The Visuomotor Transformation for Arm Movement Accounts for 3-D Eye Orientation and Retinal Geometry

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To point or reach to a visual target, you need to know its direction relative to your shoulder. That direction can be computed from the retinal image, if the brain also knows the orientation of the eyeball, head, and clavicle. To be geometrically exact, the neural computation would have to involve rotary operations.[1] When the eye was turned 30° up, for instance, the brain would take the locations of all objects relative to the eye and rotate them 30° down to find the locations relative to the head. Some theories[2,3,5–7] suggest that the brain might approximate that rotation by a simpler vector addition, merely shifting all retinal locations by the same vector. But that strategy would lead to marked errors in some situations. FIGURE 1A shows five earth-fixed, horizontal arcs wrapped around a cylinder centered on an eyeball. In front of the eye are two spheres and 90° to the right are two cubes, one sphere-cube pair at eye level and the other 30° up. When the eye fixates the eye-level sphere, the retinal image of the eye-level cube falls on the eye's horizontal meridian (FIG. 1B). But when the eye fixates the sphere at 30° up, the retinal image of the corresponding cube falls well below the horizontal meridian (FIG. 1C). That is, both pairs of spheres and cubes are horizontally separated, but in one case their retinal images are not, owing to the rotation of the eye. If the brain tried to compute these objects' locations relative to the head or the shoulder simply by shifting all their retinal locations by a fixed vector, it would misestimate the elevations of at least some objects, and would misaim its eye and arm movements. Here we study whether the visuomotor transformation for arm movements uses a vector-additive strategy or correctly accounts for the rotary geometry of retinal projection.

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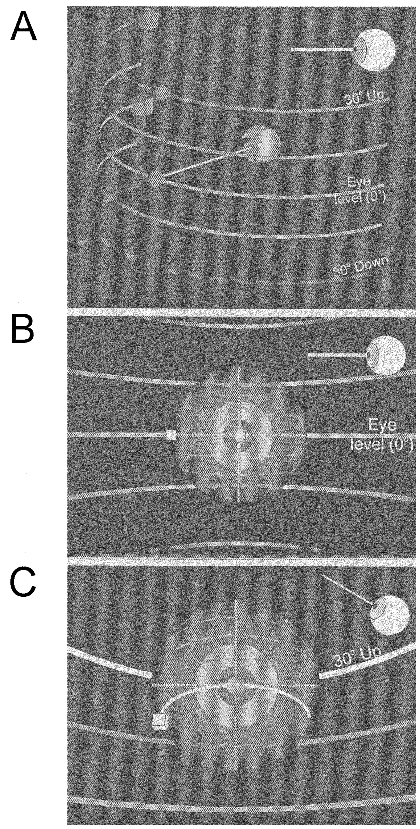

FIGURE 1. Simulated retinal projections for two horizontally paired targets as a function vertical eye position. **A:** Five horizontal lines (wrapped around the eye) with paired targets at different elevations. **B** and **C:** Behind view of the semi-transparent eye and retinal projections of the paired targets while the eye is looking straight ahead (**B**) and while the eye is rotated 30° up to view the top paired stimuli (**C**).

METHODS

Six subjects took part. With the head fixed, the subject looked at one of five target lights at different elevations in an otherwise dark room. Another LED flashed for 500 msec, 40°–80° right of the fixated light. The fixation light went out at the same time, and in complete darkness the subjects kept their eyes on the remembered location, but pointed their arm to the location of the flash. All targets lay on a vertical cylinder of diameter 1.1 m, centered on the right eye. We measured the orientation of the right eye and arm with search coils, and calculated the flashed target's location in eye coordinates (also known as retinal error).

RESULTS

FIGURE 2 shows the type of pointing error that would result if the brain used a vector-additive computation to process retinal target locations. Final pointing directions

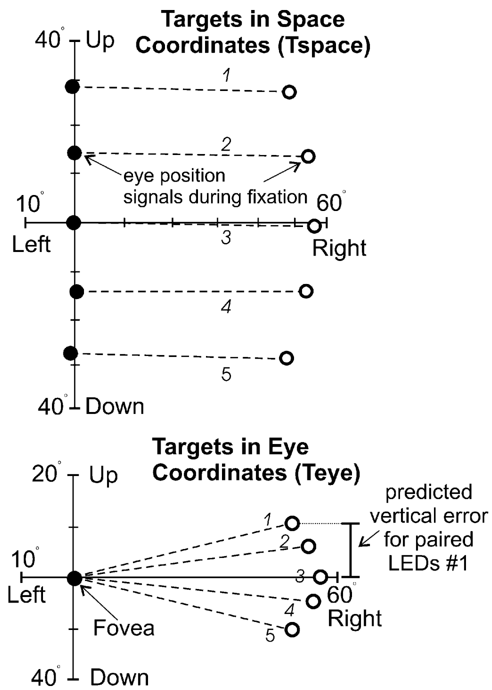

FIGURE 2. Target locations in space (*top*) and eye (*bottom*) coordinates. *Solid circles:* LED location for ocular fixation. *Open circles:* location of final pointing direction as derived from eye position signals. Five horizontal pairs are shown. To get the Teye from Tspace, we rotate the target vectors from the latter by the inverse of initial 3-D eye position (*toward solid circles*).[1,4]

would "fan out," yielding vertical errors that varied systematically as a function of vertical eye position. Only a rotary computation would allow accurate pointing to all targets.

Do subjects make the systematic fanning-out errors predicted by the vector-additive theory? FIGURE 3A shows mean vertical pointing errors for one typical subject for 24 trials. Actual vertical errors are plotted versus the vertical errors predicted by the vector-additive theory. Solid lines are regression fits to the data for the one subject and for all subjects (FIG. 3B). A slope of unity (dashed line) would suggest that the brain performed a purely vector-additive computation. A slope of zero would suggest a rotary computation. Actual slopes were near zero: subjects showed little or no tendency to make the errors predicted by the vector-additive theory, but instead closely approximated the exact, rotary transformation.

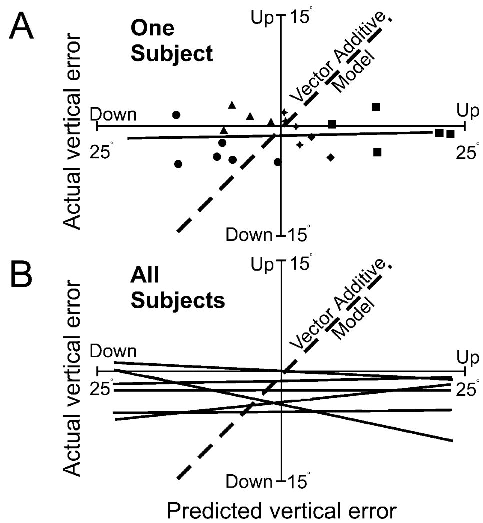

FIGURE 3. Actual vertical pointing errors plotted as a function of errors predicted by the vector-additive theory for one subject (**A**). *Solid lines* indicate the regression fit to the data for the one subject (**A**) and for all six subjects (**B**). The vector-additive model predicts a slope of one (*dashed line*) whereas correction for the rotary geometry of retinal projection predicts a slope of zero.

CONCLUSION

We have shown that the brain closely approximates the rotary computations that are needed to convert retinal images into accurate arm movements. In 1998 Klier and Crawford, studying the rapid eye movements called saccades, showed that they are accurately directed even when the retinal image of the target is rotated owing to torsion of the eye about its own line of sight. We have generalized that result to show that the visuomotor processing underlying arm movements also employs rotary computation, and that the brain also corrects for the retinal effects of vertical eye motion.

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