Implications of Ocular Kinematics for the Internal Updating of Visual Space

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INTRODUCTION

For visual information to be useful for more than a fraction of a second, its spatial content must be stored and updated across saccades. Recent neurophysiological studies have suggested that the spatial targets for eye and arm movements are updated by remapping their internal representations within retinal coordinates during each saccade (Batista et al. 1999; Duhamel et al. 1992; Gnadt and Andersen 1988; Henriques et al. 1998; Walker et al. 1995).

For example, suppose that the receptive field of a visually responsive neuron is currently encoding target A and that an intended eye movement will cause target B to fall within its receptive field. Concomitant with the eye movement, the neuron will stop responding to target A and begin responding to target B even though target B is not yet within its receptive field (Walker et al. 1995). Such neural events have been modeled by subtracting a vector representing the saccade from other vectors representing visual locations on a retinotopic map (Goldberg and Bruce 1990; Moschovakis and Hightstein 1994).

However, an important property of three-dimensional (3-D) eye rotations is their noncommutativity. By noncommutativity we mean that, unlike vector addition, different orders of rotation around the three axes of rotation will land the eye in different orientations (Tweed and Vilis 1987). As a result, vector subtraction (i.e., through the addition of the negative of a vector) does not properly represent the physical rotations of the eye and may not be the appropriate mechanism for retinocentric remapping (Henriques et al. 1998). The implications of noncommutativity for oculomotor control have been controversial (Crawford and Guitton 1997; Demer et al. 2000; Quaia and Optican 1998; Raphan 1998; Tweed and Vilis 1987), but their implications for higher level processes like visuospatial remapping remain largely unexplored.

Recently, Henriques et al. (1998) suggested a model for the intersaccadic remapping process that would incorporate the noncommutativity of 3-D rotations. In particular, the authors suggested that the brain would rotate its retinocentric representations by the 3-D inverse of each eye rotation, which is the rotary analog of vector subtraction. In theory, this would be a more correct mechanism, but it is not yet clear how important this would be for behavior or whether the actual system bothers to take into account the difference between these approaches. The purpose of this study was to generate simulations that would provide a behavioral test between the commutative and noncommutative models of the remapping process and to test these simulations experimentally.

THEORY

The cortical structures involved in remapping [e.g., lateral intraparietal cortex (LIP), frontal cortex] seem to encode saccade targets in a visual frame (Colby and Goldberg 1999; Colby et al. 1995). Moreover, Klier et al. (2001) have shown that the superior colliculus also encodes movements in an eye-centered visual frame. In light of these findings, the process of visuospatial remapping must be modeled in a visual coordinate frame. In this study, two models of visuospatial
remapping were tested: the vector subtraction model of Goldberg and Bruce (1990) and the noncommutative remapping model of Henriques et al. (1998). The details of these models are shown in Fig. 1. Briefly stated, the vector-subtraction model remaps the visual target in eye coordinates by subtracting the displacement vector (ΔE) of the intervening saccade. In contrast, the noncommutative model rotates the old coordinates of the target by the inverse of the 3-D eye rotation, which was suggested by Henriques et al. (1998). An additional feature overlooked by Henriques et al. (1998) was that an efferent copy of the headcentric eye rotation was first put into eye coordinates so that the efferent copy matched the sensory representation frame. In practice, these collapse into a single multiplicative comparison between current and desired position. To be fair, the output of both models was used to drive the same model of the saccade generator (Crawford and Guittón 1997), which is one that converts targets in a visual frame into a motor displacement command for saccades in Listing’s plane (Crawford et al. 1997; Hepp et al. 1997). The latter saccade generator model has previously been shown to produce realistic saccades that are accurate and obey Listing’s law (Klier and Crawford 1998).

Simulations

Saccades were simulated with both models using various target configurations. The configuration that most clearly distinguishes between the two models is shown in Fig. 2. This arrangement of peripheral targets formed the basis of our test paradigm, which had a central-fixation light emitting diode (LED) illuminated while two of the corner targets flashed. The task required three saccades between the remembered location of the corner targets in the dark (see Experimental paradigms for details). Figure 2, A and B, shows two simulated gaze trajectories of the test paradigm using both the noncommutative model (Fig. 2A) and the commutative vector-subtraction model (Fig. 2B). Note that the noncommutative model showed no errors in either acquiring the initial target or in the saccades between the remembered locations of the peripheral targets. The commutative model was able to acquire the first target accurately because this did not require remapping. However, the commutative model predicted a cumulative pattern of centripetal errors during subsequent saccades between the remembered locations of the peripheral targets. Further simulations suggested that this pattern of saccades provided the clearest test between the two models, so our experiment was designed to emulate this test.

METHODS

Five head-fixed human subjects, aged 22–43 years, participated in three experimental paradigms. In each paradigm, subjects faced a black tangent screen 110-cm distant while sitting in the dark. The tangent screen had an arrangement of five LEDs: a central-fixation LED located directly in front of the subject and four peripheral target LEDs 30° from the central fixation point and located at the corners of an imaginary upright square.

3-D eye position information was collected using the scleral search coil technique in three alternating magnetic fields (Klier and Crawford 1998; Tweed et al. 1990). Data were digitized and analyzed offline using in-house software. The experiment and methods were approved by the York Human Participants Review Subcommittee.

Experimental paradigms

In our test paradigm, subjects were required to saccade repeatedly between adjacent corners of a virtual square outlined by the peripheral target LEDs. Using the upper right and upper left LEDs as an example of the test paradigm (see Fig. 2B for a simulation), the subject fixated the illuminated central LED and the upper right and upper left corner targets flashed. After 400 ms, one of the two corner targets (chosen at random) was flashed again to signal which target was to be first fixated and after 250 ms the central LED was extinguished. An audio cue cued the subject to make a saccade to the remembered location of the first target and then to make three successive saccades back and forth between the two remembered locations of the corner targets. The subject’s successive saccades were also paced with an audio tone to ensure that each remembered location was fixated for a consistent amount of time. At the completion of the three successive saccades, a higher tone instructed the subject to again fixate the now illuminated central target. This entire task was then repeated for a total of 10 trials using each of the four corner pairs of LEDs, where the initial corner target was randomly selected. This was the main test between the models.

We also conducted a visual control paradigm. This paradigm was
identical to the test paradigm, except that the LEDs were illuminated sequentially such that only one LED was illuminated at any one time for 1,500 ms. Subjects fixated each LED in turn for the entire time of the illumination. In addition, the audio pacing tones were maintained for consistency. This was done as an extra calibration for ideal gaze directions at the targets (see Analysis).

Finally, as an additional control, we conducted a memory control paradigm (subjects saccaded between the remembered locations of peripheral LEDs five times, where one of the pair was randomly chosen to serve as the initial fixation point instead of the central target). This was done to quantify position dependent memory errors (Gnadt et al. 1991; White et al. 1994) independent of remapping from the center. However, because these controls did not prove to be necessary for analysis of the main test paradigm and because Henriques and Crawford (2001) have subsequently shown that position-dependent errors in human “memory saccades” are minimal in this task, we do not include this data here.

Analysis

Perceived peripheral target locations were determined for each subject by computing the centroid of a data cloud of fixations around each target during the visual control trials. Theoretical error predictions for each subject were then generated by inputting, into the commutative model, the initial fixation positions (determined by the search coils) for each task, and the order and location of the peripheral target presentation. These data were first rotated into alignment with Listing’s plane coordinates (Tweed et al. 1990), because this was the coordinate system used by the models. This was necessary because the primary position in Listing’s coordinates does not generally align with the central position (Tweed and Vilis 1990), and conversely, subjects’ eye positions at the center target were not generally aligned with primary position. In this way we could generate errors like those shown in Fig. 2B, accounting for individual differences in fixation positions within Listing’s coordinates. Again, the noncommutative model always predicted zero error.

RESULTS

Figure 2, C and D, shows the gaze trajectories of a typical subject performing the test paradigm using the upper left/right and the lower right/left targets (Fig. 2C) and the upper/lower left and lower/upper-right targets (Fig. 2D). The subject was able to perform the basic elements of the task with some errors of localization for each target. In Fig. 2C this subject tended to misjudge the location of all of the targets to the left, whereas in Fig. 2D a more skewed pattern of errors was seen. However, note that the subject consistently saccaded between the same two incorrect positions, which we called positional error, and did not show the sequentially cumulative pattern predicted by the commutative model.

On average, subjects showed a raw positional error of 2.77° (SD, 1.41°; all subjects, all tasks). To eliminate these positional errors, which simply added noise and were unrelated to remapping, and thus isolate the errors due to internal commutative
approximations, we subtracted the mean error made by a subject in acquiring the initial target (where there is no remapping) from those errors made during saccades returning to this target.

Figure 3, A and B, shows a scatter plot between the remapping errors for one subject (vertical axes) and those predicted by the commutative model for the test paradigm across all targets (horizontal axes). Note that the main component of predicted error was always orthogonal to the saccades (Fig. 2 B). We plotted the vertical error component for horizontal saccades in Fig. 3 A (see Fig. 2 C for targets involved) and the horizontal error component for vertical saccades in Fig. 3 B (see Fig. 2 D for targets involved). Note also that the commutative model predicted a slope of 1, whereas the noncommutative model predicted a slope of 0. It is clear from Fig. 3 that (although there is considerable stochastic scatter in the data) the regression line fit to the actual errors more closely follows the predictions of the noncommutative model than those predicted by the commutative model.

To determine if this result was consistent, we performed the same analysis across subjects. Figure 3 shows the slopes of all subjects for the vertical error component of horizontal saccades (Fig. 3 C) and for the horizontal error component of vertical saccades (Fig. 3 D). In the vertical saccades task, one subject’s slope (†) was close enough to include the commutative model’s prediction within the associated confidence intervals (confidence intervals not shown). The subject’s high slope in this task could reflect a partial failure in the noncommutative mechanism in this particular task. However, in all other cases the slopes more closely follow the prediction of the noncommutative model. Indeed, the average slopes for the horizontal and vertical tasks were only −0.026° (SE, 0.036) and 0.038°, respectively (SE, 0.038). Further, a t-test across the slopes of all subjects (in both the horizontal and vertical tasks) showed that, as a population, the subjects’ slopes were significantly different from the slope predicted by the commutative model (P < 0.05) and, conversely, were not significantly different from the slope predicted by the noncommutative model (P > 0.7 for the horizontal task and P > 0.3 for the vertical task).

**DISCUSSION**

Several recent studies have suggested that trans-saccadic remapping in retinal coordinates is an important mechanism in visuomotor space constancy (Colby and Goldberg 1999; Duhamel et al. 1992; Goldberg and Bruce 1990; Henriques et al. 1997). We have extended these findings by showing that the remapping process is not simply a translation of the target location in retinal coordinates but also involves a transformation of the spatial error estimated on the basis of saccade amplitude and direction. This transformation is not accounted for by the simple models that have been proposed (Colby and Goldberg 1999; Duhamel et al. 1992; Goldberg and Bruce 1990; Henriques et al. 1997). Instead, the remapping process appears to be a complex interplay between the two mechanisms, as evidenced by the fact that the slopes of the regression lines are close to zero (for the horizontal task: slope = −0.091, SE = 0.030; for the vertical task: slope = 0.023, SE = 0.057) and are consistent with the predictions of the noncommutative model. C and D: regression fits (thin line) for all subjects across all tasks. For clarity, confidence limits are not shown. Note that the mean slopes for all data (thick dark lines) are consistent with predictions of the noncommutative model (for the horizontal task: mean slope = −0.026, SE = 0.036; for the vertical task: mean slope = 0.038, SE = 0.038). In the vertical task only, 1 subject (†) shows a slope which tilts more toward the prediction of the commutative model (slope = 0.742, SE = 0.163), which may indicate a partial failure of noncommutativity in the remapping process.
1 According to our simulations, a model which used visual signals (available in the cortex) to update the spatial map produced qualitatively similar, but larger, errors than the commutative model tested here.

2 Simulations which lacked this step (not shown) failed to provide accurate remapping.


