# Implications of Rotational Kinematics for the Oculomotor System in Three Dimensions

## DOUGLAS TWEED AND TUTIS VILIS

Departments of Physiology and Ophthalmology, University of Western Ontario, London, Ontario N6A 5C1, Canada

## SUMMARY AND CONCLUSIONS

*1*. This paper develops three-dimensional models for the vestibuloocular reflex (VOR) and the internal feedback loop of the saccadic system. The models differ qualitatively from previous, one-dimensional versions, because the commutative algebra used in previous models does not apply to the three-dimensional rotations of the eye.

2. The hypothesis that eye position signals are generated by an eye velocity integrator in the indirect path of the VOR must be rejected because in three dimensions the integral of angular velocity does not specify angular position. Computer simulations using eye velocity integrators show large, cumulative gaze errors and post-VOR drift. We describe a simple velocity to position transformation that works in three dimensions.

3. In the feedback control of saccades, eye position error is not the vector difference between actual and desired eye positions. Subtractive feedback models must continuously adjust the axis of rotation throughout a saccade, and they generate meandering, dysmetric gaze saccades. We describe a multiplicative feedback system that solves these problems and generates fixed-axis saccades that accord with Listing's law.

4. We show that Listing's law requires that most saccades have their axes out of Listing's plane. A corollary is that if three pools of short-lead burst neurons code the eye velocity command during saccades, the three pools are not yoked, but function independently during visually triggered saccades.

5. In our three-dimensional models, we

represent eye position using four-component rotational operators called quaternions. This is not the only algebraic system for describing rotations, but it is the one that best fits the needs of the oculomotor system, and it yields much simpler models than do rotation matrix or other representations.

6. Quaternion models predict that eye position is represented on four channels in the oculomotor system: three for the vector components of eye position and one inversely related to gaze eccentricity and torsion.

7. Many testable predictions made by quaternion models also turn up in models based on other mathematics. These predictions are therefore more fundamental than the specific models that generate them. Among these predictions are 1) to compute eye position in the indirect path of the VOR, eve or head velocity signals are multiplied by eye position feedback and then integrated; consequently 2) eye position signals and eye or head velocity signals converge on vestibular neurons, and their interaction is multiplicative; 3) tonic neurons carrying different components of the eye position signal are interdependent, so malfunction of one component will affect the others; and 4) in the feedback control of saccades, the error signal is the desired position of the eye divided by the actual position.

## INTRODUCTION

The aim of this paper is to develop threedimensional versions of two models that are central to current understanding of the oculomotor system. The first is the oculomotor integrator, a hypothetical network which transforms eye velocity signals in the brain stem and midbrain into the eye position signals carried by extraocular motoneurons. This integrator figures prominently in the vestibuloocular reflex (VOR) and the saccadic system. The second model is the internal feedback loop of the saccadic system, in which the output of the integrator, coding eye position, is subtracted from a signal coding desired eye position to yield an error signal that drives the saccade. Both models will be seen to require significant modification before they will work in three dimensions.

The idea of a three-dimensional model of the oculomotor system is not new. Considerable work has been done on the three-dimensional properties of the direct path of the VOR, analyzing the conversion of head angular velocity signals from the semicircular canals into eye angular velocity signals (18, 22, 23). But the indirect path of the VOR, in which the eye velocity signal is transformed into an eye position signal, has not been treated in three dimensions. As we shall see, the obvious approach, sending the three components of the eye velocity vector through three integrators, will not yield what is required, namely a signal that specifies eye position. We shall show that the move to three dimensions brings much more profound change to the indirect path than it did to the direct; quite apart from the usual questions of coordinate systems and cross-coupling, three-dimensional analysis unmasks a fundamental flaw in the integrator hypothesis and forces a qualitative restructuring of the indirect path model. The new velocity to position transformation that emerges, replacing the oculomotor integrator, will also appear in the saccadic system and in any oculomotor subsystem that in one dimension requires integration of eye or head velocity signals.

Why does the move to three dimensions bring such changes to the indirect path model? The reason is fundamental: in three dimensions, one of the controlled variables, the orientation of the eye as it rotates about its fixed center, does not obey the same mathematical laws as the scalar variables of one-dimensional models and the vector variables, eye and head velocity, in three-dimensional direct path models. For example, ro-

tations, and hence the angular positions of rotating bodies, do not combine by addition. Unlike vector or scalar addition, which is commutative (that is, u + v always equals v + u), composition of rotations is noncommutative: in general, rotation p followed by q gives a different overall angular displacement than does q followed by p. The rotating knights in Fig. 1 illustrate this behavior. Starting from the same orientation, the knights undergo identical rotations in different orders. Their overall displacements clearly differ. In the figure, the rotations are identical with respect to a coordinate system fixed in space, but rotations about bodyfixed axes also do not commute.

With this nonadditivity in mind, it is perhaps not so surprising that integration of angular velocity, which is a sort of continuous summation of small angular displacements, does not yield cumulative angular displacement in three dimensions. Further, since

FIG. 1. Composition of rotations is not commutative. In A and B, the knights, starting from the same position, undergo the same rotations with respect to inertial coordinates, but their final positions differ. The figure also shows that angular position is not the integral of angular velocity. A: the knight rotates, from time t =0 to 1 s, at  $\pi/2$  radians/s about a vertical axis (shown as an arrow). Its angular velocity  $\omega$  is therefore  $(0, 0, -\pi/2)$ . For the next second, it rotates at the same speed about a horizontal axis (arrow), so  $\omega = (0, \pi/2, 0)$ . Hence the integral of  $\omega$  from t = 0 to 2 s is  $(0, \pi/2, -\pi/2)$ . B: the knight, starting from the same position, rotates with  $\omega =$  $(0, \pi/2, 0)$  for the first second,  $\omega = (0, 0, -\pi/2)$  for the next. Again, the integral of  $\omega$  from t = 0 to 2 s is (0,  $\pi/2$ ,  $-\pi/2$ ). That is, the integrals are the same, though the final positions differ.

negative feedback involves subtraction of eye position signals, we can see why the local feedback model of the saccadic system also requires modification before it will work in three dimensions.

Noncommutative composition has not been a problem in oculomotor models before now because it disappears in one special case: two rotations do combine commutatively and additively if they are about the same axis. In one-dimensional models, all movements are about a single axis; this restriction hides the peculiarities of the angular position variable and makes the oculomotor integrator and the local feedback model work. As for existing three-dimensional models, we mentioned earlier that they deal only with angular velocity transformations and avoid the eye position variable.

In what follows, we shall review how the equation relating motoneuron activity to eye motion in one dimension first prompted the integrator hypothesis. A generalization of this equation will then lead us to seek a velocity to position transformation that works in three dimensions. Four-component rotational operators called quaternions, ideally suited to the task, will be introduced. With quaternions in hand, the proper transformation follows quickly. The remainder of the paper deals with some implications of the algebraic properties of eye position for the saccadic system. Preliminary results of this work have been reported previously (27, 28).

### MODELS

### The oculomotor integrator in one dimension

We shall take the historical route to the integrator, starting from the finding that the firing rate m of a horizontal extraocular motoneuron (a neuron innervating a muscle that rotates the eye in the horizontal plane) is related to horizontal eye position H by the equation

$$\mathbf{m} = k(\mathbf{H} - \mathbf{H}_{\mathrm{T}}) + r\dot{\mathbf{H}} \tag{1}$$

where  $H_T$  is a threshold position, H is the rate of change of H, and k and r are constants (20). To be specific, the firing rate of, say, a right medial rectus motoneuron is approximately equal to the larger of  $k(H - H_T) + r\dot{H}$ and 0, with the convention that H and H are positive for deviations and motions to the left (in the pulling direction of the neuron). Negative firing rates appear when we regard m as the difference between the activity levels of a medial and a lateral rectus motoneuron with the same k, r, and H<sub>T</sub>. If we assume, for simplicity of modeling, that the shared H<sub>T</sub> is the zero or straight ahead position, we get

$$\mathbf{m} = k\mathbf{H} + r\dot{\mathbf{H}} \tag{2}$$

The position component kH of motoneuron firing reflects muscular tension exerted against the orbital tissue elastic torque -kH, which pulls the eye back toward primary, or straight ahead, position. The velocity component rH reflects muscular torque exerted against the viscous drag -rH of the orbital tissues (20).

Skavenski and Robinson used this finding in their 1973 model of the VOR (25). The reflex rotates the eyes at the same speed as, but in the opposite direction to, head rotation to keep the line of sight stationary during head movement. What are the sources of the position and velocity components of m in this reflex? Since the point of the reflex is to make eye velocity equal the negative of head velocity, and since vestibular neuron firing rates are proportional to head velocity during most natural head movements (12, 31), it was natural to suppose that vestibular neuron output, inverted and appropriately amplified, created the velocity component of motoneuron activity. The anatomical finding that vestibular neurons monosynaptically contact extraocular motoncurons supported this idea (8). As for the position component, it must be computed from the velocity signal. Since motoneurons themselves do not integrate their input. Skavenski and Robinson postulated an oculomotor integrator that receives velocity commands and drives motoneurons.

The integrator was also incorporated in models for saccadic eye movements, where it transforms a velocity signal from short-lead burst neurons into a position signal (21). Experimental evidence for integration of burst neuron activity was found by Cohen and Komatsuzaki (3). Velocity commands of the pursuit and optokinetic reflex systems may also be routed through the same integrator (4, 21, 31) (Fig. 2).

An equation analogous to Eq. 1 holds for vertical motoneurons (14), and many find-



FIG. 2. The oculomotor integrator in one dimension. Horizontal eye velocity commands from the saccadic  $(\dot{H}_s)$ , pursuit  $(\dot{H}_p)$ , optokinetic  $(\dot{H}_{ok})$ , and vestibular  $(\dot{H}_v)$ systems are all believed to pass through the same integrator to yield a single horizontal eye position command H.

ings suggesting the existence of an integrator have been replicated for nonhorizontal movements (13, 14). Thus it appears that gaze control in three dimensions requires a three-dimensional analogue of the oculomotor integrator.

## Eye movements in three dimensions

We shall make the simplifying assumption that three pairs of muscles rotate each eye about three orthogonal axes. We shall do this to provide the simplest possible setting for the question at hand: the implications for the oculomotor system of the unfamiliar mathematical properties of rotations. The resulting model is readily refinable to a more anatomically exact version by the methods of Pellionisz, Llinas, Ostriker, and others (18, 19). That the axes of muscle action may shift when the eye moves is another complication, easily incorporated in the model, but calculations by Robinson suggest that such shifting is negligible (23). For simplicity, we assume that the axes are fixed in the head.

By association, the motoneurons innervating the muscles may be divided into three orthogonal sets. Total motoneuron activity, then, may be represented by a three-component vector  $\mathbf{m}$ . For example, the vertical component of  $\mathbf{m}$  is the difference between the firing rates of two typical motoneurons, one pulling leftward and one rightward about a vertical axis (Fig. 3).

To state the relation between **m** and eve motion, we need expressions for eve position and velocity in three dimensions. We can define an eve position vector using Euler's theorem that a body with one point fixed can go from any orientation to any other by a single rotation about an axis through that fixed point. If the eye can move from primary position to some new position by a rotation of a radians about the unit vector **n** (clockwise looking in the direction of **n**), call the new position  $\mathbf{a} = \mathbf{an}$ . This designation is unique if  $-\pi < a \le \pi$ . We stress that **a** is not a vector fixed in the eye. Rather, it is a vector representation of a rotation from primary position; the vector a lies along the axis of rotation and the magnitude of a is the amplitude of the rotation.

The vector **a** is the natural representation of eye position for models of ocular mechanics because it is the only generalization of H (from Eq. 2) that is symmetric, in the sense that it treats all axes on even footing. In contrast, the systems of Fick (6a) and Helmholtz (10) are asymmetric because they express a position as a triplet of rotations, two of whose axes depend on the rotation about the third, fixed axis. Put another way, the systems of Fick and Helmholtz are physically



FIG. 3. Idealized geometry of the muscles rotating the right eye. Muscles 1 and 2, the inferior and superior recti, rotate the eye about the y-axis. The inferior and superior obliques (muscles 3 and 4) pull about the x-axis, and the medial and lateral recti (muscles 5 and 6) about the z-axis. If  $f_i$  is the firing rate of a typical neuron innervating muscle i, then  $\mathbf{m} = (f_3 - f_4, f_1 - f_2, f_5 - f_6)$ .

implemented as gimbals, or nested sequences of axes, where again the orientations of some axes depend on the rotations about others. But the eye does not move on gimbals. The three components of  $\mathbf{m}$ , which determine eye position, apply their torques simultaneously about three nearly fixed axes, so their actions are minimally, and probably mutually, interdependent. The symmetry of this arrangement favors the  $\mathbf{a}$  vector representation of eye position.

A vector expression for eye velocity is obtained similarly: an eve spinning at  $\omega$  radians/s about the unit vector **u** has angular velocity  $\omega = \omega \mathbf{u}$ . This is the standard definition of angular velocity and yields the most natural generalization of H, obtained by making the axis of rotation arbitrary. But note two, perhaps surprising, properties of  $\omega$ . First, the directions of  $\omega$  and **a** are different, and in fact the angle between the two vectors can take any value from 0 to 180°. Second, it will be very helpful to observe that, despite its name, the angular velocity vector was not defined to be the time derivative of **a**. We shall soon confirm that  $\omega$  is not the derivative of **a**, or of angular position in any sense.

If the three-dimensional relation between motoneuron activity and eye motion is to preserve the form of Eq. 2, the elastic torque vector exerted by the passive orbital tissues must be a linear function of **a**. Since any linear function taking three-component vectors to three-component vectors is equivalent to multiplication by a  $3 \times 3$  matrix, the elastic torque at any eye position **a** is  $-K\mathbf{a}$ , where K is a fixed matrix. Similarly, the viscous drag at any eye velocity  $\omega$  is  $-R\omega$ . The three-dimensional generalization of Eq. 2 is therefore

$$\mathbf{m} = K\mathbf{a} + R\boldsymbol{\omega} \tag{3}$$

During head rotation, the velocity component of **m** comes directly from the vestibular neurons, as described in current three-dimensional models of the direct path (18, 22, 23). The position component is a problem because the three-dimensional eye velocity signal  $\omega$  cannot be integrated to yield a position signal **a**. (We use the same symbol to represent a physical variable like eye velocity and its neural representation.)

The knights from Fig. 1 can be used to show that angular position is not the integral

of velocity. The angular velocity of each knight is a three-component vector which varies with time; mathematically, it is a function from the real numbers to euclidean 3-space and as such is integrated component-wise. The computations in the figure legend show that, for the motions depicted, the integral is the same for both knights, whereas the overall displacements and hence the final positions clearly differ. Note how serious this result is: the same integral corresponds to what are, in any reasonable definition, different angular positions. Thus integration of angular velocity does not yield a, or angular position in any sense, and angular position is not even a function of the integral of velocity. In general, no computation can derive angular position from the instantaneous output of a velocity integrator. The moral for the oculomotor system is that if signals from the three semicircular canal pairs went through three integrators (or 6 signals through 6 integrators), as in Fig. 4, the output of the integrators would not specify eve position.

If the theoretical advantages and the accord with experiment enjoyed by the one-dimensional integrator hypothesis are to be retained in the three-dimensional model, we must devise a replacement for the integrator to transform the eye velocity command  $\omega$ into the eye position command a. This transformation can be effected, with many steps and feedback loops, using vector operations alone. Introducing a secondary representation of eye position as a nine-component rotation matrix simplifies the process. But the simplest approach is to use a fourcomponent representation of angular position known as a quaternion, invented by W. R. Hamilton and first applied to the oculomotor system by Westheimer (32). In fact,



FIG. 4. A three-dimensional eye velocity integrator. In this model, a vector signal coding the cyc velocity command  $\omega$ , from the semicircular canals or short-lead burst neurons or elsewhere, is integrated to yield an eye position command a'. This model generates large cumulative gaze errors and post-VOR drift.

if in place of **a** we adopt the practically indistinguishable measure of eye position **q** (explained below), quaternion calculus gives the transformation from  $\omega$  to **q** in a very natural way.

## The velocity to position transformation in three dimensions

A brief introduction to quaternions, and some references, may be found in the AP-PENDIX. Throughout this section we supply the bare essentials of quaternions needed to follow the discussion. To give some intuitive meaning to the operations, and to facilitate comparison with vector models, we present the material in a way that strongly emphasizes the links to the conventional vector algebra of dot and cross products.

On this approach, a quaternion is a fourcomponent entity which can be regarded as the sum of a scalar  $q_0$  and a vector  $\mathbf{q}$ , thus

$$\mathbf{q} = \mathbf{q}_0 + \mathbf{q} \tag{4}$$

Quaternion sums, products, quotients and magnitudes are defined in the APPENDIX. Any quaternion can be expressed in the form  $|\mathbf{q}| (\cos \theta + \mathbf{n} \sin \theta)$ , where  $|\mathbf{q}|$  is the quaternion magnitude and n is a unit vector (a vector of length 1) parallel with  $\mathbf{q}; \theta$  is called the angle of the quaternion. A theorem, which is proved in the APPENDIX, says that any quaternion represents a rotation about an axis in the direction of q (or n), through twice the angle of q. Thus the quaternion  $q = 2 \cos q$  $(a/2) + 2n \sin(a/2)$  represents the same rotation as the vector **a**, namely a radians about the axis **n**. The vector **q** is very similar to **a**: it has the same direction, and its magnitude, 2 sin (a/2), differs from a by less than 4%within an oculomotor range of 55°. At primary position, both a and q equal 0, and their magnitudes grow with gaze eccentricity in any direction. If we let the position component of motoneuron firing be Kq instead of Ka, we have a model of the ocular plant

$$\mathbf{m} = K\mathbf{q} + R\boldsymbol{\omega} \tag{5}$$

which is practically indistinguishable from that of Eq. 3. To simplify the mathematics, we make one final modification to the plant equation, redefining q and K by dividing the former by 2 to get a unit quaternion and multiplying the latter by 2 to compensate. With a quaternion model we can use the following equation (proved in the APPENDIX) for  $\dot{q}$  in terms of the quaternion product of  $\omega/2$  and q

$$(\omega/2)\mathbf{q} = \dot{\mathbf{q}} \tag{6}$$

By this formula, it is clear that the network in Fig. 5 transforms an angular velocity signal to a position signal. The vector part of q is conveyed to the motoneurons;  $q_0$  is only for feedback. The main difference from the one-dimensional model is that  $\omega/2$  is multiplied by a feedback signal before integration. Angular velocity is multiplied by position feedback prior to integration even when vectors or rotation matrices are used to take velocity to position, so this unusual use of feedback is not a quirk of the quaternion approach.

Implementation of the model would pose no special problems, since the quaternion equations can be expressed in terms of scalar operations. For example, we can break up the quaternion integrator in Fig. 5 into four scalar integrators. The fourth of these is what corresponds, roughly, to the oculomotor integrator of the horizontal model. That is, the output of the fourth integrator specifies how far the eye has rotated horizontally (i.e., about a vertical axis). Expressed in the coordinate system of Fig. 3, the input of this integrator is the fourth component of  $\omega q/2$ , which is  $(\omega_1 q_2 - \omega_2 q_1 + \omega_3 q_0)/2$ , where  $q_1$  and  $q_2$  are the x and y components of q—the nonhorizontal components in the sense that z is the axis for horizontal rotation. This formula shows that the rate of change of the fourth component of q depends on the other three components and on all three components of  $\omega$ . Similar equations for the other components show that if any one component of the integrator malfunctioned, the outputs of the other three would become inaccurate,



FIG. 5. A three-dimensional velocity to position transformation. The vector  $\omega$  is ocular angular velocity. The quaternion q is ocular position with respect to the head. 'II' indicates quaternion multiplication. Multiplication of the vector  $\omega/2$  and the quaternion q is defined because a three-component vector is also a quaternion with scalar part 0.

since each component depends on input from all the others. Vector and rotation matrix models have similar properties. Thus we see the extensive cross-coupling that is required in the indirect path even with identical orthogonal coordinate systems.

### Computer simulations

In Fig. 6 we use computer simulations to compare the indirect path model in Fig. 5 (the quaternion model) with the model where the position component of  $\mathbf{m}$  is the integral of eye velocity (Fig. 4). In this way we can see in detail where and how badly the latter model fails.

As a rule, it is the angle between  $\mathbf{q}$  and  $\boldsymbol{\omega}$  that matters. As long as  $\mathbf{q}$  and  $\boldsymbol{\omega}$  remain parallel, an integrator model is approximately



FIG. 6. Computer simulations of two VOR models. Commentary in text. The vectors **h**, **g**, and **q** depict head angular velocity, initial gaze direction, and the vector of the initial eye position quaternion, respectively; **h** and **g** are set to length  $\frac{1}{2}$  so as not to dwarf the **q** vector. *A*: **h** = (0.353, 0, 0.353); **g** = (0.353, 0.25, 0.25); **q** = (0, -0.271,0.27). *B*: **h** = **g** = (0.353, 0, 0.353); **q** = (0, -0.383, 0). *C*: **g** and **q** are as in *A*. The three head velocity vectors are, in temporal order, **h**1 = (-0.141, 0, 0.48); **h**2 = (-0.079, -0.456, -0.189); **h**3 = (-0.079, 0.456, -0.189).

correct. When the angle becomes large, intolerable errors mount quickly. The simulations will show that this can happen for eye movements within the oculomotor range. The quaternion model gives the correct eye position signal for all movements.

In the simulations, we input identical head velocity functions to the two models. The outputs we consider are the indirect path signals, so we are looking at the eye positions coded by the instantaneous level of indirect path activity, not necessarily the actual eye positions. For the quaternion model, there is no difference, since the eve position signal is perfectly matched to eve velocity. For the integrator, the precise gaze path depends on the speed of head motion as well as its path. Thus, for slow head movements, where the indirect path dominates, the gaze trajectories will closely resemble those shown in the simulations. For fast movements, the actual gaze point would more closely follow the correct trajectory, but there would be superimposed drift toward the position coded by the indirect path. At the end of the head movement, there would be post-VOR drift to the position coded by the indirect path.

In Fig. 6, solid lines show the eye position trajectories coded by the quaternion model. Dashed lines show eye positions coded by indirect path activity in the integrator model. In each case, coded eye positions are shown as they would appear monitored with a scleral coil and displayed in horizontal-vertical form on an oscilloscope. Torsional errors, which occur in the integrator model in all three simulations, are not shown. Circles demarcate an oculomotor range of 55°. Vectors drawn beside each simulation depict head velocity, h, and, in Fig. 6, A and B, the initial gaze (or fixation) vector g and the vector of the initial eve position quaternion q. The coordinate system is the head-fixed system used in Fig. 3, though here we view it from behind to approximate the subjective viewpoint used in the simulations.

In Fig. 6*A*, the subject is looking  $45^{\circ}$  up and to the left when the head begins to rotate leftward about an axis in the sagittal plane tipped  $45^{\circ}$  forward and down from the straight-up direction. The initial angle between **q** and  $\omega$  is 120°. The models diverge immediately. The quaternion model, appropriately, makes the gaze point arc about the hub of the head rotation, shown as a dot. The integrator model slices upward. Gaze error in this model, defined as the angle between the gaze directions generated by the two models, runs at  $\sim 30\%$  of head rotation in this simulation. That is, when the head has rotated through 20°, the error is almost 6°; at 50° the error is 15°.

In Fig. 6*B*, the head rotates about the same axis as in Fig. 6*A*, but this time the gaze is directed along the axis at the start of head movement. Clearly, head rotation about the fixation line would cause almost no translation of the retinal image of an object on this line even if the eyes were stationary in the head. A correct VOR, therefore, would cause no change in gaze direction with respect to the head. Figure 6*B* shows that the quaternion model does in fact leave the craniotopic gaze direction unchanged. The integrator model drives the eye away from the target, right, up, and out of the oculomotor range.

Figure 6C shows how errors can accumulate in the integrator model when the head moves about more than one axis. As the head rotates, cycling twice through a series of three axes, the quaternion model draws the eye twice around the solid triangle, starting from the upper left corner. The integrator model is only  $5^{\circ}$  off at the end of the first,  $60^{\circ}$  head rotation, but an 80° turn about a new axis brings the error to 15° and it mounts steadily thereafter. An interesting feature of this simulation is that we have chosen the head rotation axes so that the quaternion model obeys Listing's law throughout, showing that integration of  $\omega$  does not yield eye position even when  $\omega$  is constrained to preserve Listing's law. An integrator model, therefore, will not work in the saccadic system any more than in the VOR.

The errors generated by the integrator model are so large that subjective observation of gaze direction before and after a closed-eye head rotation, as in Fig. 6*B*, seems to us sufficient to refute the model. But for more objective evidence, and to measure the accuracy of the quaternion model, the first two simulations would translate readily into experiments. Some relevant data are in fact available from an experiment by Fetter et al. (6), in which a subject was tipped back 60° and rotated in the dark  $\pm 24^{\circ}$  about an earthvertical axis while looking straight up along the axis. In this situation, which is very nearly a live-action version of the simulation in Fig. 6*B*, the integrator model predicts a horizontal eye excursion of about  $\pm 5^{\circ}$  and a horizontal VOR gain, as defined by Fetter et al. of 0.24. The actual finding was a stationary gaze point and a horizontal gain of 0, as predicted by the quaternion model.

In summary, then, the simulations show how the integrator model departs from the kinematically sound quaternion model when  $\mathbf{q}$  and  $\boldsymbol{\omega}$  are not parallel. We can gain some insight into both models and their differences by expressing Eq. 6 in vector terms. The formula for translating a quaternion product into vector terms and operations is the following

$$\mathbf{p}\mathbf{q} = \mathbf{p}_0\mathbf{q}_0 - \mathbf{p}\cdot\mathbf{q} + \mathbf{p}_0\mathbf{q} + \mathbf{q}_0\mathbf{p} + \mathbf{p}\times\mathbf{q}$$
(7)

Multiplying Eq. 6 through by 2 and applying Eq. 7, we obtain

$$\omega \mathbf{q} = -\boldsymbol{\omega} \cdot \mathbf{q} + \mathbf{q}_0 \boldsymbol{\omega} + \boldsymbol{\omega} \times \mathbf{q} = 2\dot{\mathbf{q}} \tag{8}$$

When **q** and  $\omega$  are parallel, their cross product vanishes, so the equation simplifies to

$$\omega \mathbf{q} = -\boldsymbol{\omega} \cdot \mathbf{q} + \mathbf{q}_0 \boldsymbol{\omega} = 2\dot{\mathbf{q}} \tag{9}$$

(10)

Extracting vector parts, we get  $q_0\omega = 2\dot{q}$ 

that is

$$\cos (a/2)\omega = 2\frac{d}{dt} [\sin (a/2)\mathbf{n}]$$
$$= \cos (a/2)\dot{\mathbf{a}}\mathbf{n} + 2\sin (a/2)\dot{\mathbf{n}} \qquad (11)$$

Hence

$$\boldsymbol{\omega} = \dot{\mathbf{a}}\mathbf{n} + 2 \tan\left(\frac{a}{2}\right)\dot{\mathbf{n}} \tag{12}$$

If **n** is not moving (i.e., if  $\dot{\mathbf{n}} = \mathbf{0}$ ) then  $\boldsymbol{\omega} = \dot{\mathbf{a}}\mathbf{n} = \dot{\mathbf{a}}$ . This result shows why an integrator works in one-dimensional models, where **q** and  $\boldsymbol{\omega}$  are always parallel and **n** never moves.

If  $\mathbf{q}$  and  $\boldsymbol{\omega}$  are not parallel,  $\boldsymbol{\omega} \times \mathbf{q}$  does not vanish, and so  $\dot{\mathbf{q}}$  has a component orthogonal to  $\boldsymbol{\omega}$ . The error in the integrator model depends on the size of the  $\boldsymbol{\omega} \times \mathbf{q}$  component, which depends in turn on the angle between  $\mathbf{q}$  and  $\boldsymbol{\omega}$ , and on the magnitude of  $\mathbf{q}$ , that is, the eccentricity of the current eye position. These results agree with our simulations, where large gaze eccentricities and large angles between  $\mathbf{q}$  and  $\boldsymbol{\omega}$  combined to yield particularly large gaze errors, though we know from simulation 6*C* that the smaller errors accrued near primary position can accumulate quickly.

## Feedback control of saccades

Another place where the algebraic properties of rotations call for changes in current oculomotor models is the feedback control of saccades. The evidence for feedback is that saccades can attain their targets, despite unpredictable interference. For example, brief electrical stimulation of omnipause cells, which inhibits the short-lead burst neurons, slows an ongoing saccade but does not make it inaccurate (1). In the one-dimensional local feedback model for saccades, the output of the integrator, coding eye position, is subtracted from a signal coding desired eye position to give an error signal that drives the short-lead burst neurons until the target is reached (29) (Fig. 8A). The move to three dimensions brings an immediate complication: the error signal must have a direction as well as an amplitude. The comparator, given desired and actual eye position, must compute the speed and direction of motion that will best reduce the error. If we were dealing with translational motion, this would be a job for vectors. The vector difference between desired and actual position would give the magnitude of the error and the optimal direction of correcting movement. But as we are dealing with rotations, vector methods are unwieldy. The vector difference between desired and actual eye position does not give the optimal direction of rotation.

Figure 7 makes this clear. Figure 7, A-C, shows the primary, present, and desired positions of the globe, respectively, together with the corresponding q vectors. (In Fig. 7A,  $\mathbf{q} = \mathbf{0}$ .) In Fig. 7D the arrow is the vector difference v between the q's of the desired and actual positions; the globe shows the orientation reached by rotating about v, through the angle specified by v, starting from position B. This orientation does not match the desired position C, showing that the vector difference between B and C is not the rotation that takes B to C. In other words, it is not an accurate error signal. In this case, the final position is correct except for torsion, but in general no rotation about the difference vector, through whatever angle, will bring even the line of sight to the right place.

The correct error direction may be found by computing an eigenvector of the quotient of the desired and actual rotation matrices. Rotation matrix methods for finding the error magnitude are also cumbersome. But with quaternions one division yields both. The quotient of desired and actual eye position quaternions is the error quaternion E. The vector of E determines the optimal ocular angular velocity. The mathematical basis for these assertions is the quaternion formula for composition of rotations (proved in the APPENDIX): if a body undergoes rotation q and then rotation E, its overall angular displacement is the quaternion product Eq. which is not in general equal to qE. Thus, if the eye is at position q and the desired eye position is q\*, the error E is the rotation that satisfies the equation  $Eq = q^*$ . Right-multiplying each side by  $q^{-1}$ —that is, dividing both sides by q—we obtain the formula E = $q^{*}q^{-1}$ . (Because q is a unit quaternion, its inverse is easily computed:  $q^{-1} = q_0 - q$ —see APPENDIX.)

To move toward the target, then, the eye must rotate about an axis in the direction of E. That is, the direction of E is the direction of the optimal velocity  $\omega$ . As in the one-dimensional model, E passes through a nonlinear element (in this model, three orthogonal pools of short-lead burst neurons) to determine the magnitude of the eye velocity command. When the feedback signal q equals the desired eye position  $q^*$ , then E = $q^{*}q^{*-1} = 1$ ; the vector of 1 (when 1 is viewed as a quaternion) is 0, so E, and therefore  $\omega$ , vanish and the movement stops. Conversely, if q\* is a unit quaternion the velocity command will not vanish unless  $q = q^*$ , so the system will not stop off target. Figure 8C is the flow diagram for a three-dimensional servomechanism based on these properties of quaternions.

If we use computer simulations to compare the multiplicative feedback model in Fig. 8C with the subtractive model in Fig. 8B, we see that they both perform well for saccades within the oculomotor range. The reason the subtractive model works is that, although its error signals are not optimal, they are close to correct for targets in the oculomotor range, and the error signals approach the optimal as the saccade progresses. Gaze trajectories, displayed as they would appear on an oscilloscope, are fairly straight for both the multiplicative and the subtractive model. Thus the subtractive feedback model cannot be ruled out immediately, based on simulated saccades to targets in the oculomotor range.

There is one situation, however, where the subtractive model runs into real trouble: the feedback control of gaze saccades (gaze shifts involving movements of the head and eyes) (9, 17). For large movements, the inaccuracy of the error signal can cause the gaze path to meander. The simulation in Fig. 9 shows  $180^{\circ}$  gaze saccades made by models 8B and 8C, with the models altered so that head position is also monitored by the comparators; that is, so that the comparators compute eye

position error in inertial coordinates. Note that Fig. 8B is well designed apart from its comparator; in particular, it has a quaternion velocity to position transformation, so any poor performance is attributable to its use of subtractive feedback. The subject is initially standing with head erect, looking 45° down in the sagittal plane. The target appears at eye level directly behind the subject. Again, gaze trajectories are shown as they would appcar monitored with a scleral coil and displayed in horizontal-vertical form on an oscilloscope, but since gaze saccades are seldom displayed this way, it may be more helpful to think of the subject as standing at the center of a large glass sphere; gaze trajectories show where the subject's fixation line



FIG. 7. Eye position error is not the difference between desired and present eye position. A: primary, or reference, position of the globe. B: present position, reached from primary position by rotating  $\pi/2$  radians about the y-axis, is represented by  $\mathbf{q} = -\sin(\pi/4)\mathbf{j}$ , (arrow). C: desired position, reached from primary position by rotating  $\pi/2$  radians about the z-axis, is represented by  $\mathbf{q}^* = \sin(\pi/4)\mathbf{j}$ , (arrow). C: desired position, reached from primary position by rotating  $\pi/2$  radians about the z-axis, is represented by  $\mathbf{q}^* = \sin(\pi/4)\mathbf{k}$  (arrow). D: the arrow is  $\mathbf{v} = \mathbf{q}^* - \mathbf{q} = \sin(\pi/4)\mathbf{k} + \sin(\pi/4)\mathbf{j} = (\mathbf{k} + \mathbf{j})/\sqrt{2} = \sin(\pi/2)(\mathbf{k} + \mathbf{j})/\sqrt{2}$ . Since  $\mathbf{q}^*$  and  $\mathbf{q}$  are both in the yz plane, so is v. The orientation reached by rotating  $\pi$  radians about v, starting from q, does not match  $\mathbf{q}^*$ . This is, the globe cannot rotate from q to  $\mathbf{q}^*$  about v. The difference vector v, therefore, is an inaccurate error signal.



FIG. 8. Feedback control of saccades. A: the one-dimensional local feedback model. H\* is the desired horizontal position of the eye. The error signal  $E = H^* - H$  passes through a nonlinear element to yield the velocity command H. B: a three-dimensional subtractive feedback model where the actual eye position quaternion q is subtracted from the desired position q\* to yield an error signal which drives the saccade. C: a kinematically sound three-dimensional model. The leftmost 'II' indicates tht q\* is multiplied by q<sup>-1</sup>, that is, divided by q. The vector of the quotient E passes through a nonlinear element to yield  $\omega/2$ .

intersects the sphere. In Fig. 9A we view the saccade from directly in front of the subject; in B, from the subject's left side. The gaze trajectory of the multiplicative feedback model, shown as a solid line, sweeps around to the target. The subtractive model (dashed line), veers too high, descends, and wobbles ever more slowly toward home, effectively stalling at the end of the dashed track.

The reason the model is having such trouble when it is so close to the target (within the range of a large nongaze saccade), is that, as we shall see in more detail below, the inaccuracy in subtractive error estimates depends not only on the size of the error, but also on the size of  $\mathbf{q}$ , where  $\mathbf{q}$ , for these gaze saccade simulations, is the position of the eye in inertial coordinates. When  $\mathbf{q}$  is large, as at the end of the 180° gaze saccade, subtractive error estimates are almost orthogonal to the true error direction. This difficulty with large angles is not a result of the sine nonlinearity

in the quaternion representation of rotations. A model that eliminates the sine functions by computing **a** from the output of the quaternion integrators and subtracting that from a desired eye position vector  $\mathbf{a}^*$  does not do any better. On attempting a 180° gaze saccade like the one above, this model veers wildly on its trip around to the target and then settles into a slowly widening oscillation near the correct gaze direction.

We can analyze the difference between the subtractive and multiplicative models in more detail if we express the multiplicative feedback equation  $E = q^*q^{-1}$  in vector terms

$$\mathbf{E} = \mathbf{q}_0^* \mathbf{q}_0 + \mathbf{q}^* \cdot \mathbf{q} + \mathbf{q}_0 \mathbf{q}^* - \mathbf{q}_0^* \mathbf{q} + \mathbf{q} \times \mathbf{q}^* \qquad (13)$$

The vector part of the error signal is

$$\mathbf{E} = \mathbf{q}_0 \mathbf{q}^* - \mathbf{q}_0^* \mathbf{q} + \mathbf{q} \times \mathbf{q}^* \qquad (14)$$

The first two addends on the right side give a linear combination of q and  $q^*$ , so their contribution lies in the same plane as q and  $q^*$ .



FIG. 9. Computer simulations of gaze saccades. Commentary in text. A: front view. B: view from subject's left side. C: the initial gaze vector  $\mathbf{g}$ , the initial  $\mathbf{q}$ , and the desired  $\mathbf{g}^*$  and  $\mathbf{q}^*$  are shown in an inertial coordinate system; gaze vectors are set to length 1. Thus  $\mathbf{g} = (0.707, 0, -0.707)$ ;  $\mathbf{q} = (0, 0.383, 0)$ ;  $\mathbf{g}^* = (-1, 0, 0)$ ;  $\mathbf{q}^* = (1, 0, 0)$ .

This plane also contains  $\mathbf{q}^* - \mathbf{q}$ , which is the subtractive estimate of error. The final addend on the right side,  $\mathbf{q} \times \mathbf{q}^*$ , is perpendicular to the plane of  $\mathbf{q}$  and  $\mathbf{q}^*$ , so when this vector is large the subtractive estimate of error will be inaccurate. There are two factors that tend to make  $\mathbf{q} \times \mathbf{q}^*$  large: large vectors  $\mathbf{q}$  and  $\mathbf{q}^*$  and a large acute angle between  $\mathbf{q}$  and  $\mathbf{q}^*$ .

When q and  $q^*$  are parallel, as in one-dimensional models, then

$$E = q_0 q^* - q_0^* q$$
  
= cos (a/2) sin (a\*/2)n\* - cos (a\*/2) sin (a/2)n  
= sin [(a\* - a)/2]n (15)

This last term is approximately equal to  $q^* - q$  when a is small. Hence the subtractive error estimate points in the same direction as the true error and is approximately equal to it in magnitude.

When **q** and **q**<sup>\*</sup> are near **0**, as in head-fixed saccades near primary position, then  $q_0$  and  $q_0^*$  are near 1, because **q** and **q**<sup>\*</sup> are unit qua-

ternions. Hence  $q_0q^* - q_0q^*$ , which is approximately equal to  $q^* - q$ , is a small vector but  $\mathbf{q} \times \mathbf{q}^*$ , the product of small vectors, is negligible. Thus the vector of  $q^{*}q^{-1}$  is approximately equal to  $q^* - q$  and the subtractive error estimate is approximately correct. As a result, the subtractive system moves the eye in about the right direction and so q and **q**<sup>\*</sup> come closer to being parallel, causing the cross-product term to shrink still further. The magnitude of **a** may be increasing, tending to enlarge the cross product, but for saccades within the oculomotor range the shrinking effect dominates, the error estimates become more accurate, and the eye reaches the desired position.

When  $\mathbf{q}$  and  $\mathbf{q}^*$  are of near unit length, as they are at the end of the gaze saccade in Fig. 9,  $\mathbf{q}_0$  and  $\mathbf{q}_0^*$  are near 0. The vector part of E is approximately equal to  $\mathbf{q} \times \mathbf{q}^*$ , which is orthogonal to the plane of  $\mathbf{q}^* - \mathbf{q}$ , so the subtractive error estimate can be  $\sim 90^\circ$  off the correct direction if  $\mathbf{q} \times \mathbf{q}^*$  is large. The eye may be guided away from the target and into a loop nearby. Before leaving the subject of gaze saccades, we mention that the gaze saccade feedback models of Guitton and Volle (9) and Laurutis and Robinson (17) incorporate integrators of head velocity, which keep track of head position. Since the head can rotate full circle repeatedly, these hypothetical integrators handle very large angular displacements. They are therefore subject, but in a more extreme way, to the same problems that beset the three-dimensional eye velocity integrator in Fig. 4. If we model three-dimensional gaze saccades using head position trackers, they will require the sort of multiplicative feedback structure shown in Fig. 5.

The system in Fig. 8C has some interesting properties that can be tested experimentally. First, it makes straight saccades (as measured with scleral coils and viewed in horizontalvertical display on an oscilloscope) toward and away from primary position. The subtractive feedback model in Fig. 8B does the same, and so do cats, monkeys, and humans, with varying degrees of precision (5, 7, 15). Saccades that are not directly toward or away from primary position are slightly curved in both models. But all saccades in model 8Chave fixed axes, whereas in subtractive models the axis may rotate as much as 30° during a movement. Thus an examination of instantaneous eye velocity during saccades that are neither centripetal nor centrifugal would provide evidence for choosing between the two models.

The subtle curvature of noncentripetal, noncentrifugal saccades in both models can make it look like the "horizontal component", say, of a saccade is over before the "vertical component." The direction of one component can also appear to reverse even though, in model 8C, the saccade is actually proceeding efficiently, as a smooth rotation about a single fixed axis. These observations show that differences in timing between the horizontal and vertical components of saccades, as measured with scleral coils, do not necessarily entail independent horizontal and vertical saccade generators. However, the asynchronous horizontal and vertical components found by King et al. (15) are probably not due to this effect because the saccades studied were approximately centrifugal. Their curvature may have been due to imprecision in the comparator or in the

nonlinear element that computes desired eye velocity from motor error by adjusting the length of the latter vector while preserving its direction. If error direction were imperfectly computed or preserved, systematic curvature of saccades could result.

A second interesting property of model 8Cis that, if the input q\* has its vector in the coronal plane, the system obeys Listing's law. The law holds that the eye assumes only those orientations that can be reached by rotation from the primary position about an axis in Listing's plane, which is a coronal plane fixed in the head and orthogonal to the fixation line in primary position. By definition, the eye position vector **a** and the vector **q** lie along the axis about which the eye would turn to get from primary position to its current position in a single rotation. Listing's law, then, can be stated in the following form: **q** is always in the coronal plane. If we use the coordinate system in Fig. 3, where the *vz* plane coincides with the coronal plane, the law becomes  $q_1 = 0$ . [This compact formulation of Listing's law is due to Westheimer (32).] If the desired eye position signal q\* has its vector in the coronal plane, the final eye position will too. That is, the eye position at the end of the saccade will fit Listing's law. Further, it can be shown that if the start position also fits Listing's law, so will all intermediate positions.

It is noteworthy that a system that rotates the eve about axes in Listing's plane may not preserve Listing's law. For example, in Fig. 7, position C fits Listing's law, and therefore any position with the same gaze direction but different torsion does not fit the law. In particular, 7D does not. But the rotations from primary position to B and thence to D are both about coronal axes. Thus confining the rotation axes to the coronal plane does not preserve Listing's law. Conversely, a system that preserves Listing's law must often rotate the eye about axes not in the plane. (For example, see Fig. 6C.) In fact, Eq. 14 shows that unless q and q\* are parallel, that is unless the saccade is purely centripetal or centrifugal, the saccade axis will have a nonzero component,  $\mathbf{q} \times \mathbf{q}^*$ , out of the plane. In other words, Listing's law requires that q always be in the coronal plane, and that  $\omega$  usually be out of the plane. [See also Helmholtz (10).]

This result has implications for the con-

nections of short-lead burst neurons, whose outputs code saccadic eye velocity commands. In 1981, Robinson and Zee (24) proposed that there are three populations of short-lead burst neurons with nearly orthogonal action vectors aligned with the sensitivity vectors of the three semicircular canal pairs. Recent studies support this contention (11, 30). Robinson and Zee suggested that Listing's law is preserved because, for visually triggered saccades, the inputs to the burst neurons are arranged so that the total eye velocity command coming from the three burst cell pools is always a vector in the coronal plane. They also suggested that the true on-direction of a nonhorizontal burst neuron could not be determined by looking for maximal responses to voluntary saccades: since all such saccades would have axes in the coronal plane, they would activate equally both populations of nonhorizontal burst neurons, whose action vectors, aligned with the sensitivity vectors of the canals, would make nearly equal and opposite  $(45^{\circ})$ angles with the coronal plane.

As we saw, however, Listing's law actually requires that the rotation axis be out of the coronal plane for most saccades. It is therefore unlikely that the nonhorizontal shortlead burst neurons are yoked so as to keep the velocity vectors of saccades in the coronal plane.

Given that Listing's law does not restrict  $\omega$ to the coronal plane, how does it constrain  $\omega$ ? The answer is that Listing's law, coupled with the proposition that all saccades have fixed axes, does not rule out any direction for eye velocity. But the further requirement that movements be restricted to the oculomotor range does constrain the eve velocity vector as follows: if an animal obeys Listing's law and makes saccades with fixed axes, those axes all lie within  $(x/2)^{\circ}$  of the coronal plane, where  $x^{\circ}$  is the limit of the animal's oculomotor range. [This result, like most of the geometric implications of Listing's law, was known to Helmholtz (10)]. For example, in monkeys, whose oculomotor range is about 45°, no fixed-axis saccade between points fitting Listing's law has an axis tilting more than 22.5° out of the coronal plane. If a short-lead burst neuron had its action vector orthogonal to the plane of a nonhorizontal canal, at say 45° to the coronal plane, no

visually triggered saccade would activate it maximally. Thus its precise on-direction could not be ascertained by looking at its activity during voluntary saccades. Nevertheless, it should be possible to distinguish burst neurons aligned with different nonhorizontal canal planes by looking for differential activation during visually triggered saccades with axes tilted in front of and behind the coronal plane.

### DISCUSSION

Three-dimensional analysis has been seen to reveal several qualitatively new features of the vestibuloocular reflex and the saccadic system. These new properties appear because three-dimensional rotations do not have the mathematical properties assumed in previous models. Thus we are able to reject the notion of an eye velocity integrator in the indirect path of the VOR because we found that when the rotation axis is free to move. integration of angular velocity does not yield angular position. In fact, no computation can derive angular position from the instantaneous output of a velocity integrator. Computer simulations of an indirect path model incorporating a velocity integrator show large, cumulative gaze errors and post-VOR drift, which are clearly unphysiological. A new velocity to position transformation is therefore required.

In the internal feedback control of saccades, we found that eye position error is not the vector difference between desired and actual eye position. A system using such subtractive error estimates must continuously adjust the rotation axis of the eye throughout a saccade. The problem is most apparent in large gaze saccades, where substractive feedback can make the gaze point follow a wandering path and stall short of the target.

Note that these two results follow from simple principles of rotational kinematics. Quaternions serve merely as a computational tool in their derivation; the results themselves require no assumptions about whether the oculomotor system actually uses a quaternion representation of eye position. Also in this category are the results clarifying Listing's law. We found that this law requires that the rotation axes for most saccades lie outside the coronal (Listing's) plane and that the axes of fixed-axis saccades between positions fitting Listing's law can lie as much as  $(x/2)^{\circ}$  out of the plane, where  $x^{\circ}$  is the oculomotor range. If we assume that there are three pools of short-lead burst neurons coding the saccadic eye velocity command, we have the corollary that the three pools are not yoked, but function independently during visually triggered saccades.

In developing three-dimensional replacements for the integrator and the comparator of the saccadic system, we have worked almost entirely with quaternions. The reason is that quaternions, while not the only possible representation of eye position, are the representation that best fits the needs of the oculomotor system. Quaternions mirror the properties of rotations with a fidelity and directness matched only by nine-component rotation matrices, and quaternions vield much simpler models than rotation matrices do: because they represent rotations in terms of axes and amplitudes, quaternions connect more smoothly with the plant equation, they are better for computing the angular velocity that will take the eye from its current position to some desired orientation, and they simplify the implementation of Listing's law. For these reasons, we believe that quaternion models of the VOR and saccadic system are the best concrete proposals now available.

The most striking specific test of the quaternion models is the fourth channel: according to these models, eye position is represented in the oculomotor system in the activity of not three but four populations of tonic neurons, the new one coding the scalar or  $q_0$  component of eye position,  $\cos(a/2)$ . The firing rates of such cells would be inversely related to the eccentricity of gaze in any direction. They would also code torsion. Within an oculomotor range of 45°, though,  $\cos(a/2)$  is always between 0.92 and 1, so if the coding were linear, the activity of these cells might appear constant and unrelated to eve position. Unless one were specifically looking for it, this fourth channel might easily escape detection. Other specific tests of the quaternion models would involve looking for neural correlates of the precise equations and operations used in the models.

Most of the predictions discussed in this paper do not yield tests specific to quaternion models, because other models (in fact,

all viable models we devised), based on other mathematical systems such as vectors and rotation matrices, yield the same predictions. Clearly, this unanimity greatly increases the plausibility of the predictions. In fact, we emphasize that the chief virtue of the quaternion models is that they generate fundamental predictions and present these predictions in the simplest possible setting. For example, whether the transformation from angular velocity to position is done using vectors alone, vectors and rotation matrices, or quaternions, angular velocity is multiplied by position feedback before integration. In the first two versions, this fundamental feature is more or less obscured in a welter of operations; in the quaternion model it stands out clearly. The fact that this feedback loop recurs in all viable models strongly suggests that the actual transformation in the brain, whatever its specifics, will share the multiplicative feedback structure of Fig. 5. Similarly, quaternion and rotation matrix models both show that in the feedback control of saccades, the error signal depends on the quotient of actual and desired eye position, suggesting that a multiplicative interaction is essential. On this view, Fig. 8C shows the basic multiplicative feedback loop required for the control of saccades. To sum up, then, we regard quaternion models as revealing the bare bones of the structure imposed on the oculomotor system by its computational tasks.

The prediction that an eye position feedback loop participates in the velocity to position transformation implies that head or eye velocity signals and eye position signals converge on cells in the vestibuloocular pathway upstream from the integrator. (Not an angular velocity integrator, but the integrator of velocity times position.) The quaternion, vector and rotation matrix realizations of Fig. 5 also require that the interaction of position and velocity be multiplicative, so that doubling the velocity input doubles the output. All models yield the further predictions that more than one canal signal contributes to each component of the eye position signal and that each component is computed using position feedback of other components. As mentioned above, this interdependence suggests that isolated malfunction of a single component of the eve position signal, say the horizontal, should be a rare event, because

such a malfunction would have to interfere with the horizontal signal that goes to the motoneurons but spare the feedback version which influences the other components. We mention again that this cross-coupling is required even with identical orthogonal coordinates for the position and velocity signals.

Finally, we note that the mathematical properties of rotations embodied in these models are relevant not only to the oculomotor system, but also to any motor system that moves the limbs about joints with more than one degree of freedom.

### APPENDIX

### Quaternions

Quaternions were invented by W. R. Hamilton in 1843. Trying to define multiplication and division for three-component vectors, Hamilton found he could not obtain a closed algebraic system of three dimensions and was obliged to consider four-component entities, the quaternions. Dot and cross products have superseded Hamilton's quaternion multiplication in the algebra of three-component vectors, but in the study of three-dimensional rotations, quaternions live on, albeit under new names. The rotation group SU(2), the Cayley-Klein parameters, spinors, and the Pauli spin matrices are some modern aliases. For our purposes, the quaternions in their original form are most convenient.

Westheimer (32) has applied quaternions to ocular kinematics in a paper which gives an oculomotor introduction to their algebra. More general presentations are available in Tait (26) and Brand (2). In this section we outline the quaternion properties used in the models in this paper.

In quaternion language a vector  $(v_1, v_2, v_3)$  is written  $v_1i + v_2j + v_3k$ , where i, j and k have the properties

$$i^2 = j^2 = k^2 = -1$$
  
 $ij = -ji = k$   $jk = -kj = i$   $ki = -ik = j$  (16)

A real quaternion q has the form  $q_0 + q_1i + q_2j + q_3k$ ; where  $q_0$ ,  $q_1$ ,  $q_2$ , and  $q_3$  are real numbers. A three-component vector is thus a quaternion with  $q_0 = 0$ . Setting  $q_0 = 0$  in q yields **q**, the vector of the quaternion. Quaternions are added and multiplied like polynomials, keeping the order of the i's, j's, and k's and using the properties in *Eq. 16*. Because i, j, and k do not commute, quaternion multiplication, though associative, is not commutative. These properties it shares with matrix multiplication, and in fact the quaternion  $q = q_0 + q_1i + q_2j + q_3k$ , is equivalent to the complex matrix

$$\begin{array}{ccc} \mathbf{q}_0 + \mathbf{i}\mathbf{q}_3 & \mathbf{q}_2 + \mathbf{i}\mathbf{q}_1 \\ -\mathbf{q}_2 + \mathbf{i}\mathbf{q}_1 & \mathbf{q}_0 - \mathbf{i}\mathbf{q}_3 \end{array}$$

(See Ref. 16). The identification with matrices shows, among other things, that quaternion multiplication is distributive over addition.

The norm, or magnitude, of a quaternion is  $|\mathbf{q}| = \sqrt{q_0^2 + q_1^2 + q_2^2 + q_3^2}$ . Every nonzero quaternion q has a unique inverse  $\mathbf{q}^{-1}$  such that  $\mathbf{qq}^{-1} = \mathbf{q}^{-1}\mathbf{q} = 1$ . The inverse of q is  $(q_0 - q_1\mathbf{i} - q_2\mathbf{j} - q_3\mathbf{k})/|\mathbf{q}|^2$ ; so we have  $|\mathbf{q}^{-1}| = 1/|\mathbf{q}|$ . Any quaternion can be written  $|\mathbf{q}| (\cos \theta + n_1 \sin \theta + n_2 \sin \theta + n_3 \sin \theta)$ , where  $(n_1, n_2, n_3)$  is a unit vector;  $\theta$  is called the angle of the quaternion.

The following property is the basis for the usefulness of quaternions in the study of rotating bodies: if q is a nonzero quaternion and **r** is a three-component vector, then  $qrq^{-1}$  is the vector obtained by rotating **r** about an axis parallel with **q**, through twice the angle of q. This theorem establishes a correspondence between quaternions and rotations of three-component vectors.

To prove the theorem, we first establish that  $q()q^{-1}$  is a linear operator on three-component vectors, that is, if  $c_1$  and  $c_2$  are any real numbers and  $v_1$  and  $v_2$  are vectors then  $q(c_1v_1 + c_2v_2)q^{-1} = c_1qv_1q^{-1} + c_2qv_2q^{-1}$ . The verification uses the fact that quaternion multiplication distributes over addition and that scalars commute with quaternions

$$\begin{aligned} \mathbf{q}(\mathbf{c}_1\mathbf{v}_1 + \mathbf{c}_2\mathbf{v}_2)\mathbf{q}^{-1} &= (\mathbf{q}\mathbf{c}_1\mathbf{v}_1 + \mathbf{q}\mathbf{c}_2\mathbf{v}_2)\mathbf{q}^{-1} \\ &= (\mathbf{c}_1\mathbf{q}\mathbf{v}_1 + \mathbf{c}_2\mathbf{q}\mathbf{v}_2)\mathbf{q}^{-1} \\ &= \mathbf{c}_1\mathbf{q}\mathbf{v}_1\mathbf{q}^{-1} + \mathbf{c}_2\mathbf{q}\mathbf{v}_2\mathbf{q}^{-1} \qquad (17) \end{aligned}$$

We now define three vectors of length one: **i** parallel with **q**; **j** orthogonal to **i** and **in** the plane of **r** and **i**; and **k** such that **i**, **j**, and **k** define a right-handed orthogonal coordinate system. If  $\lambda$  is the acute angle between **r** and **i**, then **r** = |**r**| (**i**  $\cos \lambda + \mathbf{j} \sin \lambda$ ) (Fig. 10).

Since coaxial quaternions commute, we have  $qiq^{-1} = iqq^{-1} = i$ , so  $q(|\mathbf{r}| \cos \lambda i)q^{-1} = |\mathbf{r}| \cos \lambda i$ . Further, if  $\theta$  is the angle of q we have  $qjq^{-1} = |\mathbf{q}|$ ( $\cos \theta + \mathbf{i} \sin \theta$ ) $\mathbf{j}|q^{-1}|$  ( $\cos \theta - \mathbf{i} \sin \theta$ ). Since  $|q^{-1}| = 1/|\mathbf{q}|$ , the two norms cancel and we have

$$qjq^{-1} = (\cos\theta + i\sin\theta)j(\cos\theta - i\sin\theta)$$
$$= (j\cos\theta + k\sin\theta)(\cos\theta - i\sin\theta)$$
$$= j(\cos^2\theta - \sin^2\theta) + k(2\sin\theta\cos\theta) \quad (18)$$

Hence  $qjq^{-1} = j' = j \cos 2\theta + k \sin 2\theta$ , the vector obtained by rotating j about i through an angle of  $2\theta$ , clockwise looking in the direction of i (see Fig. 10).

Thus  $\mathbf{r} = |\mathbf{r}| \cos \lambda \mathbf{i} + |\mathbf{r}| \sin \lambda \mathbf{j}$  is taken to  $|\mathbf{r}| \cos \lambda \mathbf{i} + |\mathbf{r}| \sin \lambda \mathbf{j}'$ , the vector obtained by rotating  $\mathbf{r}$  about  $\mathbf{q}$  through an angle of  $2\theta$ . This completes the proof.



FIG. 10. The operator  $\mathbf{q}(-)\mathbf{q}^{-1}$  rotates an arbitrary vector **r** about the axis **i** (parallel with **q**), through twice the angle  $\theta$  of **q**. Proof in APPENDIX.

The quaternion formula for composition of rotations is very simple: the product qp is equivalent to rotation p followed by rotation q. To prove this, we use the previous theorem to put an arbitrary vector **r** through rotations **p** and **q** in that order. At the end of the first rotation, **r** has gone to  $prp^{-1}$ . The second rotation takes the vector  $prp^{-1}$  to  $q(prp^{-1})q^{-1} = (qp) r(p^{-1}q^{-1})$ . On the other hand, putting **r** through the rotation qp yields  $(qp)r(qp)^{-1}$ . We need to show that for any nonzero quaternions **q** and **p**,  $(qp)^{-1} = p^{-1}q^{-1}$ . But this is easily verified. Note that  $(qp)(p^{-1}q^{-1}) =$  $q(pp^{-1})q^{-1} = qq^{-1} = 1$ . Similarly,  $(p^{-1}q^{-1})(qp) =$ 1. Hence  $p^{-1}q^{-1}$  is indeed the inverse of qp.

To prove that  $\omega q/2 = \dot{q}$ , we shall use the formula for the derivative of a product pq,  $\dot{p}q + p\dot{q}$ ,

#### REFERENCES

- BECKER, W., KING, W., FUCHS, A., JURGENS, R., JOHANSEN, G., AND KORNHUBER, H. Accuracy of goal-directed saccades and mechanisms of error correction. In: *Progress in Oculomotor Research (Developments in Neuroscience 12)*, edited by A. Fuchs and W. Becker. Amsterdam: Elsevier/North-Holland, 1981, p. 29–37.
- 2. BRAND, L. Vector and Tensor Analysis. New York: Wiley, 1948, chapt. 10.
- COHEN, B. AND KOMATSUZAKI, A. F.ye movements induced by stimulation of the pontine reticular formation: evidence for integration in oculomotor pathways. *Exp. Neurol.* 36: 101–117, 1972.

which is easily verified to hold for quaternions. We also need the fact that  $pq - pq = 2(\mathbf{p} \times \mathbf{q})$ , which follows from the vector formula for quaternion products, *Eq.* 7. We shall use "Vpq" to indicate the vector part of the product pq.

Now if  $\mathbf{r}_0$  is the initial position of any point in a rotating body and q is the position quaternion of norm 1 for the body (q = 1 initially), then the position **r** of the same point at any time is

$$\mathbf{r} = \mathbf{q}\mathbf{r}_0\mathbf{q}^{-1} \tag{19}$$

Differentiating with respect to time, we get

$$\dot{\mathbf{r}} = \dot{\mathbf{q}}\mathbf{r}_0\mathbf{q}^{-1} - \mathbf{q}\mathbf{r}_0\mathbf{q}^{-1}\dot{\mathbf{q}}\mathbf{q}^{-1}$$

$$= \dot{\mathbf{q}}\mathbf{q}^{-1}\mathbf{q}\mathbf{r}_0\mathbf{q}^{-1} - \mathbf{q}\mathbf{r}_0\mathbf{q}^{-1}\dot{\mathbf{q}}\mathbf{q}^{-1}$$

$$= 2(\mathbf{V}\dot{\mathbf{q}}\mathbf{q}^{-1} \times \mathbf{q}\mathbf{r}_0\mathbf{q}^{-1})$$

$$= 2\mathbf{V}\dot{\mathbf{q}}\mathbf{q}^{-1} \times \mathbf{r} \qquad (20)$$

But it is a theorem of kinematics that

$$\dot{\mathbf{r}} = \boldsymbol{\omega} \times \mathbf{r}$$
 (21)

Since **r** may be any vector in the body, we must have

$$\omega = 2\mathbf{V}\dot{\mathbf{q}}\mathbf{q}^{-1} \tag{22}$$

Since  $|\mathbf{q}|$  is constant,  $\dot{\mathbf{q}}$  and  $\mathbf{q}$ , viewed as elements of cuclidean 4-space, must be orthogonal, so their dot product  $\dot{\mathbf{q}}_0\mathbf{q}_0 + \dot{\mathbf{q}}\cdot\mathbf{q} = 0$ . But  $\dot{\mathbf{q}}_0\mathbf{q}_0 + \dot{\mathbf{q}}\cdot\mathbf{q}$  is the scalar part of  $\dot{\mathbf{q}}\mathbf{q}^{-1}$ , so  $\dot{\mathbf{q}}\mathbf{q}^{-1}$  is a vector, and we have

$$\omega = 2\dot{q}q^{-1} \tag{23}$$

$$\omega \mathbf{q}/2 = \dot{\mathbf{q}} \tag{24}$$

ACKNOWLEDGMENTS

that is,

We thank L. Van Cleeff for drawing the figures.

This study was supported by the Medical Research Council of Canada Grant MT9335. D. Tweed is a Fellow of the Medical Research Council. T. Vilis is a Medical Research Council Scientist.

Received 12 November 1986; accepted in final form 11 May 1987.

- 4. ECKMILLER, R. AND MACKEBEN, M. Velocity coded neurons: a new class of pre-motor neurons in the primate oculomotor system during pursuit. *Soc. Neurosci. Abstr.* 4: 162, 1978.
- 5. EVINGER, C., KANEKO, C. R. S., AND FUCHS, A. F. Oblique saccadic eye movements in the cat. *Exp. Brain Res.* 41: 370–379, 1981.
- 6. FETTER, M., HAIN, T. C., AND ZEE, D. S. Influence of eye and head position on the vestibulo-ocular reflex. *Exp. Brain Res.* 64: 208–216, 1986.
- 6a. FICK, A. Die Bewegungen des menschlichen Augapfelf. Z. Rat. Med. N. F. 4: 101–128, 1854.
- 7. FUCHS, A. F., KANEKO, C. R. S., AND SCUDDER,

C. A. Brainstem control of saccadic eye movements. *Annu. Rev. Neurosci.* 8: 307–337, 1985.

- 8. GACEK, R. R. Location of brain stem neurons projecting to the oculomotor nucleus in the cat. *Exp. Neurol.* 57: 725–749, 1971.
- GUITTON, D. AND VOLLE, M. Eye-Head Coordination in Humans to Targets Within and Beyond the Oculomotor Range. IUPS satellite meeting: Developments in Oculomotor Research Abstract WP-11, Glenedon Beach, OR, 1986.
- HELMHOLTZ, H. VON. Treatise on Physiological Optics (English Translation), translated by J. P. C. Southall. Rochester, NY: Opt. Soc. Am., 1925, vol. 3, p. 44–51.
- 11. HEPP, K., VILIS, T., AND HENN, V. Vertical and torsional rapid eye movement generation in the riMLF. *Soc. Neurosci. Abstr.* 12, 325.9, 1986.
- 12. KELLER, E. L. Behaviour of horizontal semicircular canal afferents in alert monkey during vestibular and optokinetic stimulation. *Exp. Brain Res.* 24: 459–471, 1976.
- KING, W. M. AND FUCHS, A. F. Reticular control of vertical saccadic eye movements by mesencephalic burst neurons. J. Neurophysiol. 42: 861–876, 1979.
- KING, W. M., FUCHS, A. F., AND MAGNIN, M. Vertical eye movement-related responses of neurons in midbrain near interstitial nucleus of Cajal. *J. Neurophysiol.* 46: 549–562, 1981.
- KING, W. M., LISBERGER, S. G., AND FUCHS, A. F. Oblique saccadic eye movements of primates. J. Neurophysiol. 56: 769–784, 1986.
- KOSTRIKIN, A. I. Introduction to Algebra (English translation), translated by Neal Koblitz. New York: Springer-Verlag, 1982, p. 529.
- LAURUTIS, V. P. AND ROBINSON, D. A. The vestibulo-ocular reflex during human saccadic eye movements. J. Physiol. Lond. 373: 209–233, 1986.
- OSTRIKER, G., PELLIONISZ, A., AND LLINAS, R. Tensorial computer model of gaze—I. Oculomotor activity expressed in non-orthogonal natural coordinates. *Neuroscience* 14: 483–500, 1985.
- 19. PELLIONISZ, A. AND LLINAS, R. Brain modeling by tensor network theory and computer simulation. The cerebellum: distributed processor for predictive coordination. *Neuroscience* 4: 323–348, 1979.
- ROBINSON, D. A. Oculomotor unit behavior in the monkey. J. Neurophysiol. 33: 393–404, 1970.

- ROBINSON, D. A. Oculomotor control signals. In: Basic Mechanisms of Ocular Motility and Their Clinical Implications, edited by P. Bach-y-Rita and G. Lennerstrand. Oxford UK: Pergamon, 1975, p. 337–374. (Wenner-Gren Cent. Int. Symp. Ser.)
- ROBINSON, D. A. Use of matrices in analyzing the three-dimensional behavior of the vestibulo-ocular reflex. *Biol. Cybern.* 46: 53–66, 1982.
- ROBINSON, D. A. The coordinates of neurons in the vestibulo-ocular reflex. In: *Adaptive Mechanisms in Gaze Control*, edited by A. Berthoz and G. Melvill Jones. Amsterdam: Elsevier, 1985, p. 297–311.
- ROBINSON, D. A. AND ZEE, D. S. Theoretical considerations of the function and circuitry of various rapid eye movements. In: *Progress in Oculomotor Research (Developments in Neuroscience 12)*, edited by A. Fuchs and W. Becker. Amsterdam: Elsevier/North-Holland, 1981, p. 3–9.
- SKAVENSKI, A. A. AND ROBINSON, D. A. Role of abducens neurons in vestibulocular reflex. J. Neurphysiol. 36: 724–738, 1973.
- 26. TAIT, P. G. An Elementary Treatise on Quaternions. Cambridge, UK: Cambridge Univ. Press, 1890.
- TWEED, D., VIIRRE, E., AND VILIS, T. The Oculomotor Integrator and Internal Feedback in Three Dimensions. IUPS satellite meeting: Developments in Oculomotor Research Abstract TP-12, Gleneden Beach, OR, 1986.
- 28. TWEED, D. AND VILIS, T. The oculomotor integrator in three dimensions. *Annu. Meet. Am. Physiol. Soc., Niagara Falls, NY*, 1985.
- VAN GISBERGEN, J., ROBINSON, D. A., AND GIE-LEN, S. A quantitative analysis of generation of saccadic eye movements by burst neurons. *J. Neurophysiol.* 45: 417–442, 1981.
- VILIS, T., HEPP, K., SCHWARZ, U., HENN, V., AND HASS, H. Unilateral riMLF lesions impair saccade generation along specific vertical planes. *Soc. Neurosci. Abstr.* 12: 325.10, 1986.
- 31. WAESPE, W. AND HENN, V. Neuronal activity in the vestibular nuclei of the alert monkey during vestibular and optokinetic stimulation. *Exp. Brain Res.* 27: 523–538, 1977.
- 32. WESTHEIMER, G. Kinematics of the eye. J. Opt. Soc. Am. 47: 967–974, 1957.