Implications of Ocular Kinematics for the Internal Updating of Visual Space

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Received 8 November 2000; accepted in final form 5 July 2001

Smith, Michael A. and J. Douglas Crawford. Implications of ocular kinematics for the internal updating of visual space. *J Neurophysiol* 86: 2112–2117, 2001. Recent studies have suggested that during saccades cortical and subcortical representations of visual targets are represented and remapped in retinal coordinates. If this is correct, then the remapping processes must incorporate the noncommutativity of rotations. For example, our three-dimensional (3-D) simulations of the commutative vector-subtraction model of retinocentric remapping predicted centripetal errors in saccade trajectories between "remembered" eccentric targets, whereas our noncommutative model predicted accurate saccades. We tested between these two models in five head-fixed human subjects. Typically, a central fixation light appeared and two peripheral targets were flashed. With all targets extinguished, subjects were required to saccade to the remembered location of one of the peripheral targets and saccade between their remembered locations. Subjects showed minor misestimations of the spatial locations of targets, but failed to show the cumulative pattern of errors predicted by the commutative model. This experiment indicates that if targets are remapped in a retinal frame, then the remapping process also takes the noncommutativity of 3-D eye rotations into account. Unlike other noncommutative aspects of eye rotations that may have mechanical explanations, the noncommutative aspects of this process must be entirely internal.

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 Highstein 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

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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 Guitton 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).

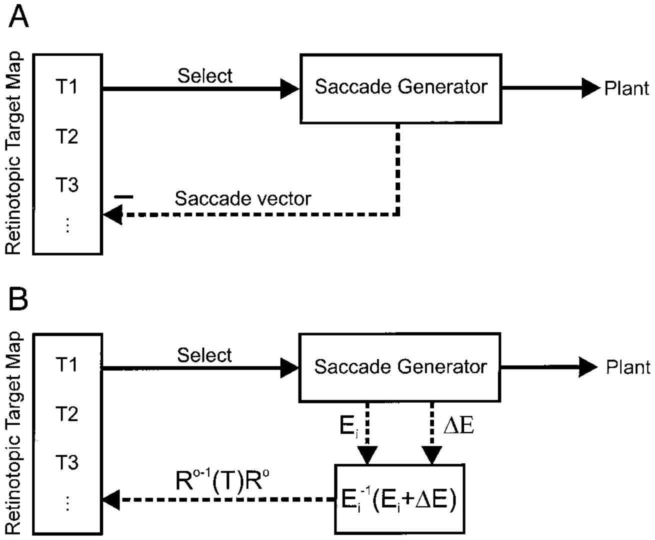

FIG. 1. Commutative/noncommutative retinotopic remapping models for saccades. The 2 models were identical except for their updating mechanisms (dashed lines). T*n*: targets in a retinotopic map. *A*: commutative vector subtraction model. The equivalent of a retinal error vector (**RE**) coding actual target location is passed to the saccade generator. Concomitant with the actual movement, all targets are remapped by subtracting the vector of the saccade ($\mathbf{RE}_{\mathbf{new}} = \mathbf{RE}_{\mathbf{old}} - \mathbf{\Delta E}$). An alternate model which subtracted the **RE** vector for the saccade was also tested, but was rejected because it produced even larger errors. *B*: noncommutative model. A target is selected, and retinal error is passed to the saccade generator. In the process of saccade generation, this model produces 2 signals: a saccade displacement command (**ΔE**) and an initial eye orientation command from the neural integrator (E_i). These 2 signals are sufficient for a noncommutative feedback mechanism (Crawford and Guitton 1997). Conceptually, 3 operations are performed by the noncommutative remapping mechanism. 1. The desired eye orientation is computed ($E_d = E_i + \mathbf{\Delta E}$). 2. The desired rotation in craniotopic coordinates (R^c) is then computed by rotating desired eye orientation by the inverse of initial eye orientation ($R^c = E_d E_i^{-1}$). 3. The rotation in crantiotopic coordinates is then converted into an equivalent rotation in oculocentric coordinates ($R^o = E_i^{-1} R^c E_i$). In practice, steps 1–3 reduce to 1 equation: $R^o = E_i^{-1}(Ei + \mathbf{\Delta E})$. All targets ($T_1$ to T_n) are rotated by the inverse of R^o to find the new retinal location ($T_{new} = R^{o-1}(T_{old})R^o$).

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. 2*A*) and the commutative vector-subtraction model (Fig. 2*B*). 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. 2*B* 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 tone 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 illumined 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

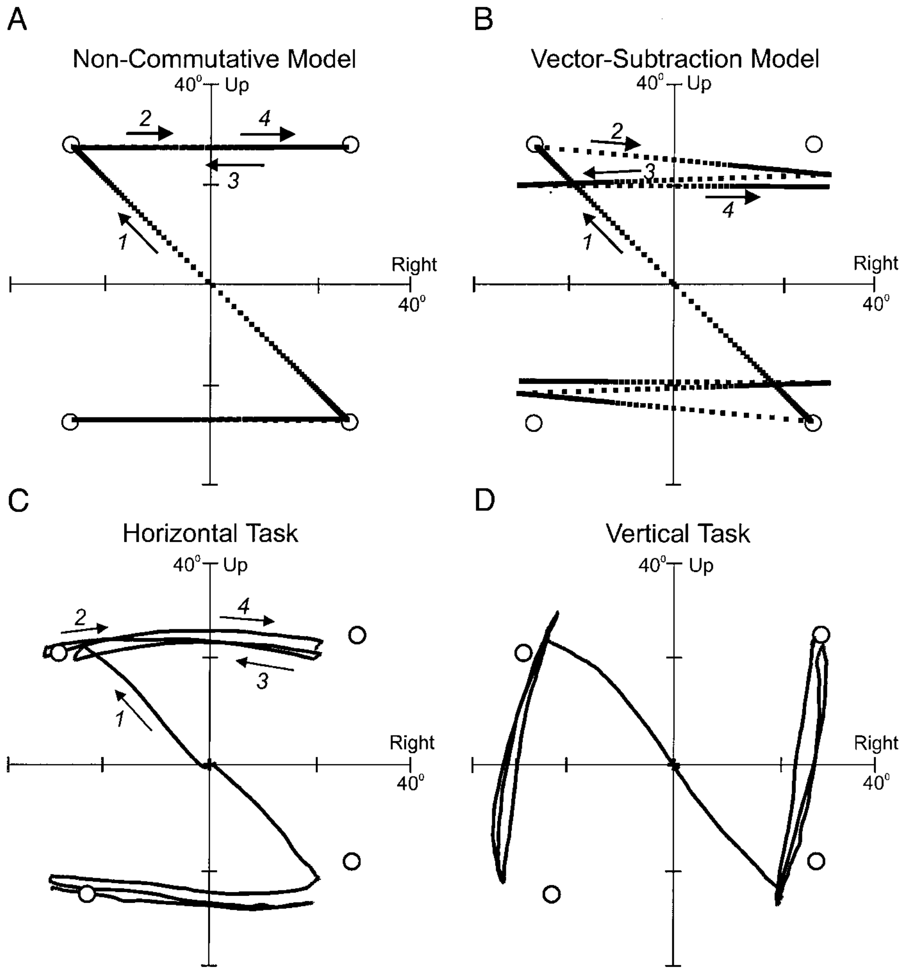

FIG. 2. Simulated (*A* and *B*) and actual (*C* and *D*) saccade trajectories. *A*: simulation of the test paradigm using the noncommutative model (Henriques et al. 1998). Only those tasks involving horizontal saccades are shown because tasks involving vertical saccades have identical results except for a 90° rotation. Note that no errors are predicted as saccades are made between the remembered locations of targets (○)—*traces 2, 3,* and *4*. *B*: same simulation using the vector-subtraction model (Goldberg and Bruce 1990). Note that a *centripetal pattern* of error is predicted for saccades between the remembered target locations. *C* and *D*: one subject's performance on the test paradigm, plotted in normal (i.e., *not* Listing's) coordinates. In these plots, perceived target locations (○) are plotted as the centroid of a cluster of eye positions around each target as recorded during the visual control task (using these positions simplified analysis by enabling us to quantify eye positions and any errors using the same coordinate system). *C*: tasks involving horizontal saccades. *D*: tasks involving vertical saccades. The subject was able to perform the task with some errors in target localization. Nevertheless, the *pattern* of gaze trajectories in all tasks follow those predicted by the noncommutative model.

identical to the test paradigm, except that the LEDs were illuminated sequentially such that only one LED was illumined 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. 2*B*, 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. 2*C*) and the upper/lower left and lower/upper-right targets (Fig. 2*D*). The subject was able to perform the basic elements of the task with some errors of localization for each target. In Fig. 2*C* this subject tended to misjudge the location of all of the targets to the left, whereas in Fig. 2*D* 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

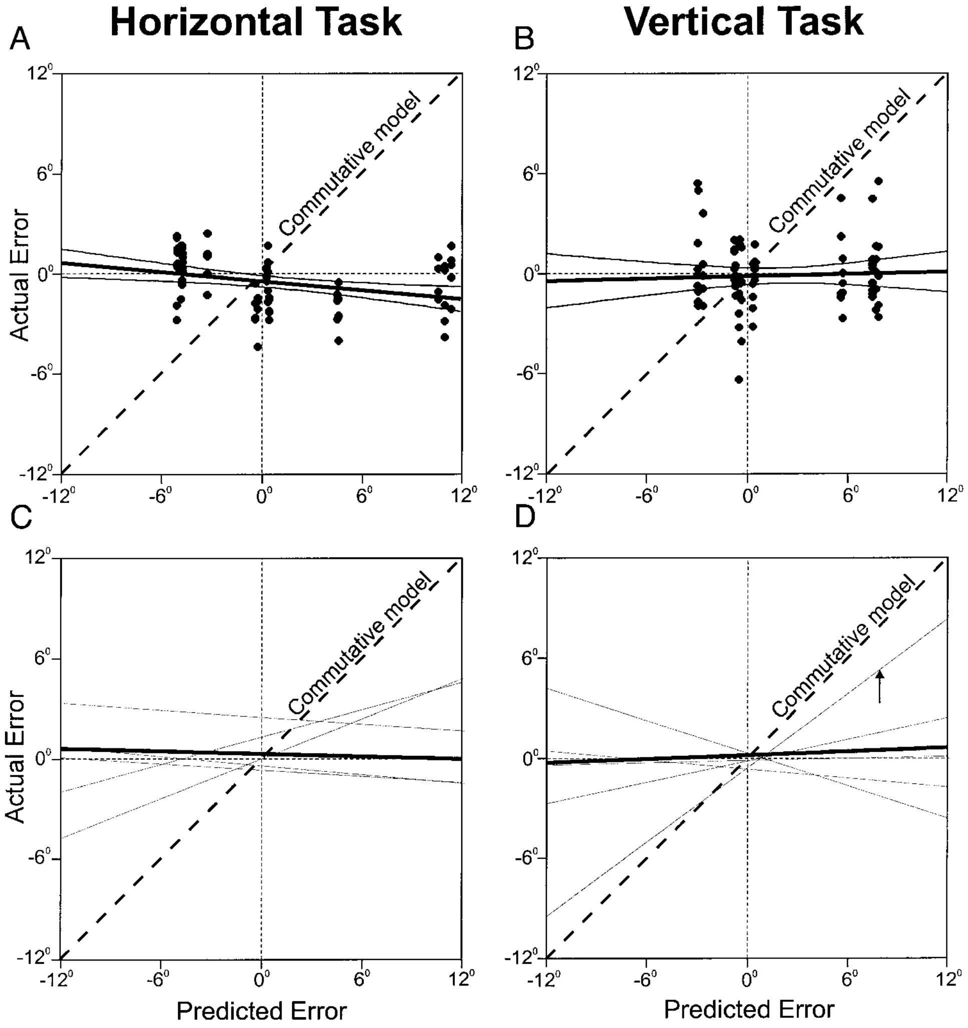

FIG. 3. Regression fits for actual vs. predicted saccade errors due to noncommutativity. Thick dashed line: prediction of the commutative vector subtraction model (slope = 1). *y* axes: actual errors in degrees (corrected for errors in localizing targets: see METHODS); *x* axes: errors (in degrees) predicted by vector subtraction model. *Left panel*: vertical error component for horizontal saccades; *Right panel*: horizontal error components for vertical saccades. *A* and *B*: errors for 1 subject (filled circles) and the regression fit for these data (dark solid line) with 95% confidence intervals (thin solid lines). Confidence intervals indicate the boundaries within which the regression line may be in any orientation. Note 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.

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 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.

1998; Moschovakis and Highstein 1994). For this remapping process to be accurate, we have seen that the noncommutativity of 3-D rotations must be taken into account or systematic errors will be made (Fig. 2*A*). Because subjects do not make the systematic errors predicted by the commutative vector subtraction model, we conclude that real behavior does take noncommutativity into account.

This is not to claim that subjects performed perfectly in our task. We saw two types of errors: a constant "positional error" (Fig. 2, *C* and *D*) and a randomly distributed error (Fig. 3). Presumably, the systematic error was related to an initial "misperception" of target location, because it occurred even in the initial saccade (before any remapping) and was not corrected. But this is not related to commutativity, and neither model can explain these errors.

The issue of noncommutativity in oculomotor control was first raised in the context of Listing's Law (Ferman et al. 1987a,b; Straumann et al. 1991; Tweed and Vilis 1987, 1990). Some have argued that the control of 3-D eye rotations requires a neural solution (Crawford and Guitton 1997; Klier and Crawford 1998; Tweed and Vilis 1987, 1990). Others have suggested that a mechanical solution may be available (Demer et al. 1995, 2000) and that a commutative controller is sufficient to control 3-D rotations of the eye (Quaia and Optican 1998; Schnabolk and Raphan 1994). However, there can be no mechanical solution to the problem of visuospatial updating since the visual cortex must update the *internal* representation of the retinal image in correspondence with the physical rotation of the eye in space, irrespective of mechanical considerations.

Moreover, the problem of noncommutativity is not unique to this particular mechanism: it has already been shown that an alternative mechanism for saccadic space constancy (rotating oculocentric vectors into head coordinates) also requires a noncommutative solution (Crawford and Guitton 1997). This is not to say that such noncommutative operations must take the form of the quaternion operations shown in our model (Fig. 1*B*). We have recently shown that artificial neural networks can implement such transformations more realistically as position modulations on vectorial visuomotor commands (Smith and Crawford 2000).

Physiologically speaking, our findings suggest that the signal that drives the remapping process must take the form of a 3-D rotation of 2-D retinal representations which, in turn, requires information about the intended 3-D saccade vector and initial eye orientation (Fig. 1*B*). The most likely source for such signals is not the cortex,[1] but the brain stem oculomotor system (Crawford 1994; Henn et al. 1989; Van Opstal et al. 1991; Waitzman et al. 1991), although these signals are probably relayed to the frontal cortex via the thalamus (Lynch et al. 1994). However, if this is correct, these brain stem signals must first be put into retinal coordinates[2] (as in our model) before they can act correctly on the retinocentric maps of the cortex and superior colliculus (Andersen et al. 1985; Cynader and Berman 1972; Munoz et al. 1990; Robinson 1972; Schall et al. 1995). Thus this model makes specific predictions about the anatomy and physiology of the internal updating mechanism for saccades.

J. D. Crawford holds a Canada Research Chair.

This work was supported by a Canadian Natural Sciences and Engineering Research Council (NSERC) grant to J. D. Crawford. M. A. Smith was supported by an NSERC scholarship.

REFERENCES

Andersen RA, Essick GK, and Siegel RM. Encoding of spatial location by posterior parietal neurons. *Science* 230: 456–458, 1985.

Batista AP, Buneo CA, Snyder LH, and Andersen RA. Reach plans in eye-centered co-ordinates. *Science* 285: 257–260, 1999.

Colby CL, Duhamel JR, and Goldberg ME. Oculocentric spatial representation in parietal cortex. *Cereb Cortex* 5: 470–481, 1995.

Colby CL and Goldberg ME. Space and attention in parietal cortex. *Ann Rev Neurosci* 22: 319–349, 1999.

Crawford JD. The oculomotor neural integrator uses a behavior-related coordinate system. *J Neurosci* 14: 6911–6923, 1994.

Crawford JD and Guitton D. Visual motor transformations required for accurate and kinematically correct saccades. *J Neurophysiol* 78: 1447–1467, 1997.

Crawford JD, Vilis T, and Guitton D. Neural coordinate systems for head-fixed and head-free gaze shifts. In: *Three-Dimensional Kinematics of Eye, Head and Limb Movements,* edited by Fetter M, Haslwanter T, Misslisch H, and Tweed D. Amsterdam: Harwood Academic, 1997, p. 43–56.

Cynader M and Berman N. Receptive field organization of monkey superior colliculus. *J Neurophysiol* 35: 187–201, 1972.

Demer JL, Miller JM, Poukens V, Vinters HV, and Glasgow BJ. Evidence for fibromuscular pulleys of the recti extraocular muscles. *Invest Ophthalmol Vis Sci* 36: 1125–1136, 1995.

Demer JL, Oh SY, and Poukens V. Evidence for active control of rectus extraocular muscle pulleys. *Invest Ophthalmol Vis Sci* 41: 1280–1290, 2000.

Duhamel JR, Colby CL, and Goldberg ME. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255: 90–92, 1992.

Ferman L, Collewijn H, and van den Berg AV. A direct test of Listing's law. I. Human ocular torsion measured in static tertiary positions. *Vision Res* 27: 929–938, 1987a.

Ferman L, Collewijn H, and van den Berg AV. A direct test of Listing's law. II. Human ocular torsion measured under dynamic conditions. *Vision Res* 27: 939–951, 1987b.

Gnadt JW and Andersen RA. Memory related motor planning activity in posterior parietal cortex of macaque. *Exp Brain Res* 70: 216–220, 1988.

Gnadt JW, Bradewell MR, and Andersen RA. Sensorimotor transformation during eye movements to remembered visual targets. *Vision Res* 31: 693–715, 1991.

Goldberg ME and Bruce CJ. Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *J Neurophysiol* 64: 489–508, 1990.

Henn V, Hepp K, and Vilis T. Rapid eye movement generation in the primate: physiology, pathophysiology and clinical implication. *Revue Neurologique (Paris)* 145: 540–545, 1989.

Henriques DYP and Crawford JD. Testing the three-dimensional reference frame transformation for express and memory-guided saccades. *Neurocomputing* 38–40: 1267–1280, 2001.

Henriques DYP, Klier EM, Smith MA, Lowy D, and Crawford JD. Gaze-centered remapping of remembered visual space in an open-loop pointing task. *J Neurosci* 15: 1583–1594, 1998.

Hepp K, van Opstal AJ, Suzuki Y, Straumann D, Hess BJM, and Henn V. Listing's law: visual, motor or visuomotor? In: *Three-Dimensional Kinematics of Eye, Head and Limb Movements,* edited by Fetter M, Haslwanter T, Misslisch H, and Tweed D. Amsterdam: Harwood Academic, 1997, p. 33–42.

Klier EM and Crawford JD. Human oculomotor system accounts for 3-D eye orientation in the visual-motor transformation for saccades. *J Neurophysiol* 80: 2274–2294, 1998.

Klier EM, Wang H, and Crawford DJ. The superior colliculus encodes gaze commands in retinal coordinates. *Nature Neurosci* 4: 627–632, 2001.

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[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.

LYNCH JC, HOOVER JE, AND STRICK PL. Input to the primate frontal eye field from the substantia nigra, superior colliculus, and dentate nucleus demonstrated by transneuronal transport. *Exp Brain Res* 100: 181–186, 1994.

MOSCHOVAKIS AK AND HIGHSTEIN SM. The anatomy and physiology of primate neurons that control rapid eye movements. *Annu Rev Neurosci* 17: 465–488, 1994.

MUNOZ DP, PELISSON D, AND GUITTON D. Movement of neural activity on the superior colliculus motor map during gaze shifts. *Science* 251: 1358–1360, 1990.

QUAIA C AND OPTICAN LM. Commutative saccadic generator is sufficient to control a 3-D ocular plant with pulleys. *J Neurophysiol* 79: 3197–3215, 1998.

RAPHAN T. Modelling control of eye orientation in three dimensions. I. Role of muscle pulleys in determining saccadic trajectory. *J Neurophysiol* 79: 2653–2667, 1998.

ROBINSON DA. Eye movements evoked by collicular stimulation in the alert monkey. *Vision Res* 12: 1795–1808, 1972.

SCHALL JD, MOREL A, KING DJ, AND BULLIER J. Topography of visual cortex connections with frontal eye field in Macaque: convergence and segregation of processing streams. *J Neurosci* 15: 4464–4487, 1995.

SCHNABOLK C AND RAPHAN T. Modeling three-dimensional velocity-to-position transformation in oculomotor control. *J Neurophysiol* 71: 623–638, 1994.

SMITH MA AND CRAWFORD JD. Self-organizing task modules and explicit coordinate systems in a neural network model for 3-D saccades. *J Comp Neurosci* 10: 127–150, 2000.

STRAUMANN D, HASLWANTER T, HEPP-REYMOND BC, AND HEPP K. Listing's law for the eye, head and arm movements and their synergistic control. *Exp Brain Res* 86: 209–215, 1991.

TWEED D, CADERA W, AND VILIS T. Computing three-dimensional eye position quaternions and eye velocity from search coil signals. *Vision Res* 30: 97–110, 1990.

TWEED D AND VILIS T. Implications of rotational kinematics for the oculomotor system in three dimensions. *J Neurophysiol* 58: 832–849, 1987.

TWEED D AND VILIS T. Geometric relations of eye position and velocity vectors during saccades. *Vision Res* 30: 111–127, 1990.

VAN OPSTAL AJ, HEPP K, HESS BJ, STRAUMANN D, AND HENN V. Two-rather than three-dimensional representation of saccades in monkey superior colliculus. *Science* 252: 1313–1315, 1991.

WAITZMAN DM, MA TP, OPTICAN LM, AND WURTZ RH. Superior colliculus neurons mediate the dynamic characteristics of saccades. *J Neurophysiol* 66: 1716–1737, 1991.

WALKER MF, FITZGIBBON EJ, AND GOLDBERG ME. Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *J Neurophysiol* 73: 1988–2003, 1995.

WHITE JM, SPARKS DL, AND STANFORD TR. Saccades to remembered target locations: an analysis of systematic and variable errors. *Vision Res* 34: 79–92, 1994.