Tweed, Douglas. Three-dimensional model of the human eye-head saccadic system. *J. Neurophysiol.* 77: 654–666, 1997. Current theories of eye-head gaze shifts deal only with one-dimensional motion, and do not touch on three-dimensional (3-D) issues such as curvature and Donders’ laws. I show that recent 3-D data can be explained by a model based on ideas that are well established from one-dimensional studies, with just one new assumption: that the eye is driven toward a 3-D orientation in space that has been chosen so that Listing’s law of the eye in head will hold when the eye-head movement is complete. As in previous, one-dimensional models, the eye and head are feedback-guided and the commands specifying desired eye position pass through a neural ‘satu-ration’ so as to stay within the effective oculomotor range. The model correctly predicts the complex, 3-D trajectories of the head, eye in space, and eye in head in a variety of saccade tasks. And when it moves repeatedly to the same target, varying the contributions of eye and head, the model lands in different eye-in-space positions, but these positions differ only in their cyclotorsion about the line of sight, so they all point that line at the target—a behavior also seen in real eye-head saccades. Between movements the model obeys Listing’s law of the eye in head and Donders’ law of the head on torso, but during certain gaze shifts involving large torsional head movements, it shows marked, 8° deviations from Listing’s law. These deviations are the most important untested predictions of the theory. Their experimental refutation would sink the model, whereas confirmation would strongly support its central assumption that the eye moves toward a 3-D position in space chosen to obey Listing’s law and, therefore, that a Listing operator exists upstream from the eye pulse generator.

**INTRODUCTION**

In most large gaze shifts, eye and head work together to bring the line of sight swiftly onto its new target. Because of the complex, fast and accurate coordination involved, these movements—called eye-head saccades—have attracted the attention of theorists (Galiana and Guitton 1992; Galiana et al. 1992; Guitton et al. 1990; Laurutis and Robinson 1986; Tomlinson and Bahra 1990), but current models of eye-head control deal with motion in only one dimension and do not touch on the new issues that arise in three dimensions, such as curvature, noncommutativity and Donders’ and Listing’s laws.

From a three-dimensional (3-D) perspective, the central question is how the saccadic system converts its two-dimensional (2-D) input signal, retinal error, into 3-D rotations of the eye and head. Retinal error, defined as the location of the target image on the retina, is 2-D simply because the retinal surface is 2-D. Eye and head rotations are 3-D because each is free to move horizontally, vertically, and torsionally. Together, eye and head have $3 + 3 = 6$ df, so the eye-head saccadic system must actually transform a 2-D input into a six-dimensional output. It is true that for some gaze shifts stereoscopic depth is important, and then one might speak of 3-D or even four-dimensional biretinal error driving a nine-dimensional system consisting of the eyes and the head, but this paper will not consider such vergence-saccades. It is also true that not all saccades are driven by retinal error—we can look toward auditory, tactile, remembered or olfactory targets—but there is evidence that auditory targets, at least, are converted to retinal coordinates within the brain and are stored, together with visual targets, in a single map in the superior colliculus, SC (Jay and Sparks 1984), a map of target direction relative to the eye (Robinson 1972; Schiller and Stryker 1972; Sparks and Mays 1980; Van Opstal et al. 1991). In this paper, therefore, I assume that the input to the saccadic system is always a 2-D signal coding target direction in eye coordinates.

The saccadic system’s job is to convert this 2-D input into 3-D rotations of the eye and head, which must fit certain constraints. Of course the most important constraint is that the gaze line land on the target, but the rotations must also obey Listing’s law of the eye in head (Ferman et al. 1987; Radau et al. 1994; von Helmholtz 1867) and Donders’ law of the head on torso (Radau et al. 1994). I shall argue that recent data on eye-head gaze shifts can be explained, and fundamental new predictions can be made, by a model that introduces just one new assumption, and that is otherwise based on ideas that are well established from one-dimensional studies. The new assumption is that the eye is driven toward a 3-D orientation in space that has been chosen so that Listing’s law of the eye in head will hold when the eye-head movement is complete. Before presenting this 3-D model and its predictions, I review the experimental data and previous models on which it is built.

**BACKGROUND**

**Superior colliculus codes gaze shifts in space**

Electrically stimulating the SC in a cat with its head free evokes an eye-head gaze shift (Guitton 1992; Guitton and Volle 1987; Guitton et al. 1990; Roucoux et al. 1980). Repeated stimulation of a single site causes repeated gaze shifts of approximately the same size and direction, but the contributions of eye and head may vary, so that for one gaze shift, the eye may move a lot and the head only a little, for another the reverse. And similar observations have recently been made in monkeys (Robinson and Cowie 1993). These findings suggest that there is a map within the SC that specifies the desired movement of the gaze line or, in other words, gaze error. Regarding terminology, note that if gaze error is
specified in eye coordinates, as we shall assume, then it is the same thing as target direction in eye coordinates, which is equivalent, in turn, to retinal error (if the lights are on and the target in within visual range); e.g., if retinal error is 20° right, then the target direction relative to the eye is also 20° right, as is the gaze shift, in eye coordinates, required to foveate the target.

Any gaze shift can be parcelled out to the eye and head in many different ways. If you want to shift your gaze point 20° rightward, you can turn your eyes 20° right in your head and hold your head fixed, or turn your head 20° right and leave your eyes fixed in your head, or turn your eyes and head 10° right, and so on. For sensible results, this division of labor must take into account the current positions of the eye and head. Thus if your retinal error is 20° rightward, your eyes are currently 20° left in your head and your head is 10° right in space, you may move your eyes 20° right in your head, i.e., center them, and leave your head where it is. But if you see the same retinal error when your eyes are already 30° right in your head and your head is centered, you are more likely to turn your head 20° right and leave your eyes fixed in your head. These scenarios show that the retinal error, or desired gaze shift, command cannot drive the eye and head by itself, but must interact, inside or downstream from the SC, with signals coding current eye and head position.

It is known that saccadic bursters in the SC code initial gaze error; e.g., the site representing 20° rightward error remains active throughout a 20° rightward saccade (Sparks and Mays 1980, 1983). Another group of SC neurons, the buildup cells, may code the evolving, or “dynamic,” gaze error throughout the movement (Munoz and Wurtz 1995a,b), but the existence of dynamic gaze error signals and their role in saccade generation are controversial. Following Galiana et al. (1992), the model in this paper drives the eye and head with a dynamic gaze error signal computed within the SC, but it is important to note that the experimental evidence for this is inconclusive, and that the crux of the model—driving the eye to a 3-D orientation in space chosen so that the eye’s final orientation in the head satisfies Listing’s law—is independent of this question.

Eye is driven to a position in space

There is convincing evidence that both eye and head are driven to their desired positions by feedback in the form of efference copy and, likely, vestibular signals (Becker et al. 1981; Guitton and Volle 1987; Guitton et al. 1990; Laurutis and Robinson 1986; Pélisson et al. 1989). Further, it is known that the eye is driven toward its desired position in space, not its desired final position in the head. For example, if the visual target is 65° right in space-fixed coordinates, then at the end of the movement, the head will be ~50° right and the eye 15° right in the head. But during the saccade, the eye does not simply move to its final position in the head, 15° right, and wait there for the head to finish its motion. Instead, it shoots well past 15° until the gaze line hits the target, and then, under the influence of the vestibuloocular reflex (VOR), it rotates back to 15° right as the head completes its motion (Guitton and Volle 1987; Laurutis and Robinson 1986; Tweed et al. 1995). This way, the gaze line reaches the target earlier, before the head finishes its motion.

**VOR is shut off in one direction**

During large saccades, the VOR is weakened or shut off, gradually turning back on as gaze error becomes small and becoming fully operational again during the final, **VOR stage** of the movement, when the gaze is on target but the head is still completing its motion (Guitton and Volle 1987; Laurutis and Robinson 1986; Roucoux et al. 1981; Tomlinson and Bahra 1986; Tweed et al. 1995). As Laurutis and Robinson pointed out, it is sensible to switch the VOR off during such saccades, because its function is to hold the gaze stable in space and that function is not desirable during a saccade. Optimally, the brain should shut off the VOR in the direction of the saccade but leave it on in other directions, because only head movements in the direction of the saccade should affect the motion of the eye in space. This design specification is at least roughly implemented in the actual VOR, which switches off in the direction of the saccade (Guitton and Volle 1987; Laurutis and Robinson 1986; Tomlinson and Bahra 1986), but remains on in the opposite (Pélisson and Prablanc 1986; Pélisson et al. 1988) and orthogonal directions (Tomlinson and Bahra 1986).

An important 3-D property of the VOR is that it does not preserve Listing’s law of the eye (Crawford and Vilis 1991; Henn et al. 1992; Misslisch et al. 1994a). This means that, if the eye is to obey Listing’s law when the eye-head gaze shift is over, it must *not* be in Listing’s plane when the gaze line hits the target, because then the VOR would just drag it back out again. Instead, the eye saccadic system must place the eye in a position, outside Listing’s plane, that has been chosen carefully so that the subsequent action of the VOR brings it into the plane. Further, this must happen despite large variations in the size and duration of the VOR stage (Fuller 1992; Tweed et al. 1995). As stated above, the model achieves this by driving the eye toward a desired final position in space that has been chosen such that eye position in the head will fit Listing’s law when the head reaches its desired position.

**Desired eye position is saturated**

Guitton and Volle (1987) showed that the command driving the eye saccade passes through a neural “saturation box” before reaching the saccadic pulse generator, so that a desired eye position command of 90° right, for example, would emerge as ~40° right. Saturation prevents the eye from running at full speed to the end of its leash, like the dog in the Bugs Bunny cartoon, a maneuver that might overstretch the muscles or damage the globe. Further, saturation prevents errors that might arise if the muscles were given commands they could not execute. But note that saturation, if it is to serve these purposes, must act on signals coding desired eye position relative to the head, not desired gaze or eye movement. For example, if the desired gaze movement is 60° to the right, is saturation required? Yes, if the eye is, say, 30° right, because then the desired eye-in-head position is 30° + 60 deg = 90° right, which is uncomfortably eccentric. No, if the eye is 30° left, because then the desired eye-in-head position is only 60° – 30° = 30° right. This shows that the saturation operator cannot act on retinal error or on commands coding only the desired movement of the eye but
requires signals coding absolute eye position in the head. In
the model, the input to the saturation function is a desired
eye-in-head position signal, computed within or downstream
from the SC.

Donders’ and Listing’s laws

Imagine a rotating object whose position is expressed us-
ing quaternion vectors. We shall say that the object follows
Donders’ law if its quaternion vector remains within a 2-D
surface (Donders 1848). If this surface is flat, i.e., if it is
a plane—then the object also obeys Listing’s law (von
Helmholtz 1867; Westheimer 1957). It is known that eye-
in-head positions obey Listing’s law, with an inaccuracy of
only a degree or so, during and between head-fixed saccades
and between eye-head saccades (Ferman et al. 1987; Radau
et al. 1994; Tweed and Vilis 1990; von Helmholtz 1867).
Head positions obey Donders’ law during spontaneous eye-
head gaze shifts (Tweed and Vilis 1992), and recent studies
have shown that the law applies much better to head-on-
torso motion than to head-in-space (Misslisch et al. 1994b;
Radau et al. 1994). Donders’ law of the head fails during
repeated gaze shifts between two targets (Tweed and Vilis
1992), and of course this law can be repealed voluntarily,
i.e., you have the power to cock your head into almost any
3-D orientation you wish. This shows that Donders’ law of
the head is a default rule that can be altered or overridden.

Model

The map in the burst cell layer of the SC specifies the
initial target direction relative to the eye, \(T_e\). In the buildup
cell layer of the SC, a comparator driven by feedback signals
coding head velocity (from the semicircular canals) and
eye position and velocity (from efference copy), computes
dynamic target direction, \(T_s\), as it changes throughout the
saccade. This signal, which is 2-D, must be converted into
3-D head and eye rotations. The operations involved in this
conversion are shown in flow diagram form in Fig. 1; for
simplicity, the computation of dynamic target direction \(T_s\)
is not shown in the flow diagram but takes place off the left-
hand side of the figure.

To drive the head, the dynamic target direction \(T_s\) is con-
verted from eye coordinates into space coordinates using
feedback signals coding eye and head position. The resulting
target direction in space signal, \(T_h\), which is still just 2-D,
drives a Donders operator to yield a 3-D desired head
position in space command, \(q^*_{eh}\), which specifies a head
position that is “comfortable” for viewing a target in that
location and that obeys Donders’ law of the head. The override
command in the flow diagram reflects the fact, men-
tioned above, that Donders’ law can be abrogated volunta-
rily, i.e., you can choose to make an eye-head saccade that
leaves your head in almost any 3-D orientation imaginable.
Most simulations in this paper use the Donders operator
because Donders’ law of the head is known to hold during
normal eye-head gaze shifts (e.g., Glenn and Vilis 1992;
Tweed and Vilis 1992; Tweed et al. 1995). For the simula-
tions in Figs. 3–5 and 7, the operator is set so that head
movement contributes ~80% of horizontal gaze shifts and
~50% of vertical gaze shifts, because these values are typi-
cal for normal subjects (Glenn and Vilis 1992). Figure 6
shows what happens when the Donders operator is altered,
changing the contribution of the head (for mathematical de-
tails of this adjustment, see the APPENDIX). Figure 8 gives
an example where the Donders operator is overridden.

Whether it arises from the Donders operator or from the
override, the desired head position command then passes to
the head pulse generator \(P_h\) where it is compared with an
internal estimate of current head position, \(q_h\), derived from
vestibular, proprioceptive and/or efference copy signals, and
yields a 3-D head velocity command, \(q_v\), that drives the neck
muscles until the head movement is complete. Note that this
velocity command, \(q_v\), is quaternion velocity, i.e., it is the
rate of change of the head position quaternion; it is not the
angular velocity vector of the head.

To drive the eye, the 2-D target direction in space signal
\(T_e\) interacts with the 3-D desired head position signal \(q^*_{eh}\) to
yield a 3-D desired eye position in the head, \(q^*_{eh}\), which fits
Listing’s law and which will point the gaze line at the target
when the head reaches its desired position. But as we saw
earlier, the eye is not driven toward its desired final position
in the head, so \(q^*_{eh}\) is combined with desired head position
\(q^*_{eh}\) to yield desired eye position in space, \(q^*_{eh}\). This signal
then interacts with an internal estimate of head position to
yield current desired eye position in the head, \(q^*_{eh}\), i.e., the
position that the eye would have to have in the head to be
in its desired position in space, given the current position of
the head. For example, if the desired eye position in space
is 90° right and the current position of the head is 10° right,
then the current desired eye position in the head is 80° right.
As this example shows, current desired eye position may be
highly undesirable because it lies beyond the oculomotor
range, and so this signal passes through a 3-D version of
Guitton and Volle’s saturation box, labeled Sat, to yield
saturated current desired eye position in the head, \(q^*_{eh}\). Fi-
ally, this 3-D signal passes to the eye pulse generator \(P_e\),
where it is compared with an internal estimate of eye posi-
tion, \(q_{eh}\), as in Robinson’s original feedback model for head-
fixed saccades (Robinson 1975), to yield a saccadic eye
velocity command which, together with the VOR, deter-
mines eye-in-head velocity \(\dot{q}_{eh}\). The equations for this flow
diagram are given in the APPENDIX.

Saturation

In the model, saturation of desired eye position operates
three-dimensionally: horizontally, vertically, and torsionally,
a generalization of Guitton and Volle’s (1987) one-dimen-
sional scheme which raises some new issues. In one dimen-
sion, saturation is a simple matter of “clipping” desired eye
position signals larger than some limit, say 40°. In 3-D,
saturation involves projecting overly eccentric desired eye
position vectors into some central, 3-D subvolume of the
oculomotor range, called the effective oculomotor range
(EOMR). We know very little about the 3-D shape of the
EOMR. Ellipsoids or cylinders seem the likeliest possibili-
 ties, so in the simulations here the EOMR is a compromise
between these two shapes (see Fig. 2); it is a clipped ellip-
soid, or pill-shape, 80° in diameter in the horizontal-vertical
plane and 16° thick in the torsional dimension in the center,
a value chosen because it is roughly the torsional eye position range seen during roll VOR (Misslisch et al. 1994a).

Geometrically, there are many ways to project an eccentric desired eye-in-head position $q^*_{eh}$ onto a saturated desired eye-in-head position $q^+_{eh}$ within the EOMR, and different projection rules have different functional advantages and disadvantages. Tweed et al. (1995) suggested that the best strategy would be to project in such a way that $q^+_{eh}$ is the point where $q^*_{eh}$ (which is continuously changing because of the head’s motion) is predicted to enter the EOMR. This strategy would get the eye-in-space to its final position at the earliest possible moment and with the least wasted eye-in-head motion. But it turns out that, in some cases when the head is prevented from completing its motion, this strategy could cause the gaze line to fall short of the target.

For this reason, the present paper uses a slightly different strategy, driving the eye to the point on the boundary of the EOMR where, it is predicted, the target will first become foveable. In other words, it drives the eye to that position within the EOMR where it will first be possible to get the target image onto the fovea. Thus whereas Tweed et al. (1995) suggested driving the eye to the position within the EOMR where the target will first be foveable with the correct eye-in-space torsion, the present model drives the eye to the position in the EOMR where the target will first be foveable, period. I should add, however, that for normal, unperturbed gaze shifts, there is little difference between the saccades produced by the two saturation schemes and, in particular, the patterns in Figs. 3-8 below are insensitive to the details of the saturation.

The new saturation strategy is illustrated in Fig. 2. If current desired eye position, $q^*_{eh}$, lies outside the EOMR in the horizontal-vertical plane, then it is projected into range along the straight path joining it to the final desired eye position $q^*_{eh}$. This signal interacts with desired head position to yield desired eye-in-head position $q^+_{eh}$ (Eq. A9a), which then combines with actual head position $q_h$ to yield current desired eye-in-head position, $q^+_eh$ (Eq. A9b). This passes through saturation box, $Sat$, emerging as saturated current desired eye-in-head position, $q^*_{eh}$ (see Fig. 2 and Eqs. A9c and A10), which then travels to eye pulse generator, $P_e$, where it is compared with a feedback signal coding actual eye position $q_{eh}$ to yield a saccadic eye velocity signal which sums with vestibuloocular reflex (VOR) to generate eye-in-head velocity $q_{eh}$ (Eqs. A11 and A12). VOR is switched off in direction of eye-in-head motor error, as described in Eq. A13.

**Simulations**

**Gaze point and facing direction**

We start the model on a relatively simple task: predicting gaze paths. This is simpler than predicting eye and head rotations, because gaze paths are 2-D whereas rotations are 3-D. Figure 3 is a computer simulation showing the predicted paths traced by the gaze point as it moves across a large spherical viewing screen centered on the subject. The simu-
are genuine predictions, confirmed by the data in Tweed et al. (1995). 2) Horizontal paths of both the gaze point and facing direction are roughly straight, but vertical paths bow out like the sides of a barrel. 3) The subtle figure-eights in the horizontal gaze point paths in Fig. 3 also are seen in all human subjects. 4) Oblique paths of the facing direction are straight. 5) Oblique paths of the gaze point are not straight, and their curvature changes with the direction of the gaze shift, so that centrifugal and centripetal saccades into this quadrant trace out a CCW loop. The mechanisms behind these curving paths, and behind the similar patterns we shall see in plots of 3-D eye-in-space position, are dealt with in the DISCUSSION.

Eye-in-space trajectories

Simulated oblique, eye-head saccades in all four quadrants are shown in Fig. 4, which plots eye-in-space orientations, depicted as quaternion vectors and viewed from behind so that the horizontal and vertical components of the motion are seen. A complex pattern of loops appears: centrifugal and centripetal saccades form CCW loops in the first and third quadrants, and CW loops in the other two quadrants. This pattern is echoed in the data shown at the bottom of the figure and indeed was present in all subjects tested by Tweed et al. (1995). But although the qualitative looping pattern is the same, data and model do not agree perfectly on the detailed paths taken by the eye. In particular, centripetal saccades usually are curved more in the data than in the model. Reasons for this discrepancy, as well as for the correct prediction of systematic looping, are covered in the DISCUSSION.

Loops also are predicted during purely horizontal and vertical saccades, but in these cases the looping is mainly in the torsional dimension. Figure 5 shows eye-in-space quaternion vectors in a right side view, so that the torsional and ho-

FIG. 2. Three-dimensional saturation. In model, when current desired eye-in-head position, \( q_{eh}^d \), lies outside effective oculomotor range, EOMR, eye is instead aimed at a saturated desired position, \( q_{eh}^s \), which is calculated as shown here. First, in plane containing the horizontal and vertical components of quaternion vectors, \( q_{eh}^d \) is projected along straight line joining it to \( q_{eh}^s \), desired final position of the eye in head (bottom). Because head motion normally causes \( q_{eh}^d \) to move along a more or less straight path in quaternion vector space, this straight projection line actually is predicted path of \( q_{eh}^d \). Its intersection with boundary of EOMR defines horizontal and vertical components of saturated desired eye-in-head position, \( q_{eh}^s \). If torsional component of projected point lies outside EOMR, it is projected along dotted line parallel with torsional, or \( q_t \), axis until boundary of EOMR is reached, thereby defining torsional component of \( q_{eh}^s \) (top). Strictly, \( q_{eh}^d \) should be projected along an isogaze line (see Fig. 6) rather than dotted line, but projection shown here is a reasonable approximation and yields a simpler formula (Eq. A10).

lated subject makes 10 saccades: the first moves from center to 70 deg up and left; the next 8 saccades take the eye first counterclockwise (CCW) and then clockwise (CW) around a square—where CW and CCW are defined from the subject’s viewpoint—and the tenth saccade returns to center. Thicker lines depict the paths of the head’s facing direction, which can be thought of as a spot cast by a laser attached to the subject’s nose, pointing straight ahead when the head is in its reference position. These simulated paths match at least five key characteristics of the 3-D data collected by Glenn and Vilis (1992) and Tweed et al. (1995). 1) The box traced by the facing direction is wider than its tall, meaning that the head contributes more to horizontal than to vertical gaze shifts. This feature was explicitly built into the model (for details see Eq. A5) to mimic Glenn and Vilis’s (1992) data, so its confirmation doesn’t provide any new support for the model, but the remaining four points

FIG. 3. Model predictions of gaze point and facing direction trajectories for saccades to targets at 70° eccentricity on the 45° oblique meridians. Gaze point traces are plotted as thin lines, facing direction traces are thick.
target DR), varying the contributions of eye and head each time, then it lands in different eye-in-space positions, but all these positions lie on the same isogaze curve, so the gaze line nevertheless reaches the target every time.

This behavior is simulated in Fig. 6, which shows final eye-in-space positions for nine saccades to each of four targets, 90° eccentric along the oblique meridians: up and left, up and right, down and left, and down and right. The nine saccades to each target differ in the contributions made by the head and eye. That is, the Donders operator (Fig. 1) was altered from saccade to saccade so that it generated different final head positions even though the target location stayed the same (for mathematical details, see Eq. A5). These alterations can be viewed as simulating either noise in the Donders operator or voluntary decisions to change or override that operator. Figure 6 shows the result: changing the head’s contribution changes the final position of the eye in space, but the eye-in-space vector continues to lie on the same isogaze curve. In other words, internal variability in the contribution of eye and head does not affect the final direction.

**Isogaze curves**

A central feature of the model is the way internal variability is manifested in its overt behavior and, in particular, in its final gaze direction and eye-in-space position. Recall that any one gaze direction can be achieved using infinitely many distinct eye-in-space positions, differing only in their orientations about the line of sight. If we plot all the eye-in-space quaternion vectors corresponding to one gaze direction, they form a curve in 3-D quaternion vector space, an isogaze curve. When the model makes a number of saccades between center and a fixed, eccentric target (e.g., the down-and-right target DR), varying the contributions of eye and head each time, then it lands in different eye-in-space positions, but all these positions lie on the same isogaze curve, so the gaze line nevertheless reaches the target every time.

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**Isogaze curves**

A central feature of the model is the way internal variability is manifested in its overt behavior and, in particular, in its final gaze direction and eye-in-space position. Recall that any one gaze direction can be achieved using infinitely many distinct eye-in-space positions, differing only in their orientations about the line of sight. If we plot all the eye-in-space quaternion vectors corresponding to one gaze direction, they form a curve in 3-D quaternion vector space, an isogaze curve. When the model makes a number of saccades between center and a fixed, eccentric target (e.g., the down-and-right target DR), varying the contributions of eye and head each time, then it lands in different eye-in-space positions, but all these positions lie on the same isogaze curve, so the gaze line nevertheless reaches the target every time.

This behavior is simulated in Fig. 6, which shows final eye-in-space positions for nine saccades to each of four targets, 90° eccentric along the oblique meridians: up and left, up and right, down and left, and down and right. The nine saccades to each target differ in the contributions made by the head and eye. That is, the Donders operator (Fig. 1) was altered from saccade to saccade so that it generated different final head positions even though the target location stayed the same (for mathematical details, see Eq. A5). These alterations can be viewed as simulating either noise in the Donders operator or voluntary decisions to change or override that operator. Figure 6 shows the result: changing the head’s contribution changes the final position of the eye in space, but the eye-in-space vector continues to lie on the same isogaze curve. In other words, internal variability in the contribution of eye and head does not affect the final direction.
and then glides back. How far and in what direction the eye overshoots depends on how much the head contributes to the saccade; in this simulation, as in most human subjects, the head contributes more to horizontal than to vertical gaze motion, and so the overshoot is largely horizontal, as seen by Tweed et al. (1995).

Figure 7 shows another confirmed prediction of the model: that the eye’s initial path is aimed at neither the visual target nor the desired final position of the eye in the head. Arrows at the center of the graph show the initial directions of current desired eye position, \( q_{\text{eh}} \) (white arrow) and final eye position \( q_{\text{eh}}^* \) (black arrow) for one centrifugal saccade. Note that the eye’s initial path lies between these two directions, as in the data of Tweed et al. (1995).

The model also predicts eye-in-head overshoot in the torsional dimension. These overshoots are small for normal eye-head saccades of \(<90^\circ\), but they can be quite marked for larger saccades, or for saccades involving unusual head postures, as in the simulation in Fig. 8. Here the simulated subject starts out with the head tilted 30 deg CCW (i.e., left ear down) and the eyes 10 deg up relative to the head. After the gaze shift, the head is tilted 30 deg CW and the eyes are again 10 deg up relative to head. To get these unusual head postures, the initial and final head positions were generated by overriding the Donders operator. As shown in Fig. 8, the head trajectory is simply a straight line in the torsional dimension, going from 30 deg CCW to 30 deg CW. The eye-in-space trajectory is also mainly torsional but with a small rightward component. What is interesting in the figure is the eye-in-head trace: it begins and ends at the same position in Listing’s plane, but during the gaze shift, it loops a full 80 deg out of the plane in the CW direction. To maximize the loop, I allowed the eye to begin moving 50 ms before the head, a typical lead time for human subjects (Tweed et al. 1995). We return to this simulation, which is the central untested prediction of the model, in the DISCUSSION.

Eye-in-head trajectories

Simulated eye-in-head trajectories for centrifugal and centripetal saccades are plotted in Fig. 7. Eight saccades are shown in all, moving between center and the targets from Fig. 3, oblique targets at 70 deg eccentricity. Centrifugal movements are plotted in thin lines and centripetal in thick. These simulated saccades show the features seen in the human data of Glenn and Vilis (1992) and Tweed et al. (1995), e.g., the eye overshoots its desired final position in the head, \( q_{\text{eh}}^* \), and then glides back. How far and in what direction the eye overshoots depends on how much the head contributes to the saccade; in this simulation, as in most human subjects, the head contributes more to horizontal than to vertical gaze motion, and so the overshoot is largely horizontal, as seen by Tweed et al. (1995).

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Fig. 8. Large, transient deviations from Listing’s law are predicted for eye-head saccades involving head torsion. Here, a simulated subject begins with head tilted 30° CCW and ends with head 30° CW. Eye-in-head position is same at beginning and end of gaze shift—10° up and lying in Listing’s plane—but en route, it loops 8° CW out of the plane.

Discussion

The model is good at predicting the complex, curving paths of head-in-space, eye-in-head, and eye-in-space, even though it was not devised with these 3-D trajectories in mind but was built from a handful of “axioms,” all with clear functional justification: 1) the VOR is switched off in the direction of eye-in-head error because its gaze-stabilizing function is counterproductive during saccades; 2) eye and head are driven by internal and vestibular feedback for speed and accuracy; 3) desired eye-in-head position is saturated to avoid driving the eye to its mechanical limits; 4) the eye moves toward its desired position in space, rather than its final position in the head, to bring the gaze line to the target as fast as possible; and 5) this desired eye position in space is chosen so that Listing’s law of the eye in head will hold at the end of the head motion. As discussed above, the first four axioms are inherited from previous models and are well confirmed by 1- and 2-D eye-head data (Galiana and Guitton 1992; Guitton and Volle 1987; Guitton et al. 1990; Lauritis and Robinson 1986; Pelisson and Prablanc 1986; Pelisson et al. 1988; Tomlinson and Bahra 1986). The fifth will stand or fall based on its key prediction that the eye-in-head should leave Listing’s plane during eye-head saccades (see Site of the Listing operator, below). In what follows, I discuss some issues arising from the simulations in Figs. 3–8 and describe some further predictions of the model.

Trajectories, saturation and Donders’ law

The looping paths in Figs. 3 and 4 occur, at least in the model, because the eye is bearing for a desired position in space, \( q_s \), but is deflected systematically by the saturation function. As described earlier, saturation prevents the eye leaving the oculomotor range; i.e., if \( q_s \) is so far eccentric, relative to the head, that the current desired eye position in the head, \( q_{eh} \), lies outside the effective oculomotor range, EOMR, then the brain computes a saturated desired eye position, \( q_{eh}^s \), which is the position within the EOMR where it will first be possible to foveate the target. This saturated position depends on how the head is going to move, because it is head movement that causes \( q_{eh}^s \) to move toward the EOMR. Because the head moves more horizontally than vertically in most subjects (Glenn and Vilis 1992; Tweed et al. 1994), \( q_{eh}^s \) lies on a more vertical meridian than the unsaturated target, \( q_{eh} \) (see Fig. 2). In other words, the eye initially moves more vertically than the direction of the target because it predicts that the head will do much of the horizontal work. It may seem like a lot of work to predict where the target will enter foveation range, but Eq. A10 shows that a rather simple algorithm does the job.

The model does not perfectly predict the detailed paths of the eye in Fig. 4; in particular, centripetal saccades are usually more curved in the data than in the model. Part of the problem is that paths vary idiosyncratically among subjects (Tweed et al. 1995), so any model would need personalized parameter settings to mimic individuals’ patterns. Another problem is that in the model, curvature is mostly due to the saturation function, whereas in reality, additional factors are at work. For instance real subjects show systematic curves even during head-fixed saccades (Bains et al. 1992), where the current desired eye position is always inside the EOMR, and so saturation should play no role, or at best a small role if we imagine a “soft” saturation. But even if saturation is not the whole explanation for curved saccade paths, Figs. 3 and 4 suggest that it does play an important role, because the 3-D saturation function in Fig. 2, designed on purely functional grounds, predicts the qualitative pattern that is shared by all subjects: CCW loops in the first and third quadrants, CW loops in the second and fourth. This same saturation mechanism explains why the eye-in-head paths in Fig. 6 start out on a path intermediate between the direction of the visual target and the final position of the eye in head: the saturated target, \( q_{eh}^s \), lies on a path between \( q_{eh} \) and \( q_{eh}^s \).

Figure 5 shows that eye-in-space positions violate Listing’s law both statically and dynamically, i.e., between and during eye-head saccades, in both simulations and data. Thus eye-in-space torsion is not fixed at 0; in the simulation traces, the saccade from down and left (DL) to down and right (DR) involves a change in torsional position of ~25° CW, whereas the saccade from UL to UR moves ~25° CCW. As a result, the static, intersaccadic positions DL, DR, UL, and UR cannot all fit in one plane, i.e., Listing’s law fails for the eye in space. The main reason is that the head does most of the horizontal work in eye-head saccades, whereas the eye does the vertical, and so the eye in space moves as if mounted on Fick gimbals (see Glenn and Vilis 1992), an arrangement which produces the kind of twisted, nonplanar distribution of static positions seen in Fig. 5. This arrangement is also responsible for the barrel-shaped gaze paths in Fig. 3: with Fick gimbals, horizontal paths are flat, following lines of latitude, whereas vertical paths bulge out, tracing lines of longitude.

The looping paths in Fig. 5, like those in Fig. 4, are due to the saturation function, but here it is the saturation in the torsional dimension that matters. For example, the movement from DL to DR plotted in Fig. 5 involves a 25° CW change in eye-in-space position. Torsional saturation pre-
vent the eye-in-head from moving too far CW, with the result that the eye-in-space path initially has too little torsion and later arcs toward its target. One consequence of this torsional looping is that the eye in space violates Donders’ law during these movements: it is not possible to fit all these looping paths into any single 2-D surface.

Further, the model predicts that the eye in space also will break Donders’ law statically between gaze shifts. For example, if a subject stands facing a tangent screen, turns the head 20° left, and makes head-fixed saccades between targets on the screen and then does the same with the head turned 20° right, the eye-in-space quaternion vectors are predicted not to lie in a single surface, but to fill out two distinct planes: a plane tilted ~10° left when the head is 20° left, and a plane tilted ~10° right when the head is 20° right. This prediction has recently been confirmed experimentally by Hubert Misslisch (1995; see also Tweed et al. 1993).

Site of the Listing operator

The central new claim of the model is that the eye is driven to a position that has been chosen to fit Listing’s law, and therefore this position must be set by a Listing operator upstream from the comparator that computes eye-in-head motor error. Theoretically, this is not the only possible way to implement Listing’s law. For example, if the oculomotor integrator is leaky in torsion, as suggested by Seidman et al. (1995), eye positions gradually will leak into Listing’s plane, thereby restoring Listing’s law whenever it is broken. However, it is clear that humans and monkeys do not rely on this mechanism for Listing’s law because when supine subjects are rotated in roll, they make torsional quick phases to return to Listing’s plane (Crawford and Vilis 1991; Seidman et al. 1995); i.e., they do not wait for a leaky integrator or any other slow mechanism to restore Listing’s law, rather they make saccades aimed at Listing’s plane. Clearly, then, there is a saccadic mechanism for Listing’s law. This mechanism appears in the model as the Listing operator in Fig. 1, but that operator goes one step further: during eye-head saccades, it aims the eye, not at a position fitting Listing’s law, but at a position that will fit Listing’s law when the entire eye-head movement is complete. This predictive feature can explain Crawford and Vilis’s (1991) observation that monkeys, when they are rotated so that their VOR slow phases carry them out of Listing’s plane, make quick phases that carry them well past the plane.

Another important consequence of this predictive Listing operator is that the eye should leave Listing’s plane transiently during eye-head saccades. The reason, again, is that the desired eye position in space is chosen so that Listing’s law will hold when the head movement is finished. In the middle of the gaze shift, when the head is still far from its final position, the desired eye-in-space position will not generally be consistent with Listing’s law; i.e., to put the eye in its desired position in space, \( q_{bh} \), given the current position of the head, the eye in head must violate Listing’s law. Therefore current desired eye-in-head position, \( q_{bh} \), generally does not obey Listing’s law during an eye-head saccade, and so the eye is predicted to leave Listing’s plane.

Tweed et al. (1995) observed the predicted effects in human eye-head saccades, but the observed and predicted departures from Listing’s plane were small for the saccade tasks they recorded. A more dramatic test will be to have a subject perform the gaze shift that is simulated in Fig. 8. During this movement, the head rotates purely CW, so in the middle of the saccade, the desired eye position in space is rotated far CW relative to the head. As a result, the eye is driven to the CW torsional boundary of the EOMR, a full 8 deg out of Listing’s plane. A complicating factor, neglected for simplicity in the simulation, is that Listing’s plane moves in the head depending on head orientation (Hashwanter et al. 1992), so a 60° CW head rotation, as in this simulation, shifts Listing’s plane ~5° CCW. Therefore the actual prediction is a large CW motion, still reaching the forward boundary of the EOMR, but then looping back to ~5° behind the starting position. If experimental data bear out this prediction, they will provide direct support for the fifth axiom of the model, which implies a Listing operator upstream from the eye pulse generator.

Further predictions and extensions

1) According to the model, head-only saccades, in which the eyes stay fixed in the head, should be impossible; i.e., when subjects attempt head-only saccades, their eyes should still shoot toward the target and then roll back during the VOR stage of the movement. The reason is that the eye is driven toward a target in space and therefore cannot be ordered to stay still in the head.

2) Many human subjects routinely make large gaze shifts with several small eye saccades superimposed on one smooth head saccade. This can be explained by the model if a series of gaze shift commands are sent from the saccade related bursters in the SC to the eye saccadic system, while the head is driven to a single desired position chosen by the override mechanism (see Fig. 1). Alternatively, perhaps a set of gaze targets are coded simultaneously in the SC and all of them are sent, in series, to the eye saccadic system whereas only the most eccentric gaze target is used to drive the head. Either way, the model predicts that the eye in head should deviate systematically from Listing’s law between and during the consecutive eye saccades, landing in Listing’s plane only when the head finishes its motion.

3) Real gaze shifts involve movements of eyes, head, torso, and limbs, and some of these motions are translational as well as rotational. A starting point for modeling translational saccades is provided by the “target locator” equations for 3-D translational and rotational VOR in Virire et al. (1986).

4) As far as it can, the model avoids guessing about the anatomic loci for various computations, because it aims to describe quantitatively what the eye-head saccadic system as a whole is doing rather than how or where. The what question comes logically before the others and enjoys a much stronger database; i.e., current behavioral data give major clues to the overall input-output behavior of the system, whereas the electrophysiological and anatomic data are controversial regarding, e.g., the locations of the comparators relative to the SC, the signals emerging from the SC, the site(s) of the Listing operator(s), and the 3-D kinematic variables coded by the short lead burst neurons and the extraocular motoneurons. As the anatomic database grows, it will fill in the details in whole-system models such as this one or its successors.
APPENDIX: MODEL EQUATIONS

Mathematical representations

For computational convenience, I express the model equations using quaternions, vectors, and matrices. There is no evidence that the brain uses these representations, but then there is no evidence that it uses any other standard notation either. Probably the brain uses some exotic representations, as yet unknown to mathematicians. In this paper, however, I am concerned primarily not with how the computations underlying gaze shifts are implemented neurally, but with expressing clearly what I think the computations are, so I shall stick to standard, quaternion-vector-matrix notation. (For readers unfamiliar with the relevant 3-D geometry, the necessary background is given in Brand [1948], or any kinematics text with a section on quaternions or Clifford algebra.) Formulas in this paper use arithmetic operations, such as multiplication and square root finding, that are somewhat unusual in oculomotor models but this is no cause for concern. It is clear that individual neurons are versatile information-processing devices (see e.g., Poggio and Torre 1978), and even if they were not, work on artificial neural networks has shown that assemblies of very simple elements can perform arbitrarily complex mathematical operations. And finally, I have no doubt that the model described here can be simplified considerably, without significant loss of performance, by using approximations to its equations. But approximations can blur the essential structure of the model, and therefore it is better to describe the theory in exact form first. If the framework is sound, simplification can come later.

Gaze comparator

A comparator in the SC computes dynamic target direction relative to the eye, \( T_e \) (= retinal error = gaze error, or better: desired gaze shift in space expressed in eye coordinates). This, I am assuming, is the command coded by the buildup cells. In Eq. A1 below, \( T_e \) is represented as a unit vector pointing in the direction of the saccade target. By a theorem of kinematics (see any text, e.g., Goldstein 1980), the time rate of change of \( T_e \), called \( \dot{T}_e \), equals the vector cross product of \( T_e \) and \( \omega_{ec} \), the angular velocity of the eye relative to space, expressed in an eye-fixed coordinate system. This cross product formula is shown in the first line of Eq. A1, but because \( \omega_{ec} \) is not one of the variables shown in the flow diagram in Fig. 1, the subsequent lines in Eq. A1 derive an expression for \( T_e \) based on variables that are available.

\[
\dot{T}_e = T_e \times \omega_{ec} = T_e \times q_{eh}^{*} \omega_{eh} d\theta_h
\]

\[
= T_e \times q_{eh}^{*} (\omega_{eh} + \omega_{ah}) d\theta_h
\]

\[
= T_e \times q_{eh}^{*} (\omega_{eh} + 2q_{eh} q_{ah}^{*}) d\theta_h
\]

\[
= T_e \times q_{eh}^{*} (\omega_{eh} d\theta_h + 2q_{eh}^{*})
\]

(A1)

Here the quaternion \( q_{eh}^{*} \) is a neural representation of eye position in the head, \( q_{ah} \) is its time rate of change, and \( q_{eh}^{*} \) is its inverse. \( \omega_{ah} \) is the angular velocity vector of the head relative to space, expressed in head-fixed coordinates; in other words, \( \omega_{ah} \) is the head velocity estimate delivered by the vestibular system. (Strictly, \( q_{ah} \) should be written \( q_{ahb} \), meaning the quaternion of eye position relative to the head in head-fixed coordinates, but because \( q_{ah} \) never is expressed in any other coordinates in this paper, I have omitted the final \( h \) for simplicity.) The symbol \( \times \) indicates the vector cross product, and the juxtaposition \( \omega_{eh} d\theta_h \) is the quaternion product of the vector and the quaternion, in which the vector is treated as a quaternion with a scalar component of 0. Once \( \dot{T}_e \) has been obtained, it is integrated within the SC to obtain the updated estimate of \( T_e \).

Desired head position and the Donders operator

Desired head position is computed from \( T_e \) by the formulas

\[
q_{eh} = q_{eh} q_{ah}^{*}
\]

(A2)

Equation A2 multiplies head position in space \( q_{eh} \) with eye position in the head \( q_{ah}^{*} \) to yield eye position in space, \( q_{eh} \), which then conjugates \( T_e \) in Eq. A3, converting it from eye to space coordinates to yield \( T_e \), target direction in space. The latter then feeds into the operator called Donders to yield \( q_{eh}^{*} \), the quaternion of desired head position (relative to space, expressed in space-fixed coordinates).

As described earlier, Donders’ job is to choose a head position that is comfortable for viewing the target. Because the head usually moves more horizontally than vertically (Glenn and Vilis 1992; Tweed et al. 1995), Donders scales the horizontal and vertical components of desired head position differently, and then it scales the torsional component to fit Donders’ law of the head. For clarity, Donders is best defined in three steps

\[
x = (-T_j)^{1/2}
\]

(A5a)

\[
y = b_x x + b_y y + b_z z
\]

(A5b)

\[
Donders(T_e) = y + (1 - y \cdot y)^{1/2}
\]

(A5c)

Here \( i, j, \) and \( k \) are the unit vectors pointing along the three axes of the coordinate system, \( i \) pointing forward, \( j \) left, and \( k \) up; \( x \) and \( y \) are the coordinates of the vector \( x \) along the \( j \) and \( k \) axes, and \( T \) indicates the dot product of two vectors. Equation A5a quaternion-multiplies \( -T_j \) with \( i \) and then takes the quaternion square root. (If \( p \) is the quaternion square root of \( q \), then the quaternion product \( pp = q \); in terms of rotations, \( p \) has the same axis and direction as \( q \) but only half the amplitude.) This operation yields a quaternion \( x \) representing the shortest rotation taking the vector \( i \) to the vector \( T \). In other words, \( x \) is the head orientation that would point the nose at the visual target while obeying a head version of Listing’s law, with Listing’s plane of the head orthogonal to the vector \( i \). But because the head doesn’t normally rotate far enough to point the nose at the target, Eq. A5b scales the rotation by the factors \( \delta_i \) and \( \delta_j \). In all simulation plots except Fig. 6, \( \delta_i \) is near 0.9 and \( \delta_j \) is near 0.3, reflecting the fact that the head contributes more to horizontal than to vertical gaze shifts; (in Fig. 6, \( \delta_i \) is varied between 1 and 1.4 and \( \delta_j \) between 0 and 0.4 to simulate noise or alteration in the Donders operator.) And because the head doesn’t obey Listing’s law, its position quaternion needs a torsional component, \( \delta_i x + \delta_j y \), where \( \delta_i \) is set at \(-0.15 \) (approximately equal to \(-\delta_i \delta_j / 2 \)) to yield a quadratic Donders surface for the head that matches those seen in the data (Glenn and Vilis 1992) (\( \delta_i = 0 \) would yield a planar surface, i.e., Listing’s law). Finally, Eq. A5c converts the vector \( y \) into a unit quaternion representing desired head position in space.

Again, the values given for \( \delta_i \), \( \delta_j \), and \( \delta_k \), and indeed the whole computation in Eqs. A5a–c, are merely defaults. It is clear that we can control voluntarily how much motion the head contributes in all three dimensions; i.e., the Donders operator can be voluntarily altered or overridden. Further, a more realistic model, particularly one involving torso movements, would require a more sophisticated way of choosing the final head position than just scaling by three factors \( \delta_i \), \( \delta_j \), and \( \delta_k \) as in Eq. A5b, but this simple scheme seems satisfactory for torso-fixed saccades.

Head pulse generator

The head is driven by a velocity command \( \dot{q}_h \) representing the rate of change of head position

\[
\dot{q}_h = P_v [V_v (q_{eh}^{*} q_{ah}) \cdot q_{ah}]
\]

(A6)

where \( V_v \) is the operator that takes the vector part of a quaternion.
If we write \( v \) for \( V_p(q \vec{z} q^{-1}) \), then the head pulse generator \( P_h \) can be defined by

\[
P_h(v, q_h) = 50 v q_h/(1 + 20|v|) \tag{A7}
\]

Pulse generator nonlinearities usually are modeled using exponentials (Robinson 1975; van Gisbergen et al. 1981), but the division by \( 1 + 20|v| \) used here is nearly equivalent and computationally simpler. Also, a more realistic model would have the head driven by a signal coding some mixture of jerk, acceleration, velocity, and position, rather than simply velocity, and would pass this signal through a higher-order plant, but such complications would not alter the basic kinematics under study here. Note that the output of the pulse generator is the \textit{quaternion} velocity of the head, \( q_h \)—i.e., the time derivative of the quaternion of head position, \( q_h \)—and not the \textit{angular} velocity of the head, which would be given by \( \omega_{\text{head}} = 2q_h q_h^\dagger = 100 v/(1 + 20|v|) \).

\textbf{Desired eye position and the Listing operator}

Desired final eye position in the head, \( q_{\text{des}}^* \), is computed by the formula

\[
q_{\text{des}}^* = \text{Listing}(q_{\text{desired head position}}^* \cdot T \cdot q_{\text{desired direction}}^*) \tag{A8}
\]

The \textit{Listing} operator takes as input the unit vector \( q_{\text{desired head position}}^* \cdot T \cdot q_{\text{desired direction}}^* \), representing the direction that the saccade target will have relative to the head when the head is in its desired position \( q_{\text{head position}}^* \), and yields as output a quaternion \( q_{\text{desired eye-in-head position}}^* \) representing desired eye-in-head position, which fits Listing’s law. To create this output, Listing quaternion multiplies \(-q_{\text{desired eye-in-head orientation}}^* \cdot T \cdot q_{\text{desired eye-in-head position}}^* \) by \( g_r \), which is the primary gaze direction of the eye expressed in head-fixed coordinates, and takes the quaternion square root, to yield a desired eye-in-head orientation, \( q_{\text{desired eye-in-head orientation}}^* \), that obeys Listing’s law and that points the gaze line in the desired direction. In the simulations, \( g_r \) is set equal to \( i \), the forward pointing coordinate axis although in reality it moves slightly depending on head position (Haslwanter et al. 1992).

\textbf{Eye saturation and pulse generation}

For clarity, the computation yielding saturated desired eye position in the head can be broken down into three steps

\[
q_{\text{desired eye position}}^* = q_t q_{\text{desired eye position}}^* \tag{A9a}
\]

\[
q_{\text{saturated desired eye position}}^* = q_{\text{desired eye position}}^* q_{\text{sat}} \tag{A9b}
\]

\[
q_{\text{saturated desired eye position}}^* = \text{Sat}(q_{\text{desired eye position}}^*, q_{\text{saturating eye position}}^*) \tag{A9c}
\]

Equation A9a combines desired head-in-space position with desired eye-in-head position to yield \textit{desired eye-in-space position}, \( q_{\text{desired eye position}}^* \). This is then divided by \( q_h \), the system’s internal estimate of actual head position, to yield the \textit{current desired eye-in-head position}, \( q_{\text{desired eye position}}^* \), in Eq. A9b.

Equation A9b introduces the important function \textit{Sat}, a 3-D version of Guitton and Volle’s (1987) one-dimensional saturation box. As we saw in Fig. 2, 3-D saturation involves projecting an overly eccentric current desired eye position \( q_{\text{desired eye position}}^* \) into the effective oculomotor range, EOMR, so that the saturated desired eye position \( q_{\text{saturated eye position}}^* \) is that position on the boundary of the EOMR where the target will first be foveable. The model’s algorithm for this projection rule is given by

\[
q_{\text{saturated eye position}}^* = \text{Sat}(q_{\text{desired eye position}}^*, q_{\text{saturating eye position}}^*) \tag{A10}
\]

\textbf{VOR shutoff}

As noted earlier, we know from 1- and 2-D studies that the VOR is weakened or shut off in the direction of the saccade. In 3-D, new questions arise, e.g., should the VOR be shut off in the direction of gaze error or head-in-space motor error or eye-in-head motor error? There are no experimental data on the precise direction of VOR shutoff, and, in any case, the model in this paper operates very well even if this direction is very imprecisely controlled. But it is an interesting theoretical point that if the VOR were switched off in the direction of current eye-in-head motor error, then it could do a surprising amount to steer the gaze line to the target, even in the absence of other signals guiding the eye. In other words, this sort of precisely directed VOR could provide a valuable backup if other parts of the saccadic system were malfunctioning. The following equations achieve precise VOR shutoff of this type.

\[
x = q_{\text{desired eye position}}^*; u = V_e(x)/|V_e(x)| \tag{A11}
\]

If \( x_0 < C \), \( m = 1 \); else, \( m = (1 - x_0)/(1 - C) \);

\[
M = \text{max}^m - 1; \tag{A12}
\]

\[
\dot{q}_{\text{vort}} = (M u_{\text{max}} q_{\text{null}})/2; \tag{A13}
\]

\( M \) is a 3-by-3 matrix, \( I \) is the 3-by-3 identity matrix, and \( u_{\text{max}} \) is the 3-by-3 matrix obtained by matrix-multiplying the column vector \( u \) by its transpose \( u^T \). The quaternion \( x \) represents current, unsaturated eye-in-head motor error, and \( C \) is a constant equal to \( \cos(A/
2), where \( A \) is the VOR shut off amplitude. That is, when eye-in-head error exceeds \( A \), the VOR is switched off completely. Then as eye-in-head error falls from \( A \) toward 0 (i.e., as its scalar component \( x \) rises from \( C \) toward 1), the VOR gradually turns on again. In the simulations, \( A = 20^\circ \) and therefore \( C = 0.985 \). It is a simple matter to verify that the above equations switch off the VOR in the direction of eye-in-head motor error \( x \), and turn it on again gradually as motor error falls.

**Code**

The following 2 m-files, esdot.m and eyespace.m, implement the model in Matlab. In these files, quaternions are expressed as 4-by-4 matrices of real numbers, with the result that all the quaternion algebra is done using Matlab’s built-in matrix operators, so no extra m- or mex-files are needed. It is also possible to represent quaternions in Matlab as 2-by-2 matrices of complex numbers, but then the code runs slightly slower and certain operations involving quaternion vectors are more complicated.

```matlab
function xdot = esdot(t,x)
% Convert input vector x into 4-by-4 matrices (quaternions)
% Convert to derivative vector xdot for output
% Gaze comparator
% Head motor error, Head velocity
% Desired eye position in space and head pulse generator
% Desired head position in space; Eye-in-head error Auges.
% Basis quaternions, defined in eyespace.m (below)
% VOR
% VOR matrix; Head angular velocity
% VOR eye velocity command
% Saturation
% Square eccentricity of current desired eye position in hor-vert plane
% Radius of EOMR in hor-vert plane if alpha > radius * radius, beta = s(2) * f(2) + s(3) * f(3); gamma = f(2) * f(2) + f(3) * f(3); alpha = -2 * beta + gamma; b = 2 * (alpha - beta); c = alpha - radius * radius; Quaternion coefficients
% Project s into EOMR in hor-vert plane
% MaxTorsion = sqrt(1.25 - alpha/(radius * radius)) * sin(4 * pi/180); if abs(s(1)) > maxTorsion, s(1) = sign(s(1)) * maxTorsion; end
```

References


Crawford, J. D., and Vilis, T. Axes of eye rotation and Listing’s law during VOR rotations of the head.


Guitton, D. and Volle, M. Gaze control in humans: eye-head coordination...


