

OCULOCENTRIC FRAMES OF REFERENCE FOR LIMB MOVEMENT

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INTRODUCTION

A little more than a decade ago, two of us (MF and JFS) developed a hypothesis to account for the manner in which visual and proprioceptive information could be processed in a common frame of reference in order to guide limb movements (29). The proposal generated considerable discussion and controversy (13) and spurred other investigators to tackle this problem (e.g. 2, 20, 21). With the passage of time, and since this volume is meant as a retrospective, it seemed appropriate to re-examine the hypothesis. We begin by summarizing the initial hypothesis, and our reinterpretation of the problem in light of recent experimental evidence. We will then summarize some of the electrophysiological evidence that supports a new scheme and conclude by describing some of our recent behavioral observations that led us to it.

The original hypothesis. - We originally set out to account for the first stage of the processes whereby visual information about a target's location in space would be mapped into a pattern of muscle activation adequate to bring the arm to the target. This study was actually inspired by a prior study one of us (JFS) had conducted with Carlo Terzuolo, which dealt with the question of how figural motions (such as circles and ellipses) could be produced (31). There, we proposed a simple algorithm according to which figural aspects of the motion of the hand in space (the slant of the ellipse and the plane in which it was drawn) were regulated by controlling the phasing of the oscillatory motion of the joint angles of the arm (32).

The original hypothesis was also inspired by principles developed in robotics, where the problem of controlling motion is split into two stages: a kinematic phase, in which a plan of motion is generated, and a kinetic phase, in which this plan of motion is translated into the forces required to achieve it (6, 15, 34). Our hypothesis dealt strictly with the kinematic transformations in the first stage and it was based largely on an analysis of errors in memory-guided reaching movements. When subjects were presented with visual targets, asked to close their eyes, and then to put their finger on the remembered position of the target, they made errors that were spherically symmetrical about a point close to the shoulder (28, 33). From this, we argued that information about target location originally encoded in a retinocentric frame of reference was transformed into a body-centered representation, using a spherical coordinate system centered at the shoulder. We also suggested a simple

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mapping between this latter representation and the orientation angles of the arm and forearm. Once visual target information was remapped into an arm-centered frame of reference, the desired movement could be defined by a vector subtraction of present arm position (encoded kinesthetically) from the desired arm position.

Revisions to the hypothesis. - Subsequent work did not support the idea of a hierarchical separation of modules dealing with kinematics and with kinetics. Wrist location in space does not uniquely define the arm's posture; in fact, the orientation of the plane of the arm can vary over a wide range of values. We investigated reaching movements to one target initiated from a variety of starting locations and found that the plane of the arm at the target depended on where the movement began (26, see also 5). We found that we could account for the variations in the plane of the arm by invoking energetic principles, i.e. by assuming that the torque (or the amount of muscle activation) required to generate the movement was taken into consideration in planning the trajectory. Accordingly, kinematics and kinetics would be intertwined at some stages in the sensorimotor transformations for arm movements (23, 30).

Nevertheless, it is still possible that earlier stages deal purely with kinematics. In that context, recent evidence highlights the importance of a retinocentric frame of reference, in preference to one that is body-centered. (We will describe the evidence that leads us to this suggestion in a subsequent section.) Specifically, we suggest that both the location of the target and the initial location of the hand are encoded in a frame of reference that is gaze-dependent and that the desired movement vector is computed in this frame of reference, rather than in a body-centered frame of reference (see also 14). In subsequent stages, this kinematic movement vector would be transformed into a body-centered (or arm-centered) frame of reference and then, as in our previous model, an inverse-dynamic model would transform the movement vector into the requisite forces.

What would be the advantage of such a scheme? Our previous proposal had the advantage that it provided for a simple mapping between a target location and the desired arm posture at that target location and that the change in posture could be achieved simply by subtracting the present posture from the desired posture. In our new hypothesis, this is no longer possible. However, we believe the new hypothesis possesses other advantages. It may be easier to deal with situations where the target is in motion (or the trunk is moving relative to a stationary target) if information is initially encoded in a gaze-centered frame of reference (12). This is because the oculomotor system is exquisitely equipped to deal with target motion in an inertial frame of reference (smooth pursuit, see 19) as well as with head and trunk motion for stationary targets (vestibulo-ocular reflex, see 25 and Angelaki, this volume).

Electrophysiological evidence for coordinate transformations. - In this section we will deal briefly, and selectively, with evidence obtained from single unit recording in behaving monkeys that is consistent with our hypothesis. Posterior parietal cortex appears to be involved crucially in the spatial planning of limb movements. There is

evidence for an encoding of target location in a gaze-centered frame of reference (1) in the 'parietal reach region' and also for a coding of the intended movement vector in this frame of reference in cortical area 5 (3). The evidence for this comes from experiments in which the monkeys' gaze and their initial hand location were varied in a task requiring them to reach to visual targets. Buneo, Batista and Anderson (3) have interpreted their findings in a manner consistent with our hypothesis; target and hand location are initially encoded in a retinocentric frame of reference, and an intended movement vector in this frame is obtained by a vector subtraction of these two signals.

Motor and premotor cortical areas appear to re-encode this movement vector in a body-fixed frame of reference, leading to a transformation to kinetic signals in primary motor cortex (16, 17). Evidence for this conclusion comes from an elegant series of experiments in which monkeys were trained to make wrist movements in various directions, with the arm pronated or supinated. These authors could thus distinguish among a body-fixed frame of reference and one fixed to the arm. The frame of reference for muscle forces is intermediate to the other two (4, see also Buneo this volume). Neurons in the ventral premotor area were predominantly tuned in a body-fixed frame of reference (17), as were about 50% of neurons in primary motor cortex (M1). However, another 25% of neurons in M1 were tuned in a muscle-like frame of reference (16).

Can the two hypotheses be reconciled? - Our evidence in favor of a shoulder centered representation of target location was based on movements performed in the dark (13, 29), whereas our present hypothesis of oculocentric coding is based on experiments where visual information was always available. In our original experiments we had also found evidence for a head-centered representation of target location in the light, but we had suggested that this resulted from a plan developed in a body-centered frame of reference, with visually-mediated corrections subsequently realigning the hand in a retinocentric frame (33). However, it is possible that, when vision is suddenly removed, there is a gradual shift away from a retinocentric frame of reference to one that is body-centered. This scheme would be compatible with our previous results as well as with other behavioral evidence (21). If so, one might predict that the frame of reference in which parietal neurons encode information about target location and hand location would be different in the dark.

RESULTS

In this section, we will summarize our recent experimental data that led us to revise our hypothesis. Some of these results pertain to the correspondence between gaze and pointing errors. In other experiments we found a close correspondence between eye and hand motion during tasks in which a moving target was tracked.

Duncker Illusion. - In the Duncker illusion, a moving background affects the perceived direction of target motion. For example, a leftward moving background adds

an illusory rightward component to a target's motion. Accordingly, a spot moving vertically down against a background moving to the left will be perceived to move diagonally, down and to the right (7). Our experiment tested whether this illusion also held when the motion of the object was occluded, i.e. when its motion had to be inferred or predicted (27). We used an experimental design in which a target disappeared behind a band of coherently moving random dots and subjects moved the hand to intercept the target at the place where it would reappear.

Subjects made errors in pointing on the manual interception task that were consistent with the Duncker illusion. Leftward background motion induced rightward errors in pointing, and vice versa. We found that errors in the gaze direction prior to the hand's contact with the screen gave an excellent prediction of the errors in pointing. Subjects typically initiated a saccade around the time the target disappeared, in a direction that was affected by the Duncker illusion. However, the random dot motion induced an ocular following response (22) in the direction of background motion. Thus gaze reflected a combination of two opposing tendencies: saccades deviating in the direction opposite to the background motion, and ocular following in the direction of background motion. Pointing errors were best correlated with gaze; they did not correlate as well with the end point of the saccades, implying that a gaze signal, of extraretinal origin (because it reflects a combination of saccades and ocular following), appears to provide the input for the limb motor system.

Hand and Eye Tracking. - In these experiments, we asked subjects to track an object that initially moved at a constant speed in a constant direction. At a random time, the target changed to a new, randomly selected direction (8, 9, 10). Typical responses are shown in Figure 1.

For manual tracking (Fig. 1A), after a reaction time, subjects changed the direction of finger movement and then moved in a fairly straight line to reintercept the target. Note that the hand's motion anticipated target motion; the hand was directed to a point ahead of the target as can be ascertained from the lines connecting the hand position to the target position. In Figure 1B, which shows the ocular response to a similar stimulus, there was a gradual change in the direction of smooth pursuit after the target had changed direction. The smooth pursuit was interrupted by a saccade toward the target (note the saccade direction compared to the line connecting gaze position to target location). Typically, the saccade was hypometric.

There are remarkable similarities between smooth pursuit eye movements and hand motion during tracking. To analyze the smooth pursuit movements, we removed the saccades. Figure 2 shows the results of this analysis and a comparison of the responses of the eye with analogous results obtained for manual tracking. The traces on the left show the change in direction of smooth pursuit eye movements and of the hand following step changes in target direction ranging from 30° to 150°. Smooth pursuit has a shorter latency than does the hand. Remarkably, the slopes of the two sets of traces are very similar; the hand and the eye changed direction at a similar rate. The panels on the right show the modulation in speed for the hand and the eye. As was the case for direction, the latency for changes in speed was less for

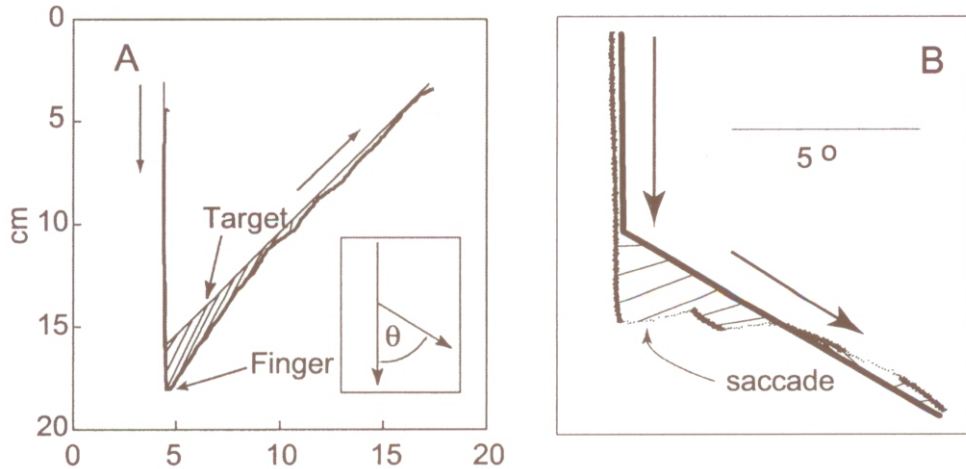


Fig. 1. Examples of manual tracking (left) and ocular tracking (right). Lines connect target to finger or eye every 100 ms (left) or 50 ms (right). In both instances, the target initially moved down and then abruptly changed direction.

the eye, and again there are remarkable similarities. Both eye and hand decelerated. Subsequently, the hand accelerated beyond the tracking speed, whereas smooth pursuit velocity generally did not exceed this value. There is a simple explanation for the difference in the velocity profiles of smooth pursuit eye movements and of hand tracking. Hand motion reflects a combination of velocity as well as positional error signals, whereas smooth pursuit velocity appears to be governed purely by a target velocity signal (24).

The similarities between smooth pursuit and hand motion suggest a high degree of coordination of the hand and eye during tracking and may indicate that they share common neural mechanisms. While inertia may limit the arm's ability to change direction quickly, the inertia of the eye is much less, and saccades can be executed at sharp angles to the direction of smooth pursuit, without requiring any deceleration of ocular motion (Fig. 1B). Thus there appears to be no mechanical reason for smooth pursuit direction to change gradually or for smooth pursuit speed to decrease while direction is changing.

There are interactions between eye and hand motion during tracking. We showed this in another experiment by recording eye and hand motion under three conditions: a) ocular tracking alone, b) hand tracking alone, and c) the combination of the two. The experimental condition had a dramatic effect on the time course of the modulation in direction. For eye and hand tracking together, the latency of the change in direction of pursuit eye movement *increased* compared to the latency for eye tracking alone, whereas the latency of the hand *decreased*. When the eye alone tracked the target, there was an initial decrease in speed, as direction changed, and a return up to the speed of the target (as in Fig. 2). However, for combined tracking of eye and hand, eye velocity overshoot target

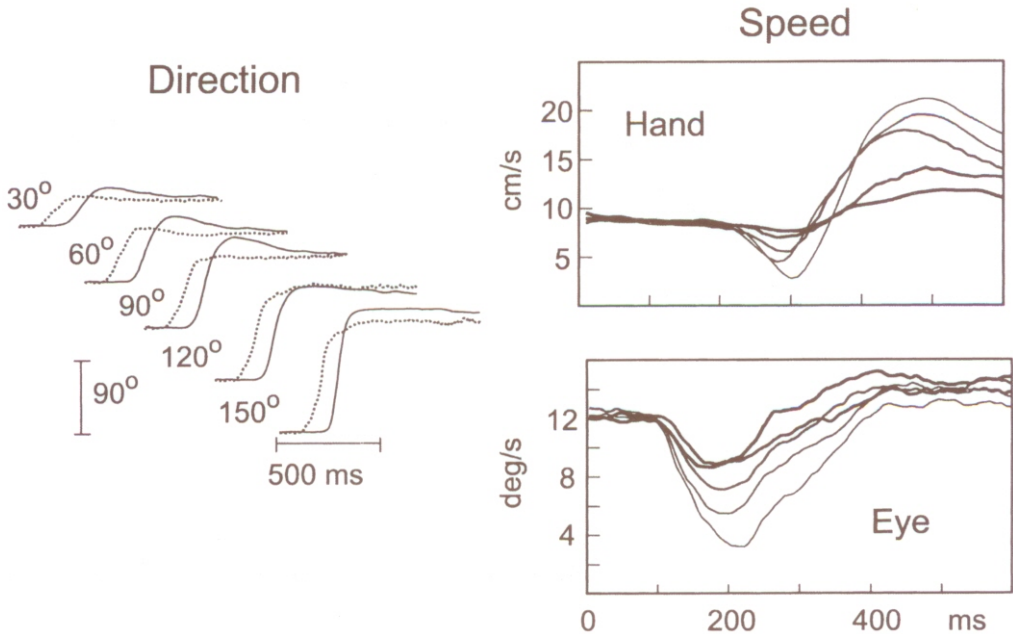


Fig. 2. Comparison of hand and eye direction (left) and tracking speed (right).

The target changed direction at time 0. Direction of smooth pursuit eye motion is shown by the dotted traces; the solid traces denote the direction of manual tracking. In the panels on the right, the thickest traces are for responses to the smallest directional change of the target.

velocity, beginning to resemble the time course of the modulation of hand speed. This finding suggests that similar error signals drive smooth pursuit and the hand when both are engaged.

Deficits in eye and hand tracking in patients with cerebellar ataxia also show remarkable similarities (Fig. 3). The figure shows results from a subject diagnosed with episodic ataxia type 2 (EA-2), an autosomal dominant cerebellar ataxia resulting from a voltage-gated Ca^{++} channel gene truncation mutation (11, 18). This subject exhibited positional nystagmus when instructed to deviate gaze from the primary position and pursuit gain was close to zero. A typical performance on ocular tracking is shown in Figure 3B, the thin portions of the trace denoting saccades and the thicker parts of the trace indicating low velocity eye movements. While the subject's eye did follow the target trajectory, this was accomplished entirely with saccades; the slower eye movements after the target had changed direction resulted from a post-saccadic drift up and to the left. Performance on a different trial involving manual tracking is shown in Figure 3A. In this example, the subject was able to follow the target reasonably well when its trajectory was predictable (downward phase). However, after the target had changed direction, hand movement was composed entirely of fast phases, overshooting the target position. (These phases are indicated by the thinner portions of the trace.) Between these saccadic-like segments of hand movements, the hand essentially came to a stop for extended periods of time. There

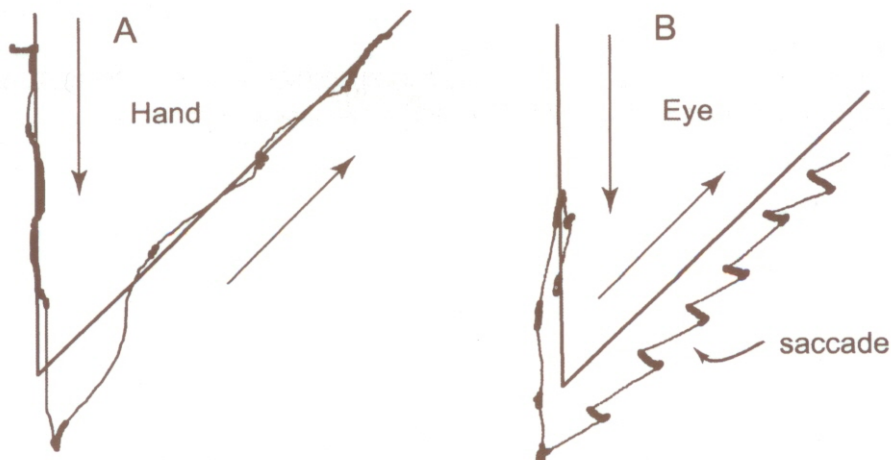


Fig. 3. Example of manual tracking (left) and ocular tracking (right) in a patient with severe episodic ataxia (EA2).

Speed of movement is indicated schematically by the thickness of the lines. Hand and eye movements were recorded in separate trials.

was a remarkable similarity in the time course and the pattern of eye and hand movements by this subject. Results from other patients, whose deficits were not as severe, also supported this conclusion.

SUMMARY

We have reviewed evidence that suggests that the target for limb motion is encoded in a retinocentric frame of reference. Errors in pointing that are elicited by an illusion that distorts the perceived motion of a target are strongly correlated with errors in gaze position. The modulations in the direction and speed of ocular smooth pursuit and of the hand show remarkable similarities, even though the inertia of the arm is much larger than that of the eye. We have suggested that ocular motion is constrained so that gaze provides an appropriate target signal for the hand. Finally, ocular and manual tracking deficits in patients with cerebellar ataxia are very similar. These deficits are also consistent with the idea that a gaze signal provides the target for hand motion; in some cases limb ataxia would be a consequence of optic ataxia rather than reflecting a deficit in the control of limb motion per se.

These results, as well as neurophysiological data summarized here, have led us to revise a hypothesis we have previously put forth to account for the initial stages of sensorimotor transformations underlying targeted limb motions. In the original hypothesis, target location and initial arm posture were ultimately encoded in a common frame of reference tied to somatosensation, i.e. a body-centered frame of reference, and a desired change in posture was derived from the difference between the

two. In our new scheme, a movement vector is derived from the difference between variables encoded in a retinocentric frame of reference. Accordingly, gaze, with its exquisite ability to stabilize a target image even under dynamic conditions, would be used as a reference signal. Consequently, this scheme would facilitate the processing of information under conditions in which the body and the target are moving relative to each other.

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