

GEOMETRIC RELATIONS OF EYE POSITION AND VELOCITY VECTORS DURING SACCADES

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Abstract—Measurements of angular position and velocity vectors of the eye in three human and three monkey subjects showed that: (1) position vectors lie roughly in a single plane, in accordance with Listing's law, between and during saccades; (2) primary position of the eye is often far from the centre of the oculomotor range. (3) saccades have nearly-fixed rotation axes, which tilt out of Listing's plane in a systematic way depending on current eye position. Findings 1 and 3 show that saccadic control signals accurately reflect the properties of three-dimensional rotations, as predicted by a new quaternion model of the saccadic system; models that approximate rotational kinematics using vectorial addition and integration do not predict these findings.

Eye movements	Saccades	Listing's law	Eye torsion	Integration	Motor error
Quaternions					

INTRODUCTION

According to a new model of the saccadic system based on the three-dimensional properties of eye rotations (Tweed & Vilis, 1987), the angular position vectors of the eye should all lie in a single plane during both fixation and saccades. Further, the velocity vectors of the eye should also lie in planes, but in distinct planes which depend on current eye position. The purpose of this study was to test those predictions.

The idea that eye positions are associated with planes goes back to the 19th-century physiologists Donders, Listing and Helmholtz. The starting point of their investigations was the geometric fact that to every gaze direction there correspond infinitely many possible eye positions, differing only in their orientations about the line of sight. Donders (1847) discovered that, for steady fixation with the head upright, the actual positions of the eye are restricted in such a way that there is only one eye position for every gaze direction (Helmholtz, 1867). Put another way, Donders found that the eye is restricted to a two-dimensional subspace of the three-dimensional space of all possible orientations.

By observing the systematic tilt of after-images in different gaze directions, Listing and Helmholtz (Helmholtz, 1867) were able to determine which two-dimensional subspace the eye

is restricted to. Their result, now known as Listing's law, is most simply described if we express eye positions in terms of the axes of their rotational displacements from a particular eye position known as primary position. Then Listing's law states that the eye assumes only those positions that can be reached from primary position by a single rotation about an axis in Listing's plane, which lies orthogonal to the gaze direction in primary position.

The above is a standard statement of Listing's law, but it is incomplete because it relies on the notion of primary position, which we have not defined. A more self-contained statement, which was proved by Helmholtz (1867) to be equivalent to the one above, is that for any eye position, e , there is an associated plane—which we shall call the displacement plane of e , DP_e —such that the eye assumes only those positions that can be reached from e by a single rotation about an axis in DP_e . It can be shown mathematically that the displacement planes for different eye positions do not coincide, and that there is exactly one eye position in which the gaze direction is orthogonal to the displacement plane. This unique eye position is called primary position; its displacement plane is called Listing's plane. A derivation of these facts is given in Tweed, Cadera and Vilis (1990).

Listing's law is illustrated in Fig. 1. The centre eye position is primary position, and Listing's plane is the plane of the paper. The eight

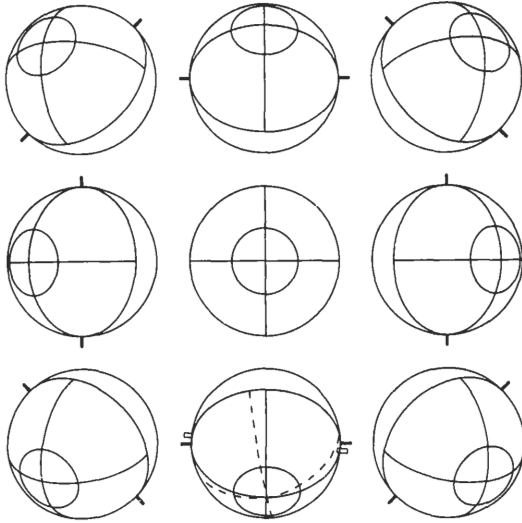


Fig. 1. The nine eye orientations drawn in solid lines accord with Listing's law, because they are attainable by rotating from primary position (centre) about axes lying in Listing's plane (the plane of the paper). The position drawn in dashed lines at bottom centre does not fit Listing's law, because the rotation to this position from primary position occurs about an axis tilted out of Listing's plane.

eccentric eye positions drawn with solid lines fit the law; the axes of their rotational displacement from primary position, all lying in Listing's plane, are drawn as thin black lines. At bottom centre, the eye position indicated by dashed lines violates Listing's law; the axis of its displacement from primary position, drawn as a white line, tilts out of Listing's plane. Again, since every eye position fitting Listing's law has its own displacement plane, this figure could have been drawn with any eye position e at the centre, and DP_e lying in the plane of the paper. But then the gaze direction in position e would not be straight out, orthogonal to the paper.

Listing and Helmholtz used their afterimage technique to demonstrate Listing's law in human subjects during steady fixation with the head upright. A more precise assessment of the law, also with human subjects and under the same conditions, but using the search coil method to measure eye position, was conducted by Ferman, Collewijn and Van den Berg (1987b). They found that the eye positions corresponding to a given gaze direction varied by about 5 deg of rotation about the line of sight, implying stochastic deviations of ± 2.5 deg from Listing's law. Ferman et al. also found a systematic deviation from Listing's law, showing that in nasal gaze directions, the eye

was consistently rotated as much as 50% more than would be predicted by the law. They noted, however, that this deviation could be removed by changing the estimate of the primary position of the eye, leaving a smaller systematic deviation from the law in all quadrants. In the present study, we show that a careful determination of primary position removes almost all systematic deviation from Listing's law.

The study of Listing's law is of basic importance for understanding the three-dimensional operation of the oculomotor system, and also has wider significance within motor physiology. It has been known for some time that the law does not hold under all conditions. It fails, for example, during sleep (Nakayama, 1975). Thus the law is not a consequence of orbital geometry or extraocular muscle mechanics. Rather, it is a clue to the organization of the neural signals that activate the muscles. Listing's law is therefore a precisely characterized example of a synergy, or neurally-imposed constraint on the coactivation patterns of muscles, which is an important concept in general motor control.

Velocity planes

To keep the angular position vectors in Listing's plane, the angular velocity vectors of the eye must also lie in planes (proof in Tweed et al., 1990). While this fact is implicit in Helmholtz's work on ocular kinematics, explicit predictions regarding the geometry of eye velocity vectors are much more recent. In 1981, Robinson and Zee proposed that eye velocity vectors during saccades all lie in Listing's plane. However, this arrangement would actually disallow fixed-axis saccades between positions fitting Listing's law. The quaternion model of the saccadic system (Tweed & Vilis, 1987) makes the contrary prediction that the velocity vectors lie in distinct planes which depend on eye position. This arrangement, which is the one needed for fixed-axis saccades preserving Listing's law, requires precise, position-dependent control of the activation ratios of the three pools of burst neurons which are believed to supply the eye velocity commands to motoneurons during saccades. The quaternion model therefore implies that the mechanisms responsible for Listing's law are at the level of, or upstream from, the burst neurons. In this paper we confirm that eye velocity vectors are distributed as predicted by the quaternion model.

Thus the observations that eye position vectors and velocity vectors lie in particular

planes during saccades provide corroboration for the quaternion model for the saccadic system. The essential novelty of this model is that it incorporates operators that reflect the mathematical, nonvectorial properties of three-dimensional rotations where previous models—here called vector models—have assumed that eye position and velocity signals could be added and integrated like vectors. The models and their connections with Listing's law are described in detail in the Discussion.

METHODS

Data acquisition

Experiments were performed on three adult male human subjects and three *Macaca fascicularis* monkeys. To measure eye position and velocity in three dimensions, we used the modification of the eye coil-magnetic field technique described in Tweed et al. (1990).

In human subjects, the movements of the left eye were monitored using a Skalar annulus: a silicone rubber ring containing two effectively orthogonal search coils that adheres to the sclera by suction (Ferman, Collewijn, Jansen & Van den Berg, 1987a). In a darkened room, the subject made saccades between target LEDs arrayed on a black hemispheric dome 1 m from his left eye. LEDs were lit and extinguished in programmed sequences by a Radio Shack Color Computer. The subject sat in three alternating orthogonal magnetic fields (frequencies 62.5, 125 and 250 kHz) with its head stabilized on a bite board. The board was positioned so that the sagittal plane of the subject's head was vertical and the pitch angle felt natural, and his left eye was at the centre of the three magnetic fields, which coincided with the centre of the dome with the target LEDs. The pitch angle of the subject's head was measured. Three voltages from each eye coil were sampled either 100 or 1000 times/sec. Eye position quaternions and eye velocity vectors were computed off line. Positions and velocities so computed were accurate to within less than 10% throughout the oculomotor range.

Data collection was identical for monkey subjects, with the following exceptions. In preparation for the experiments, each monkey underwent two sterile surgical procedures under sodium pentobarbital anesthesia. First, a skull cap of dental acrylic was securely fastened to the animal's head. Later, two preformed enameled copper search coils of 5 mm diameter were

implanted subconjunctivally in the left eye. Since the locations of the coils on the eye do not significantly affect the accuracy of the eye position computations (Tweed et al., 1990), the coils were positioned for maximum stability: both were placed nasally, one inferior and one superior, approximately orthogonal to each other. Monkeys were trained to make saccades, for grape drink reward, between target LEDs located on a black tangent screen at a distance of 1 m. During experiments, the monkey sat in a primate chair, its head immobilized in the magnetic fields using bolts implanted in the skull cap.

Coil stability

Accurate measurement of eye position requires that the eye coils remain stationary on the eye. In monkeys, the coils become attached to the globe by scar tissue within a week of implanting. In humans, however, a coil will sometimes fail to adhere to the sclera and may slip, particularly in the torsional direction, during an experiment. These cases are identifiable in several ways. First, the coil may be seen to move on the subject's eye before recordings begin. Second, the records may show a steady drift in torsion such as is never seen in monkey records. And third, during or after the recording session, the lead wires will not be lined up with the same scleral vessels as at the beginning of the experiment. Data rendered dubious by any of these findings were not used. The possibility of undetectable coil slip—noncumulative back and forth rolling of the annulus on the eye—while probably small, cannot be ruled out. However, we believe that all qualitative findings made in human subjects in this study are physiological, because they have also been observed in the monkey data.

Data presentation

We use the angular position vector \mathbf{q} and the angular velocity vector $\boldsymbol{\omega}$ for describing eye position and velocity. Details of these representations and the algorithms for computing them from search coil signals are given in Tweed et al. (1990).

The angular position vector \mathbf{q} (actually the vector part of the quaternion for that position) expresses the three-dimensional orientation of the eye in terms of its rotational displacement from some reference position—usually primary position. The vector lies along the axis of the rotation according to the right hand rule; its

length is $\sin(a/2)$, where a is the amplitude of the rotation. The length of \mathbf{q} is thus nearly proportional to a within the oculomotor range. The component q_T indicates the amount of rotation away from reference position in the clockwise direction (i.e. about a forward-pointing axis); q_V is the downward component and q_H is the leftward component.

The angular velocity vector ω is defined similarly: at any moment, a rotating body has an instantaneous axis of rotation; the angular velocity vector is defined to lie along this axis, oriented according to the right hand rule. The length of the vector is proportional to the speed at which the body is spinning about its axis, in deg/sec. That is, the vector lies along the spin axis and its length equals the rate of spin.

Coordinate system

In almost all our data plots of eye position vectors, the origin of the coordinate system ($\mathbf{q} = \mathbf{0}$) corresponds to primary position, and the plane $q_T = 0$ (i.e. the plane in which the torsional

component of eye position is zero) corresponds to Listing's plane. Exceptions to these conventions are noted where they occur.

As described in Tweed et al. (1990), eye position vectors are first computed relative to the eye position corresponding to the centre light in the target array (rather than relative to primary position) and in a coordinate system defined by the magnetic fields. It is then necessary to locate primary position and to transform the data so that they describe rotations relative to primary position and in a coordinate system where Listing's plane is aligned with $q_T = 0$. Our procedure, based on 10,000 different eye positions, yields a robust estimate of primary position for this purpose.

RESULTS

Saccade trajectories

Position and velocity traces for six saccades made by a monkey are shown in Fig. 2. Position

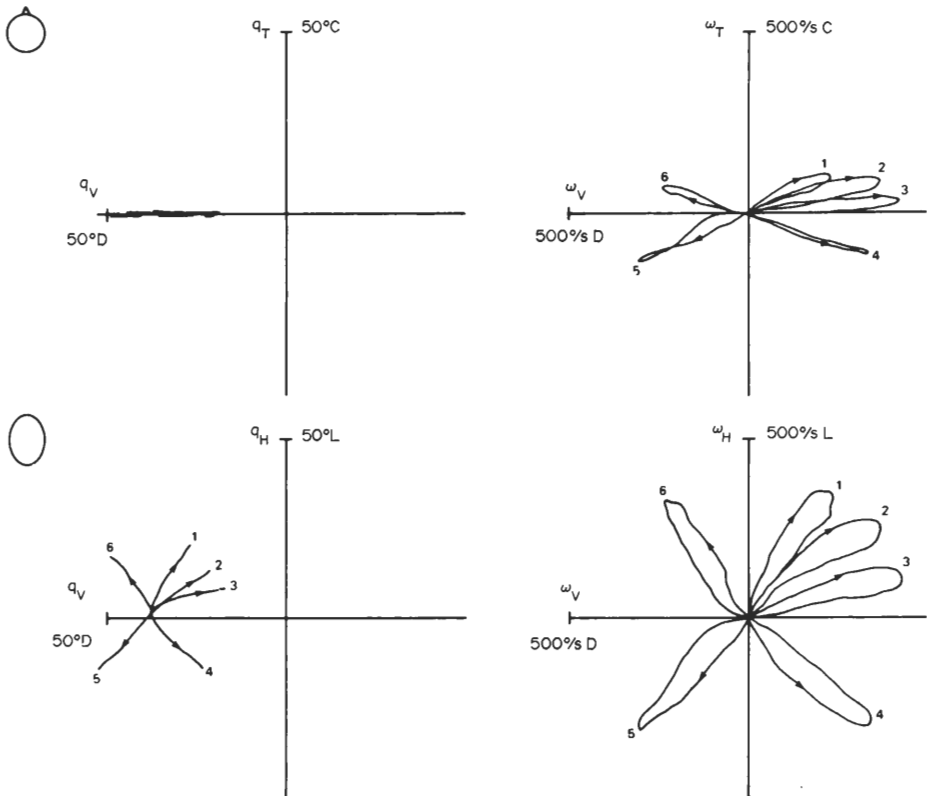


Fig. 2. Position and velocity traces for six saccades by a monkey. Position traces are on the left, velocity on the right. As indicated by the heads, the top row shows views from above the subject, bottom row shows views from behind. Coordinate axis labels C, D, L indicate Clockwise, Down and Left rotation directions. The position traces lie very close to Listing's plane (abscissa in the above views), while the velocity traces do not. Subject BA.

traces are on the left. The upper plot shows the angular position vectors from a viewpoint above the subject; the small inset head indicates that, in this view, the subject's nose points in the positive direction along the ordinate and his right ear is to the right. The lower plot shows the position vectors from a viewpoint behind the subject. The origin of the coordinate system is primary position, and the $q_T = 0$ plane (the abscissa in the above view) is Listing's plane.

These position traces are best interpreted using the right hand rule. For example, consider the saccade labeled 1. The initial eye position is to the left of the centre in the behind plot. The above view shows that the torsional (q_T) component is small, so by the right hand rule this saccade begins about 35 deg directly down from primary position. At the end of the saccade, the vector is to the left and above primary position, again with negligible torsion: by the right hand rule, this final eye position is rotated about 32 deg down and left from primary position. This plot also illustrates a short cut to angular position interpretation: if torsion is negligible, then rotating the behind view 90 deg counterclockwise gives an accurate picture of the movement of the gaze point. But we have kept the plots unrotated to preserve the consistency of the three-dimensional traces and the interesting geometric relations between eye position and velocity vectors and gaze direction.

The velocity traces for these same six saccades are plotted on the right side of Fig. 2, using the same viewpoints as for the position plots. Again, the right hand rule is the key to interpretation. For example, saccade 1 begins at zero velocity (the origin). During the acceleration phase, the velocity vector grows, in the up and right direction, toward peak velocity. Thereafter the velocity vector shrinks as the eye decelerates to zero. By the right hand rule, the eye is rotating up and left throughout this movement.

The narrow loops formed by the velocity vectors illustrate the important point that, for almost all saccades, the direction of the angular velocity vector is nearly constant throughout the saccade. That is, to good approximation a saccade has a unique axis of rotation. In fact, the loops in Fig. 2 are about as wide as any velocity trajectories (excluding occasional idiosyncratic movements and blinks) that were observed in monkeys or humans (Fig. 8 is more typical): thus if we restrict attention to mid-

saccadic velocities (> 150 deg/sec), the largest commonly observed variation in rotation axis direction was about 30 deg. The curvature that was present was very consistent for a particular starting and final position, with the velocity trajectory approximating the same trace with each repetition. Figure 2 also shows that ω , unlike \mathbf{q} , is not confined to Listing's plane. Rather, the velocity vectors tilt out of the plane, and this tilt is present from the very beginning of the saccade to the end.

Listing's law

The geometric arrangement of the eye position vectors of one human subject is illustrated in Fig. 3. The dots in this figure are about 10,000 eye position vectors, sampled over about 100 sec while the subject made spontaneous saccades in the light throughout the oculomotor range. The left side shows the cloud of vectors as it appears from a viewpoint behind the subject. The oculomotor range in this case is about 80 deg left to right and the same up and down.

The side view shows that the cloud of vectors is actually a pancake: it is squashed flat in the forward/backward dimension. Since an unconstrained rotating body would generate position vectors distributed uniformly in three-dimensional space, these plots reveal that eye position is severely constrained, restricted to within about 5 deg of a single plane, in keeping with Listing's law. The eye positions have been plotted over a human face in profile to show the orientation of Listing's plane with respect to the head: in this case, the plane is roughly coronal and makes an angle of about 75 deg with a line between the external auditory meatus and the centre of the eye.

At the bottom of the figure, right-side views of a series of five slices through the plane show that it is of roughly uniform thickness, shape, orientation and location.

Quantitative accuracy of Listing's law

We calculated the planes of best fit to 16 clouds of eye position vectors collected from six subjects. A measure of the deviation of each cloud from Listing's law is provided by the standard deviation, σ , of the distance from the quaternion vectors to the plane (i.e. the *error*). This measure of deviation is justified because plots of errors (distances of quaternion vectors from the plane) show them to be roughly normally distributed. The average σ for humans (from six measurements in three subjects) was

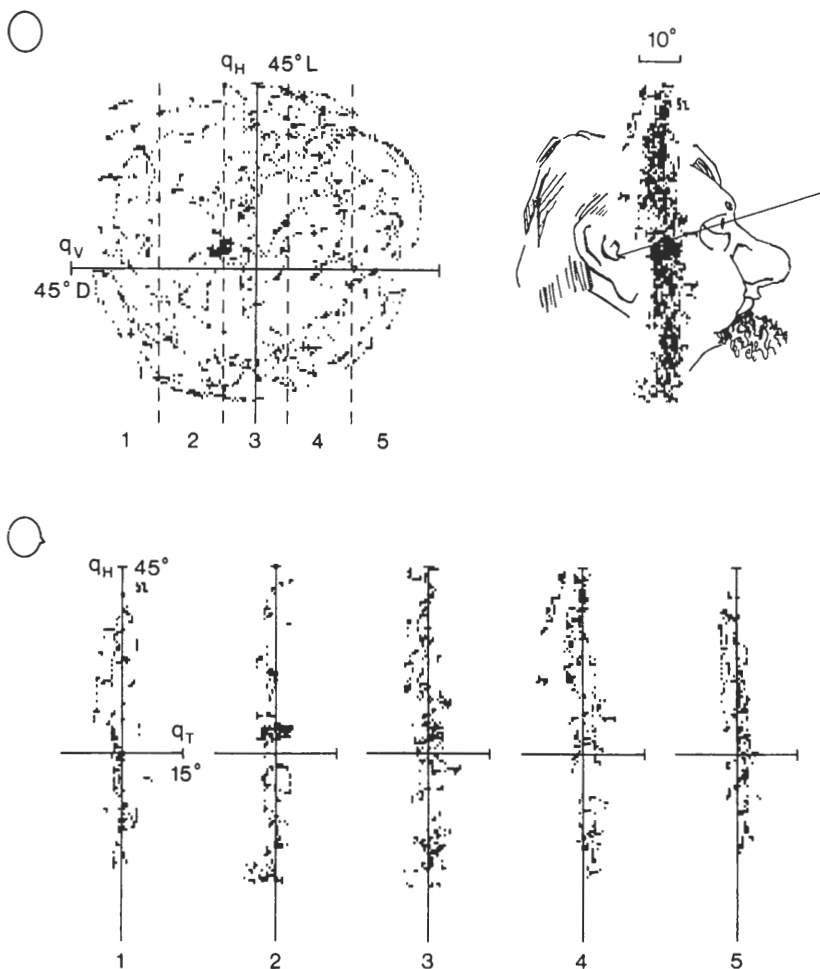


Fig. 3. Angular position vectors lie in a single plane in accordance with Listing's law. Top row: the side view on the right reveals the planar arrangement of the vectors. Bottom row: side views of five slices through the cloud (cuts indicate by vertical dashed lines in behind view, top row). Subject TV.

1.5 deg (range 1.2–1.9); for monkeys (from 10° measurements, in three subjects) it was 0.8 deg (range 0.5–1.1). Plots of error vs time for spontaneous saccades show rapid fluctuations between positive and negative values, with little in the way of long term trends.

Curvature of Listing's surface

What is the source of the deviation from Listing's law: do the quaternion vectors form a curved surface rather than a strict plane, or are they arranged in a flat plate whose thickness accounts for the observed deviation? A quantitative measure of the contribution of surface curvature to σ is obtained by fitting \mathbf{q} to a quadratic surface instead of a plane. That is, instead of approximating the torsional component of \mathbf{q} , q_T , with an affine, or first-order polynomial, function of the vertical and hori-

zontal components q_V and q_H thus:

$$q_T = f + f_V q_V + f_H q_H, \quad (1)$$

we use a second-order function:

$$q_T = f + f_V q_V + f_H q_H + f_{VV} q_V q_V + 2f_{VH} q_V q_H + f_{HH} q_H q_H. \quad (2)$$

The second-order coefficients (f s with two subscripts), which indicate the curvature of the surface, averaged 0.15 for humans (range 0–0.37) and 0.19 for monkeys (range 0.05–0.48). Because q_V and q_H are < 0.4 within the oculomotor range, the second-order coefficients multiply very small numbers, which diminish their contribution to the shape of the surface. Thus these values correspond to rather subtle curvature. A typical cloud of eye position vectors from a human subject (position plane

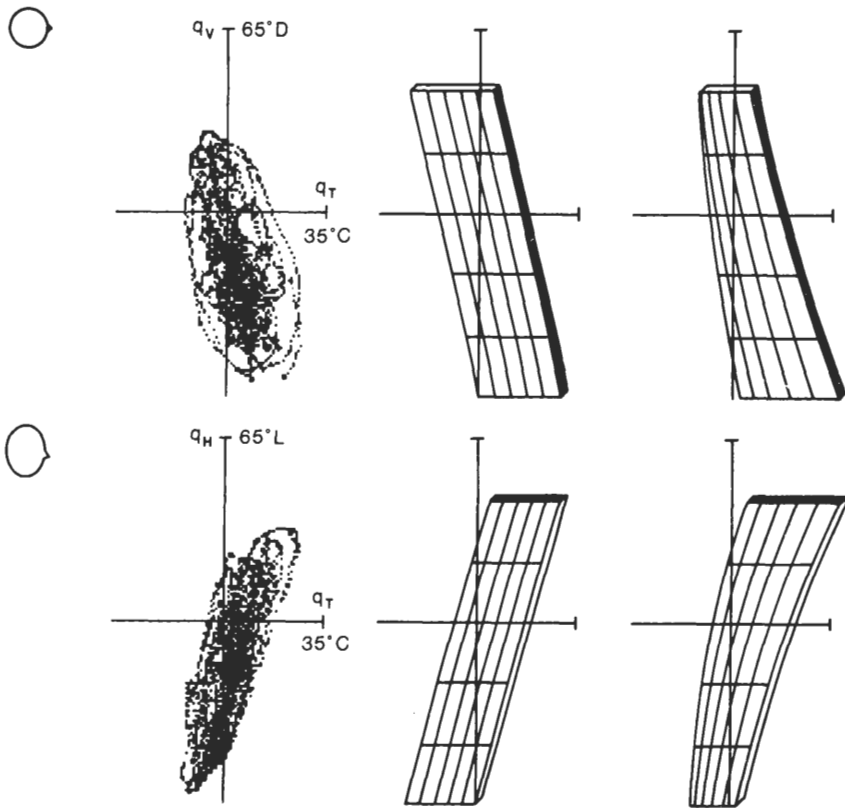


Fig. 4. The cloud of eye position vectors is approximately planar. Left column: Eye position vectors sampled during 100 sec of spontaneous saccades by a human subject. Unlike other eye position plots in this paper, the coordinate system here is aligned with the magnetic fields and not with Listing's plane and the primary gaze direction. Thus the plane formed by the eye position vectors (Listing's plane) is not viewed edge-on. Middle: A plane of best fit tilts slightly left and down. Right: A second-order curved surface of best fit deviates only slightly from the planar approximation. Subject DT.

not viewed edge-on) is shown at the left in Fig. 4, with its first and second-order approximations at centre and right.

To see whether these curved surfaces gave a better fit than the planes to the eye position data, we computed the standard deviations σ' of the errors (distances from \mathbf{q} to the surface along the q_T direction) and compared them with the corresponding σ for the planes. On average, the deviation from the curved surface was smaller by only 10% (range 0–30%). Plots of error vs time were qualitatively indistinguishable from similar plots for planar approximations. Since it seems unlikely that a higher-order curved approximation to the vector cloud would give a significantly smaller deviation, we conclude that curvature of the cloud formed by the angular position vectors accounts for only about 10% of the deviation from Listing's law on average. Further evidence that curvature was unimportant is that the second-order coefficients were

not so consistent for any one subject as were the first-order ones. Part of the observed curvature could also have been measurement artifact: electronic irregularities in the coil system can sometimes introduce slight curvature into "synthetic" Listing's planes generated by a gimbals system, but the curvatures of these are less than half the maximum seen in real subjects.

Qualitatively, shapes of the second-order surfaces showed some consistency within subjects, so that a subject who gave a, say, concave forward Listing's surface in one experiment was likely to show the same qualitative shape in the other session. However, different subjects showed a variety of different shapes. The most common shape was a shallow, warped saddle, which was observed in half of the 16 measurements. All saddles were oriented to indicate excess clockwise eye torsion in the upper medial and lower temporal quadrants, and excess counterclockwise torsion in the other two quadrants.

The finding is in qualitative agreement with the findings of Ferman et al. (1987b) regarding systematic deviations from Listing's law.

In summary, we conclude that 90% of the deviation from Listing's law originates from the thickness of the eye position vector cloud as it clusters around Listing's plane. The thickness of the cloud we attribute to biological noise in the oculomotor system, since noise introduced by the electronics was less than 0.3 deg. Whether this biological noise arises in signals coding torsional eye position, or originates further upstream, is not revealed by our analysis. And finally, there was some trend to the torsional deviations: in two cases where human subjects made large numbers of successive clockwise gaze shifts uninterrupted by any counterclockwise movement, the displacement plane of the eye was moved about 2 deg backwards; that is, the eye maintained an unusually counterclockwise torsion. Conversely, during uninterrupted counterclockwise gaze motion, the eye maintained a comparable clockwise torsion. These findings accord with the observations of Ferman, Collewijn and Van den Berg (1987c).

Location of primary position

The orientation of Listing's plane relative to the head is best described using the vector of length one which points forward orthogonal to the plane. This is the gaze vector of primary position, \mathbf{g}_p . Figure 5 shows the \mathbf{g}_p 's for the left eyes of six subjects. Where more than one plane was measured for a subject, the two most widely-separated \mathbf{g}_p 's are plotted. It is clear that \mathbf{g}_p 's were fairly reproducible: the directions for any one subject tended to lie within about 5 deg of some average value, though the monkey represented by the open diamonds had two vectors separated by 15 deg. Agreement between subjects was much poorer, particularly when subjects from different species were grouped together.

In the coordinate system of Fig. 5, the horizontal plane tilts 20 deg below the plane joining the external auditory meati and the centres of the eyes; that is, it coincides with earth horizontal when the human subject's head is at a natural pitch angle. In the side view (at bottom) primary position for the monkeys can be seen to range from 15 to 37 deg up above this plane, while for humans it ranges from about 5 deg up to 17 deg down. In most subjects primary position was not at the centre of the oculomotor range. For example, the plot of the oculomotor range of the

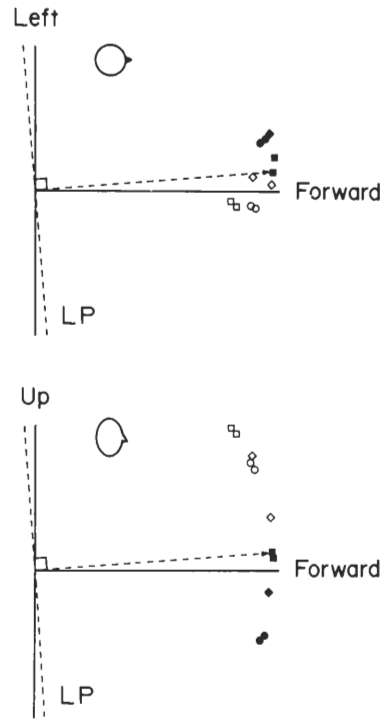


Fig. 5. Primary gaze directions for the left eyes of six subjects are shown from above and the right side. Open symbols represent monkeys, solid symbols represent human subjects. Dashed lines indicate how the primary gaze directions are related to the orientations of Listing's plane (LP): the directions are orthogonal to the planes. Primary gaze direction tends to be horizontally straight ahead and up for monkeys, left (temporal) and vertically straight ahead or down for humans. Subject key: \square , BA; \circ , MA; \diamond , FR; \blacksquare , TV; \blacklozenge , EV; \bullet , DT.

human subject in Fig. 4 shows primary position (the origin of the coordinate system) halfway to the edge of the cloud of position vectors, a position approx. 15 deg below the centre of the range.

Horizontal deviations of primary position were small. All subjects had primary gaze vectors within about 15 deg of a parasagittal plane; the 3 monkeys in particular showed nearly straight forward \mathbf{g}_p 's. Human subjects tended to point slightly left (temporal), as was also found by Ferman et al. (1987b), but the horizontal deviations were mostly within the range of measurement error.

Measurements of the absolute orientation of Listing's plane (and therefore of primary position) are less accurate than measurements of eye position relative to any given reference, because to find primary position we need to know the direction of gaze and the orientation of the head relative to the magnetic fields at some instant.

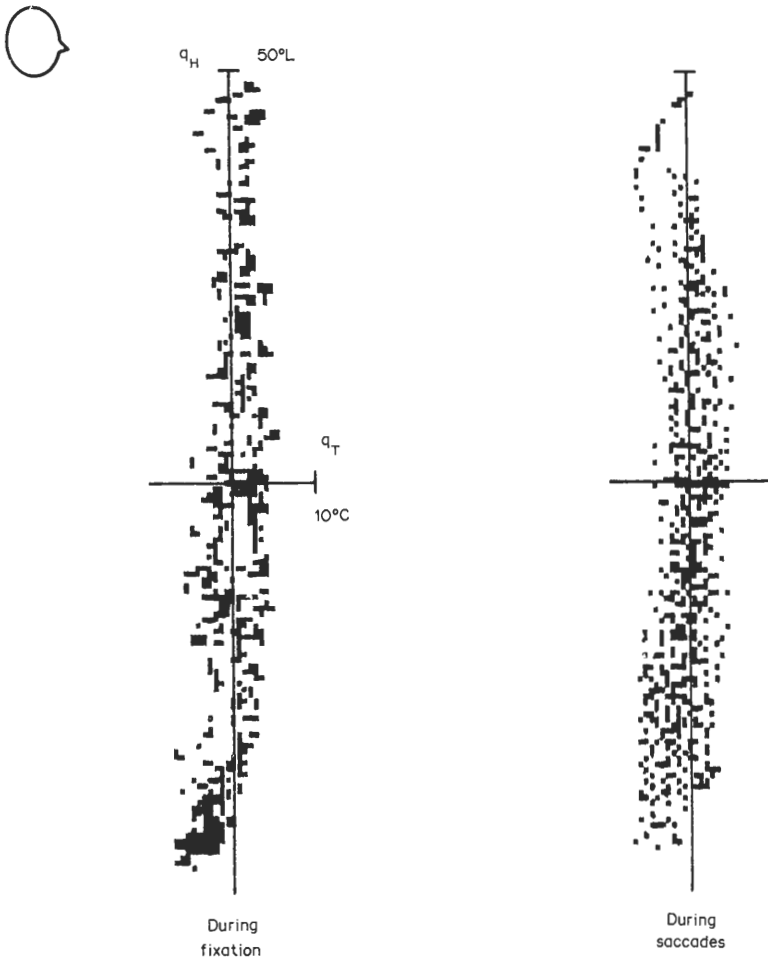


Fig. 6. Listing's law holds during saccades as well as in between: eye position vectors sampled from human subject DT.

Misestimates of either of these by a couple of degrees could yield comparable-sized errors in the determination of primary position, superimposed on the up to 10% error in finding relative eye positions, to yield a total uncertainty perhaps as large as 12 deg—though tests with a plexiglas eye rotating on gimbals suggest that in practice the error would be less than 6 deg. Thus, while Fig. 5 probably indicates that some human subjects show a real leftward, temporal deviation of the primary position of the left eye, confirmation with a more accurate coil system would be useful.

All these planes were measured with the subject viewing targets at a distance of 1 m, when binocular convergence was about 3.5 deg for humans and 1.5 deg for monkeys. Planes measured with the visual targets at infinity might differ somewhat. However, preliminary observations in monkeys (Ro & Vilis, unpub-

lished observations) show that moving the target plane in from 1 to 0.1 m, increasing convergence to 14 deg, rotated Listing's plane no more than about 5 deg, so the effect of moving the targets from 1 m out to infinity would probably be slight.

When one human pitched his head 30 deg forward and then 30 deg back, and Listing's plane was calculated in both positions, the computed planes were pitched 58 deg relative to one another. This 2 deg discrepancy, well within our measurement error, is consistent with the idea that Listing's plane is fixed in the head during pitch, though small relative movements cannot be ruled out.

Listing's law during saccades

Figure 6 shows that Listing's law holds during saccades. The eye position vectors of a human subject, sampled when the eye is moving

at less than 30 deg/sec, are shown in side view on the left side of the figure. On the right side are the position vectors for the same subject sampled only when the eye is moving at more than 170 deg/sec—that is, during saccades. In both plots the eye position vectors lie in planes, and the planes in the two conditions coincide. Similar results were obtained from the other five subjects: on average, Listing's planes calculated during saccades were rotated only 2.1 deg away from those calculated during fixation, and the standard deviation σ was only 1.3 times as large during saccades as during fixation.

Instantaneous eye velocity

The plot of velocity traces in Fig. 2 showed that any given saccade has a roughly fixed rotation axis. We now turn to the question: *which* axis does the eye spin around when it makes a saccade? Figure 7 makes the point that, theoretically, the eye might accomplish the same gaze change using many different axes. On top, the gaze direction—indicated by the line emerging from the quartered iris—moves horizontally by rotating about a vertical axis, indicated by the thick line. It is easy to see that a rotation of about 90 deg around this axis will move the gaze horizontally as shown. At bottom, the eye achieves exactly the same shift in the gaze direction by rotating about an axis that points straight forward, towards us. It is not so easy to visualize, but an 180 deg rotation about this axis will sweep the gaze line down, around and back up to complete the same horizontal gaze shift. This shows that the same horizontal gaze shift could be done using two different axes. In fact, it could be done by rotating about any axis in the plane indicated by the vertical dashed lines on the left.

But while infinitely many different axes can accomplish the same gaze shift, only one of these axes will keep the eye position vector in Listing's plane. The required axis depends on current eye position in the following way: for a saccade toward or away from a gaze direction \mathbf{g} , the rotation axis (i.e. the velocity vector) must lie in the plane orthogonal to the bisector of the angle between \mathbf{g} and \mathbf{g}_0 (proof in Tweed et al., 1990). For horizontal gaze shifts at different vertical elevations, this means that the velocity vector must tilt away from Listing's plane by an angle equal to half the elevation. In the next sections we confirm that the saccadic system chooses its rotation axes according to this rule.

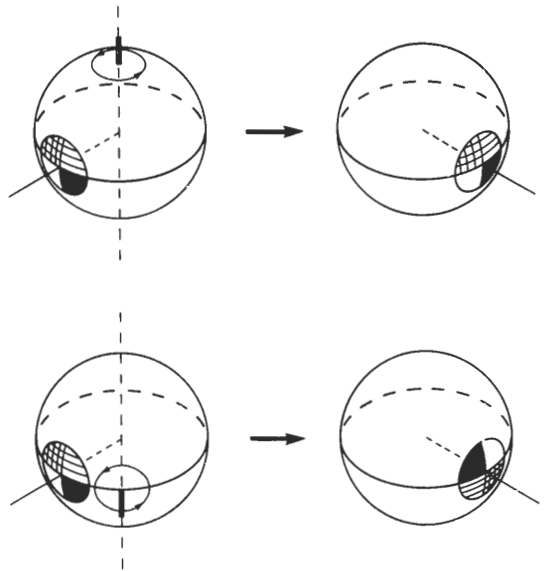


Fig. 7. Identical shifts in the gaze direction can be achieved by rotating about different axes.

We had subjects make several horizontal gaze shifts, symmetric about the sagittal plane, at various vertical elevations. If these movements were done by rotating about a vertical axis, the angular velocity vector of the eye would point straight up throughout the saccade. If they were done by rotating about any other axis in the parasagittal plane, the velocity vector would be oriented accordingly.

The velocity trajectories of one human subject, depicted in Fig. 8, show that the instantaneous spin axis tilts systematically away from vertical in the parasagittal plane. The top row of the figure shows the velocity traces for horizontal gaze shifts at a vertical level of 30 deg up; the bottom row shows the velocity traces for horizontal gaze shifts at 30 deg down. Each dot is an angular velocity vector, sampled at 1-msec intervals. The left column shows the velocity traces from a viewpoint behind the subject, and the right columns shows the traces as seen from the subject's right side. The right side view shows that the velocity vectors for horizontal gaze shifts at 30 deg up point slightly forward, into the clockwise torsional direction, throughout the rightward saccade, and slightly back throughout the leftward saccade. The opposite is true for horizontal gaze shifts as 30 deg down (bottom pair in Fig. 8): velocities tilt back during the rightward saccade and forward during the leftward saccade. In each case the tilt is about 15 deg, or half of the vertical elevation of the eye, as required by Listing's law.

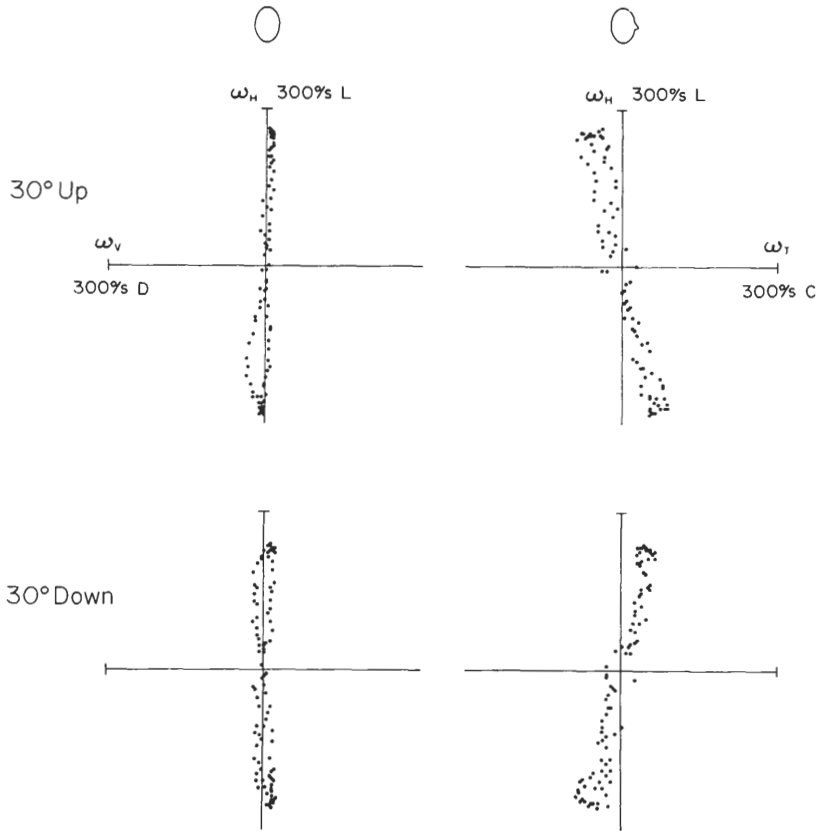


Fig. 8. Saccadic velocity vectors tilt systematically out of Listing's plane. Top row: velocity vectors of a human subject during horizontal gaze shifts at 30 deg up. Bottom row: 30 deg down. Velocities tilt about $30 \text{ deg}/2 = 15 \text{ deg}$ out of Listing's plane (ordinate in side view), but in opposite directions depending on the vertical elevation. Subject TV.

A more quantitative demonstration of these axis tilts is shown in Fig. 9: a plot of the angle of forward or backward tilt of velocity vectors as a function of the vertical elevation of horizontal gaze shifts. Each symbol represents the average tilt of the peak velocity vectors of about 10 saccades between a pair of targets. The three symbols correspond to three subjects. Diagonals indicate the tilts predicted by Listing's law: the solid line for rightward saccades and the dashed for leftward. Actual tilts are distributed close to the predicted values.

Velocity planes

The saccades in Fig. 9 are all horizontal, but to demonstrate the full planes formed by the velocity vectors, we must examine saccades in multiple directions. We had subjects make saccades in eight directions toward and away from a gaze point 30 deg above reference position, and the same for a target 30 deg down. To fit Listing's law, the velocity vectors should be arranged in planes tilted half as far as the gaze

line, so the 30° up saccades should all have their velocity vectors in a plane tilted 15 deg back; velocity vectors for the 30° down saccades should lie in a plane tilted 15 deg forward.

Figure 10 confirms that prediction, showing typical samples of 1000 velocity vectors from a human subject. The behind views show the vectors fanned out in all directions. The side views show that the velocity vectors lie in planes, and that the planes tilt by 15 deg as predicted. Oblique lines indicate the predicted orientations of the planes. Analogous results were found for saccades at different horizontal locations.

DISCUSSION

We have seen that for both human and monkey subjects, the angular position vectors of the eye lie roughly in a plane, as Listing and Helmholtz predicted a century ago. We found that the error in Listing's law, expressed as the standard deviation of the distances from eye

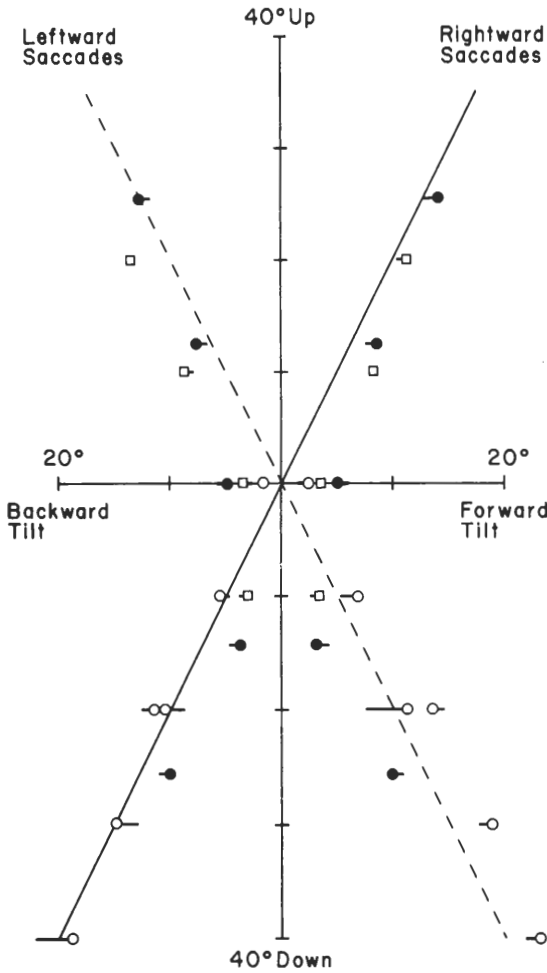


Fig. 9. Peak velocity vectors sampled during horizontal gaze shifts show position-dependent tilt as required for Listing's law. Subject key as in Fig. 5.

position vectors to their plane of best fit, was about 1.5 deg in humans and 0.8 deg in monkeys. About 90% of this error was due to scatter of eye position around the plane; only 10% to the vectors forming a nonplanar, curved surface.

The location of Listing's plane was described in terms of \mathbf{g}_p , the gaze vector in primary position, which points forward orthogonal to the plane. For any one subject, \mathbf{g}_p was fairly constant, staying within about 5 deg of an average vector on successive days. This variation was usually within the range of measurement errors attributable to day to day variations in field characteristics and in the placement of the head. Different subjects, however, showed large, consistent differences in the direction of \mathbf{g}_p . In all three monkey subjects, primary position was in the upper half of the oculomotor range. In the

three humans, it was vertically straight ahead or down, and also slightly temporal. Surprisingly, in two monkeys and one human, primary position was far from the centre of the oculomotor range.

Our investigation of eye position and velocity vectors during saccades turned up three interesting findings (1) plots of eye position showed that Listing's law holds during saccades as well as in between, and there is minimal torsional drift between saccades; (2) velocity plots showed that the loops traced by the velocity vector during saccades are narrow and consistent, indicating a roughly constant rotation axis for any given saccade task; (3) for each eye position there is an associated plane—the velocity plane (or displacement plane) of that position—such that when the eye saccades away from or towards that position, the velocity vector of each saccade lies in the plane. In primary position, the velocity plane is orthogonal to the gaze direction; when the gaze direction moves, the velocity plane tilts in the same direction as the gaze vector but only half as far (see Fig. 13).

Findings 1, 2 and 3 above are logically related. Specifically, 1 and 2 together imply 3; that is, it can be shown that fixed-axis rotations between positions fitting Listing's law must have their rotation axes distributed as described in 3. This geometric fact was certainly known to Helmholtz, and so the prediction of velocity planes for the saccadic system can be traced back to his writings (1867). The quaternion model of the saccadic system, which is based on the mathematical properties of three-dimensional rotations, predicts this same arrangement of velocity planes because it generates fixed-axis saccades between positions fitting Listing's law (Tweed & Vilis, 1987). The model also provides a mechanism for the generation of appropriate velocity axes that is consistent with current knowledge about the neural circuitry underlying saccades. The following sections review how this quaternion model was developed and then show how the geometric relations between position and velocity vectors and gaze directions support the model.

Models of the saccadic system

The local feedback model of the saccadic system, which was developed by Robinson and coworkers in the 1970s based on one-dimensional experiments and mathematics (van Gisbergen, Robinson & Gielen, 1981), is illustrated in Fig. 11a. In the model, an eye velocity

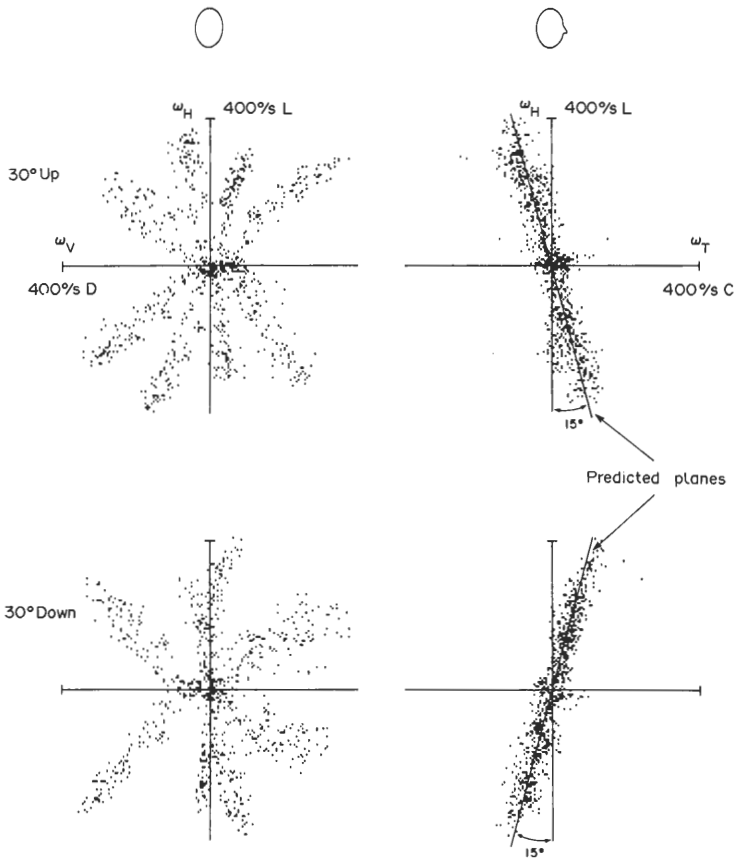


Fig. 10. Saccadic velocity vectors form planes which tilt at an angle equal to half the gaze eccentricity in the target position.

command ω carried by short lead burst neurons passes through an integrating neural circuit to yield the eye position command e carried by the tonic cells. The position signal is fed back and subtracted from a signal coding the desired position of the eye to yield an error signal that drives the burst cells until the saccade is complete. This model has been shown to mimic many behavioural properties of saccades, as well as the firing patterns of various brainstem neurons.

This circuit was first worked out for horizontal eye movements. But more recently, studies of nonhorizontal movements and associated neurons have uncovered two other circuits like the horizontal one, with the same burst cells and cells carrying position signals, and the same evidence for integration and feedback (King & Fuchs, 1979; King, Fuchs & Magnin, 1981; Hepp, Henn & Vilis, 1988). Hence it appears that there are two other circuits like the horizontal one, dealing with the nonhorizontal components of eye movements.

To extend the local feedback model to three dimensions, one might assume that each scalar should simply be replaced by a three-component vector. But a model derived this way would predict large errors in gaze control, because ordinary vector algebra does not correctly describe the properties of three-dimensional ro-

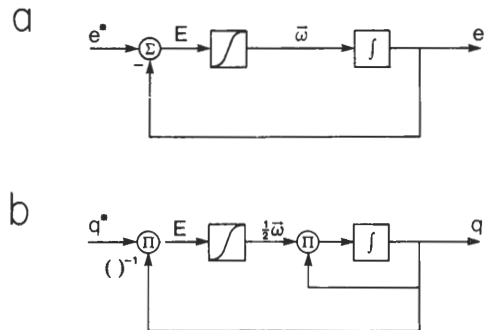


Fig. 11. Models of the saccadic system. (a) Vector model. Burst neurons are symbolized by a sigmoid curve representing the nonlinear relation between their input: motor error E and their output: eye velocity ω . (b) Quaternion model.

tations (Tweed & Vilis, 1987). In the kinematically correct, three-dimensional, quaternion version of Robinson's model (Fig. 11b), it is assumed that the three pools of short lead burst neurons code the eye velocity vector ω . To transform this eye velocity signal into a position signal, the former is multiplied by the latter and then the product is integrated. The reason this multiplication is necessary is that, in three dimensions, the rate of change of angular position depends not only on angular velocity, but also on angular position itself. A change is also required in the error computation: the angular velocity required to rotate from position q to q^* is a function, not of the difference $q^* - q$, but of the quotient q^*q^{-1} (Tweed & Vilis, 1987). The multiplication operation invoked in both the velocity to position transformation and the motor error computation differs fundamentally from familiar vector addition in being non-commutative: i.e. the product qp is not, in general, equal to pq . (For mathematical background on quaternions see Westheimer, 1957; Tweed & Vilis, 1987; Tait, 1890; Brand, 1948.)

The vector model 11a and the quaternion model 11b have similar structures, but only the latter, which incorporates the mathematical properties of rotations, can account for the observed distributions of angular position and velocity vectors during saccades. For example, the observation that eye position traces are restricted to a two-dimensional surface while the velocity vectors are distributed three-dimensionally, in many different planes, shows that position signals are not derived by integrating velocity commands. The arrangement of the velocity planes is such that, if velocity signals from short lead burst cells were integrated by tonic cells as in the vector model 11a, then eye positions would also be distributed three-dimensionally, with a torsional spread of about 40 deg. But we saw that eye position vectors actually lie within 5 deg of Listing's plane between and during saccades (as predicted by the quaternion model).

The arrangement of velocity planes also causes trouble for the subtractive computation of motor error used in the vector model. A simple argument shows that no model with the basic structure shown in Fig. 11a—i.e. a model where the difference between desired and actual craniotopic eye position determines craniotopic eye velocity—can generate the observed distribution of velocity vectors, regardless of the eye position representation used. Figure 12 shows

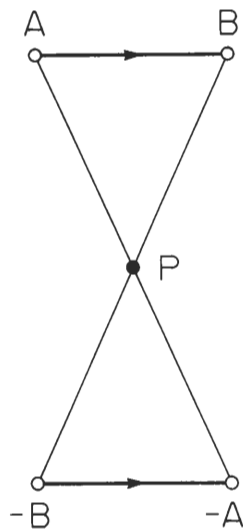


Fig. 12. A subtractive craniotopic feedback cannot generate the observed distribution of saccade axes. Explanation in text.

two eye positions A and B, at an eccentricity of say 40 deg; diagonally opposite them are the positions $-A$ and $-B$. We know that the rotation axes of the two saccades, A to B and $-B$ to $-A$, should tilt at about 40 deg relative to one another. However, subtractive error estimates will give the same initial errors for both saccades because the differences between the two position pairs are the same:

$$B - A = -A - (-B). \quad (3)$$

That is, the rotation axes of the two saccades will be the same rather than tilting 40 deg to each other. Thus any subtractive model with the form of Fig. 11a will be wrong about the initial rotation axes of at least some saccades by at least 20 deg.

Of course, there are many options besides the models in Fig. 11. One important possibility is that the motor error computation may be performed by subtracting displacements rather than positions—i.e. by subtracting the actual eye displacement since the beginning of the saccade from a signal coding the desired displacement of the eye—in which case all saccades would be centrifugal as far as the error computation was concerned, and (it can be shown) a subtractive feedback system would recreate the observed axis tilts. To preserve Listing's law, the initial computation of the desired eye displacement would have to be done multiplicatively, but thereafter the dynamic computation of motor error within the local feedback could be done subtractively. This is an important alterna-

tive interpretation of the data, especially since studies of the role of the superior colliculus in saccade generation suggest that the error computation does in fact involve eye displacements (Tweed & Vilis, 1985). However, a recent model of saccade generation by the superior colliculus (Tweed & Vilis, 1990) provides independent evidence that the error computation within the local feedback loop is multiplicative, by showing that a multiplicative computation automatically generates the weighted vector averaging effects that are observed with electrical stimulation of the superior colliculus.

Another possibility is that the initial assumption of the quaternion model, that short lead burst neurons code eye velocity, may be incorrect. Thus if burst cells instead coded the derivative of eye position (e.g. \dot{q}), then an integrator could transform this signal to a position signal; a velocity to position transformation would not be needed in the saccadic system (though it would still be required in the vestibuloocular reflex). Examination of this possibility will require careful measurement of three-dimensional eye movements during stimulation or cell recording in the burst cell and burst-tonic regions. A related question is whether activation of a given site in the superior colliculus, which drives the burst cells, consistently generates the same eye rotation (in some coordinate system) regardless of eye position—i.e. whether loci in the superior colliculus map represent eye rotations—or whether activation instead generates, say, consistent translations in some space of eye position coordinates (e.g. the three-dimensional space of Fick coordinates).

Implementation of Listing's law

Our findings regarding the behaviour of eye position and velocity vectors during saccades show that Listing's law is not implemented by directly restricting the patterns of motoneuron tonic firing, as suggested by Nakayama (1975). That is, there is no "Listing's box" that alters eye position commands just before they reach the motoneurons so that they are in accord with Listing's law. Rather, the position signals on motoneurons obey Listing's law because they are derived from velocity commands that fit the law. Robinson and Zee (1981) were the first to make this suggestion but they proposed that the correct velocity commands could be generated merely by yoking the nonhorizontal burst neurons so that the velocity vector always lay in Listing's plane. We have seen that the velocity

vectors must actually be arranged in many different planes which depend on current eye position. Thus when the eye is looking 30 deg up, a rightward gaze shift requires an axis tilted 15 deg forward out Listing's plane. The same gaze shift performed when the eye is 30 deg down requires a 15 deg backward tilt. Thus if the short lead burst neurons carry an eye velocity command, then for the same gaze shift, the three pools of burst neurons must be coactivated in different ratios; in one case generating clockwise velocity and in the other case counterclockwise. This fact suggests that Listing's law is implemented upstream from the burst neurons, at or above the level of the motor error computation. It also suggests that the same retinal error must evoke different coactivation patterns among the short lead burst neurons depending on initial eye position.

Purpose of Listing's law

Several proposals have been made regarding the purpose of Listing's law, most suggesting that the law reduces the computational or physical work of some system. For example, making eye orientation constant for each gaze direction (Donders' law) may simplify the work of the perceptual systems that compute the positions of visual objects, and the particular orientations embodied in Listing's law may have specific advantages (Helmholtz, 1867; Hering, 1868). There is an interesting untested corollary of this hypothesis: if Listing's law exists mostly for the benefit of the perceptual systems, then shifting or warping visual perceptions, as with distorting spectacles, should cause adaptive shifting or warping of Listing's plane.

Alternatively, Listing's law may simplify computations on the output side of the oculomotor system. The idea is that, since many eye positions give the same gaze direction, the oculomotor system must choose one of the infinitely many different patterns of extraocular muscle activation that correspond to a given visual target location. Fixing one, "torsional" component of eye position might simplify this choosing process. Another possibility is that Listing's law may minimize the work of the extraocular muscles. It is worth noting, however, that a plausible explanation of the law cannot depend heavily on the detailed geometry of these muscles, because spontaneous visually-directed head movements fit their own Listing's law—i.e. in humans, the angular position vector of the head is restricted to a single plane (Tweed

& Vilis, 1988)—but the geometry of the head and neck muscles seems much different from that of the eye muscles.

Of course, the law may have both perceptual and motor aspects. For example, suppose that for perceptual reasons the brain implements Donders' law—that is, it makes eye orientation a function of gaze direction. Given this constraint on eye position, and given some commonly used, or otherwise distinguished, "primary" eye position, Listing's law ensures the most efficient gaze shifts toward and away from primary position; that is, Listing's law ensures that, for saccades toward and away from primary position, a gaze shift of x deg is achieved by the smallest possible eye rotation, namely x deg. However, if this hypothesis were correct, one might expect primary position to lie near the centre of the oculomotor range, contrary to the findings for three subjects in this paper.

Geometry of saccadic control

Figure 13 summarizes the basic geometric relations of eye position and velocity vectors and gaze direction that hold during saccadic eye movements. Expressed relative to primary position, the eye position vectors lie, roughly, in a single plane known as Listing's plane. The eye velocity vectors also lie in planes, but in distinct

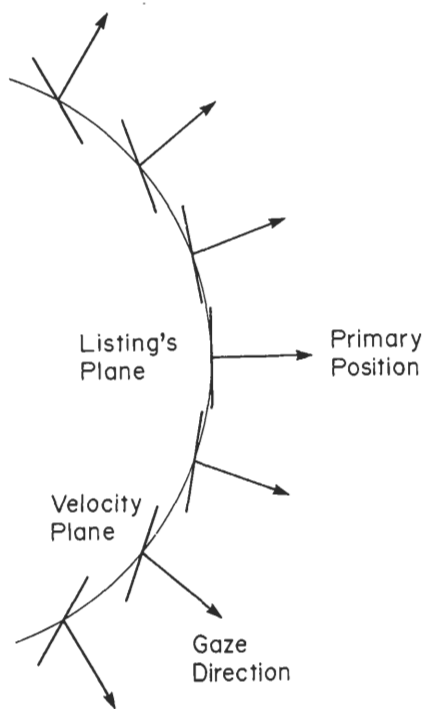


Fig. 13. Geometry of saccadic control.

planes which depend on eye position. The dependence on eye position is somewhat intricate: the plane is aligned with Listing's plane when the eye is in primary position, and it is rotated half as much as the gaze line when the eye looks elsewhere. The velocity planes for any two positions intersect in a common axis which will take the eye from one position to the other. For example, if the eye looks 40 deg up, then the velocity plane tilts 20 deg back. However, this plane contains the horizontal axis required to rotate the eye back down to primary position.

The vector model 11a, because it ignores the properties of three-dimensional rotations, does not predict this fundamental geometry of the saccadic control system. We have put forward a new model, based on first principles of rotational kinematics, that accounts for the preservation of Listing's law during saccades and for the observed distribution of the rotation axes of the eye.

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