation and that our findings implicate a broader range of elements in movement planning and implementation than is generally recognized. When an initial Coriolis force de- viates an arm movement from its intended path, the pattern of spindle feedback associated with the movement will be abnormal for the pattern of efferent innervation of the arm muscles. For example, unplanned stretch of the biceps brachii and shortening of the triceps brachii occur during the Coriolis force perturbation and should lead to increased spindle activity in the biceps brachii and decreased spindle activity in the triceps brachii relative to that expected for the pattern of efferent innervation present. From our discussion above of correlating efferent commands and spindle activity to generate position sense, it can be seen that the pattern of increased spindle activity in biceps brachii coupled with decreased triceps brachii activity would lead to a sense of rightward deviation of the right arm relative to the torso. Put in the context of the original reafference model of Mittelstaedt and von Holst, the reafferent primary and secondary spindle signals are inappropriate for the efference copy signals, and will produce a change in experienced movement path.

In the absence of vision, this discordance between expected and received spindle signals likely serves as a basis for initiating recalibration. Compensatory innervations are generated that effectively cancel the Coriolis force influence on the arm movement, perhaps by increasing the alpha drive to the biceps brachii to "normalize" the spindle feedback for the movement.
These compensatory innervations are not conscious reactions, but automatic compensations initiated by the central nervous system. As a subject continues to make reaching movements during rotation, his or her movements feel more and more normal and, in fact, are straighter and straighter, though the subject does not know why. These compensations result in a straight-line reaching path being required by the sighted subjects (in the case of the blind subjects, a trajectory with the original degree of curvature), despite a Coriolis force still being present during movement. When compensation is complete, the movement is again straight and feels straight, and the Coriolis force is no longer consciously perceived.

For endpoint adjustment to occur as well, it is necessary to have terminal surface contact. Although such contact in our experiments did not provide direct feedback about the position of the target, it did provide information about movement termination, finger contact force at touch down, as well as finger orientation to the surface at the end of the movement. These details provide strong cues about finger location on the horizontal surface. The nature of the surface stimulation of the finger thus conveys spatial information that can be compared with “expected” contact features. In other experiments, we have demonstrated that fingertip contact with a stationary external surface provides powerful orientational information that enhances postural and orientation control (14,15). We have presented elsewhere a more detailed model that incorporates such contact cues and a host of other factors involved in adaptive limb movement control (12).

In the experiments summarized here, adaptive compensations to Coriolis forces were shown to occur in the absence of vision. We have found, in other studies, that allowing sight of the moving hand during exposure to Coriolis force perturbations reduces by about 50% initial deviations of movement path and endpoint and enhances by about 25% the rates of both trajectory and endpoint adaptation. The importance of visual feedback can also be seen from an experimental paradigm that is a human variation on a technique used by Mittelstaedt to show the importance of reafferent signals in the Erisalis fly. When put in a rotating striped enclosure, the fly will turn in keeping with the direction of stripe motion, an optomotor response that minimizes visual slip. If its head is twisted 180° relative to its body, the sequence of visual receptors stimulated by the stripes is reversed. The fly will now turn in the opposite direction for the same stripe motion. The apparatus illustrated in Figure 4 allows us to reverse in the human the direction of visual flow associated with voluntary locomotion (16).

A subject is illustrated walking forward in place on a rotating treadmill while holding onto a stationary handle bar. The visual flow provided by the moving drum is in the direction that would normally be associated with walking backwards in a stationary surround. Subjects

![Figure 4. Illustration of a subject walking in an apparatus that allows independent control of walking movements relative to the floor, the visual surround, and inertial space. For the experiment described here, the bar is inertially fixed and the floor turns at a fixed speed, creating a circular treadmill. The rate and direction of stripe motion around the subject is manipulated.](image-url)
exposed to such a situation often feel that they are voluntarily walking backwards on a stationary platform in a stationary striped drum. The physically stationary bar that they grasp is perceived by them to be moving backwards forcing them to step backwards. They feel the bar as pushing against their hands so that they have to move backwards. Thus, there is 1) a misperception of the commands issued to the musculature; the subjects are stepping forward, but perceive themselves to be stepping backwards, and 2) a misperception of the forces on the hands, the bar is physically stationary and not moving toward them. Strain gauge measurements of the forces on the hands show that the physical forces present do not correlate with the subjects' perceptions of those forces.

The significance of these observations and of our studies of adaptation to Coriolis forces lies in their implications for mechanisms of self-calibration. They indicate that reafferent and efference copy signals form part of a larger computational context that serves to maintain perceptual stability of self and environment during voluntary locomotion and movement. They also show that Mittelstaedt's concept of reafference and efference copy are important for understanding recalibration of position sense and motor control as well as for spatial orientation.

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