Reprinted from:
Vergence Eye Movements C.M. Schor
and K.J. Ciuffreda Butterworths
1983

16

Kinematics of Normal and Strabismic Eyes

Ken Nakayama

Most contemporary investigators have measured eye rotations in only one direction, usually along the horizontal. In so doing, the very rapid movements of the eyes have been described with great precision, and significant classification of different types of movements has been possible: saccades, vergence, pursuit, and nystagmus (Robinson, 1968). In rarer instances, both horizontal and vertical movements have been considered, in which case the eye is treated as if it were a pointer (defined by the foveal axis). As such, two-dimensional descriptions of eye rotations specify the orientation of this pointer in space.

Much earlier, however, it was recognized that the eye can also make torsional movements about this pointer axis (Helmholtz, 1910). Therefore a full description of the rotary behavior of the eye also requires measurement of torsion. Far from being a formal exercise in completeness, consideration of all three degrees of freedom of eye rotation leads to some unique neurological conclusions regarding oculomotor organization. It may also provide an additional way of viewing the mechanics of eye musculature in health and disease.

Supported by NIH grants 5 R01 EY-01582, 5P30-EY-01186; and the Smith-Kettlewell Eye Research Foundation.

KINEMATIC LAWS OF EYE ROTATION

Although this subject can be explained simply, it can be confusing. Some of the difficulty stems from the need of previous writers to define the kinematic laws quantitatively, setting up a coordinate system based on a rigorously determined set of spherical angles. Although this is useful for empirical verification of these laws (see below), it is a poor way to introduce the subject. There is widespread lack of familiarity with three-dimensional spherical angle representations, and the choice of reference coordinates usually obscures the basic ideas.

Rather than describing eye kinematics with respect to a horizontal and vertical angular coordinate system as is usually done, this discussion begins intuitively and geometrically, without explicitly defining a coordinate system in any notational sense. A simple physical "ball and membrane" model of the eye is used (Nakayama, 1978). Figure 16.1 shows such a model positioned in the head of a supine observer gazing upward. The model consists of a spherical globe attached to a very tightly stretched elastic membrane carefully secured to the end of cylinder so that the membrane is equally taut in all directions. Because of the elastic quality

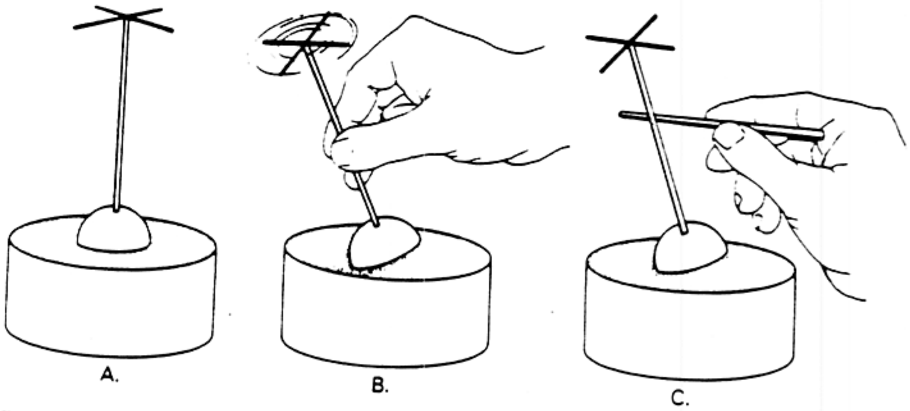

FIGURE 16.1. Ball and membrane model of the eye of a supine observer gazing upward. A Resting position of the "eye," when it is in the primary position. The foveal axis (see stalk) is perpendicular to the membrane and is oriented in the primary direction of regard. B Rotational displacement of the "eye" showing 3 degrees of rotational freedom: horizontal, vertical, and torsional rotations are possible. The stalk can be displaced as well as twisted between the fingers. C Rotational displacement of the "eye" having the capability of only 2 degrees of rotational freedom. Note that the smooth rod can displace the eye in only two dimensions. It has no control of the third dimension, torsion. This model obeys both Donders' law and Listing's law (see text).

of the membrane, there is a natural resting place for this eye model. Note the existence of a stalk attached to this globe. It represents the foveal axis and is perpendicular to the membrane. A cross is mounted on the end of the stalk to reveal the amount of twist of the globe around the axis. This position of rest is defined as the primary position, and the direction of the foveal axis, as represented by the stalk, corresponds to the primary direction of regard. The plane of this membrane when the model is at rest corresponds to Listing's plane for the eye. It is the frontoparallel plane passing through the center of the globe or sphere. The figure 16.1B depicts a situation in which the globe is rotated with three full degrees of rotational freedom. It can be rotated horizontally and vertically by displacing the stalk and torsionally by twisting the stalk between the fingers.

A third and most important case is shown in Figure 16.1c. Instead of moving the globe by grasping the stalk between the fingers, the fixation axis can be moved to any desired direction of gaze by pushing the foveal stalk with a smooth rod. In this case the model has sufficient rotational freedom to fixate any object, but it is limited to just two degrees of freedom, not three. The twist or torsion of the eye is no longer under external control because it cannot be twisted between the fingers. Its orientation is dictated by the elastic properties of the membrane, which ensures that it corresponds to the position having the lowest potential energy. Thus each direction of the foveal axis is associated with one and only one orientation of the globe.

What is essential to remember is that the behavior of this particular ball and membrane model is isomorphic with two of the most fundamental laws of human eye rotation: Donders' law and Listing's law. Donders' law states that for each gaze direction, that is, for each direction of the foveal axis in space, there is only one orientation of the globe in the orbit. Listing's law is much more specific, assigning the exact torsion of the eye in any gaze direction according to the model presented in Figure 16.1c.

This definition gives the most concise example of eye torsion and its relation to Listing's law. It says that the behavior of the eye (and of the model) shows a radial or axial symmetry, such that there is no net torsion of the eye with respect to an axial reference direction (the primary direction of regard). An equivalent and more common way to phrase Listing's law is to say that orientation of the eye can be predicted by assuming that the eye has made a geodesic (shortest path) rotation from the primary position to any other fixation position. The axis of this shortest path rotation is perpendicular to the intended direction of gaze, and thus lies in Listing's plane. For the case of the rubber membrane model, it means that the axis of the shortest path rotation lies in the plane of the membrane.

As with many other geometric and physical relations, the reason why the law can be stated with such simplicity is that we have a model that is couched in the proper coordinate representation to express Listing's law. Confusion has surrounded eye kinematics precisely because this most natural radial coordinate system has been neglected.

CONVENTIONAL COORDINATE REPRESENTATION OF LISTING'S LAW

To make actual kinematic measurements of the eye, it is often advantageous to use such nonradial angular coordinate systems. In particular, the angular coordinate systems that are usually chosen to describe eye rotation are based on the familiar concept of horizontal and vertical rotation. Two different systems, Fick and Helmholtz, specify rotations in this manner, although they are not identical (Alpern, 1969). For an appropriate model of the Fick system, consider a terrestrial telescope mounted on a set of two axes (Figure 16.2). The telescope can rotate horizontally about a vertical axis fixed to a stationary (earth-referenced) bearing and a vertical rotation can be made about a mobile horizontal axis. Thus any fixation direction can be specified in terms of two spherical angles.

In many ways, these two angles comprise a natural and suitable coordinate system that corresponds well with our sense of horizontal and vertical, and that is mechanically convenient for mounting the telescope. It can scan the visual field with ease and its gaze direction can be precisely specified by the two spherical angles (Θ, Φ) (Figure 16.2). The arrangement has one other advantage in that telescopic vertical always remains ori-

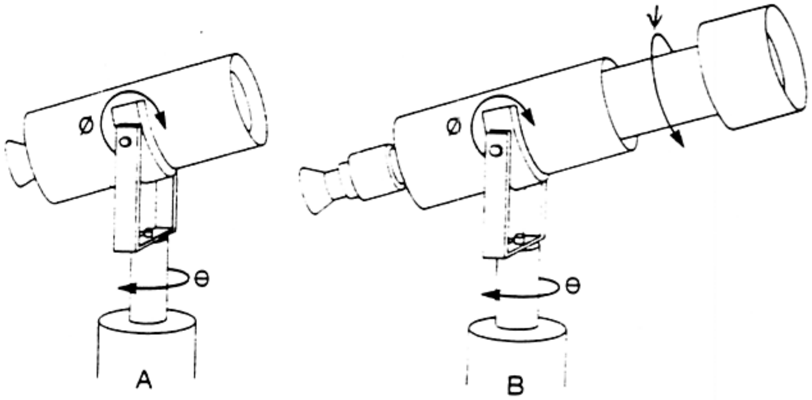

FIGURE 16.2. Fick coordinate system equivalent to a telescope model to describe the rotational behavior of the eye. A Description of a two-dimensional system that can be pointed to any desired direction of regard. It consists of freedom to rotate about a vertical axis, θ, and the freedom to rotate about a horizontal axis through an angle ϕ. B Same as in A with the addition of a third degree of rotational freedom. The telescope can also rotate about its optical axis by the angle ψ.

ented with respect to the environmental vertical. If we scanned the skyline of the city, for example, the vertical sides of any distant building would always line up with the vertical cross-hair in the telescope eyepiece. Although such a model is easy to understand, is easy to build, and has the property of preserving the parallel alignment of telescope and environmental verticals, it is very different from the behavior of the eye. It differs because it lacks the radial symmetry of Listing's law.

To describe adequately the radially symmetric rotational states of our normal eye fixations in this Fick system, we require an additional angular parameter, namely, a torsional one. The telescope needs to be twisted about its own axis (see Figure 16.2) according to the following equation:

$$\psi = \sin^{-1}\left(\frac{\sin\theta\sin\phi}{1 + \cos\theta\cos\phi}\right) \tag{a}$$

where θ is the horizontal rotation, ϕ the vertical rotation, and ψ the required rotation to adjust the eye's orientation in accordance with Listing's law. This angle ψ is also called false torsion, as it is an apparent twist of the eye with respect to the vertical that needs to be "added" to make the eye conform to Listing's law. An extra parameter of this type is required for any coordinate representation of Listing's law that is not radially symmetric with respect to the primary direction of regard. As we can see from the ball and membrane model, however, no real torsion occurs as it moves from primary to oblique positions of gaze.

Empirical support for Listing's law comes from a number of measuring techniques. The simplest is to put a vertical afterimage on the retina when the eye is in the primary direction of regard, thus providing a visible indication of the "vertical" meridian of the eye as it makes different steady fixations on a target screen (Helmholtz, 1910; Hering, 1879). If the eye were to obey the telescope rule (as in Figure 16.2), such afterimages would always appear congruent with vertical lines on a target screen. This is because the longitude lines in Figure 16.3 project to vertical straight lines on a target screen. If the eye obeyed Listing's law, however, such afterimages should be tilted away from true vertical (Figure 16.3). If we were to project the afterimages on a normal planar surface they would be congruent to a family of hyperbolic arcs, as depicted in Figure 16.4 (Southall, 1961; Helmholtz, 1910).

IMPLICATIONS FOR NEUROMOTOR CONTROL

Listing's law has been stated. It holds under a wide variety of conditions, in particular when the observer is unconverged looking at distant targets and the head is erect (Nakayama, 1978). How is it maintained and why

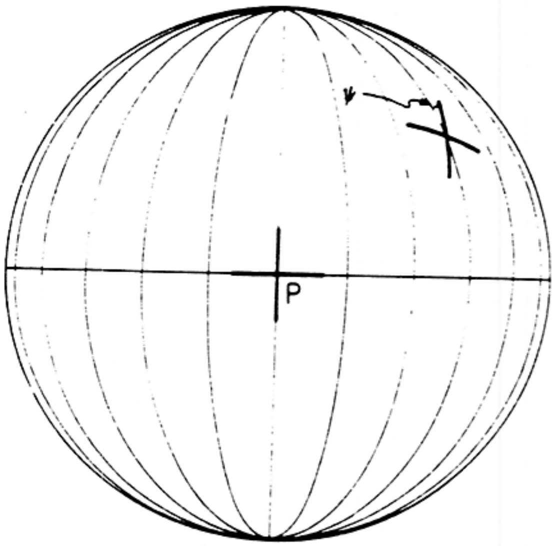

FIGURE 16.3. Representation of false torsion of the eye on a spherical field of fixation if the eye were to obey Listing's law. Vertical arcs represent longitude lines of the Fick system. They represent lines of constant horizontal angular displacement as well as as being congruent with vertical edges in the environment. Cross in the primary direction (represented by P) moves to a position in the upper right as a consequence of an eye movement in conformity with Listing's law. The vertical limb of the cross makes an angle of ψ with the true vertical in accordance with equation (a). This angle is defined as false torsion.

is it maintained? Is there a stiff rubber membrane in the orbit as described in Figure 16.1. mechanically obliging an adherence to Listing's law? A set of passive restraining tissues does exist in the orbit, comprised primarily of the stiff passive properties of each muscle and supplemented by nonmuscle tissue that surrounds the globe (Robinson, 1975). A partial cutaway drawing of some of the muscles and their attachments can be seen by looking ahead to Figure 16.11. Of importance is the arrangement of the muscles with respect to the primary direction of regard. The vertical rectus muscles pull back at an angle of 30° with respect to the primary direction. If Listing's law were to be explained by passive tissue elasticities, it would be very surprising if the primary axis of radial symmetry would lie in the primary direction of regard (see arrow). One might predict, for example, that the primary direction of regard would also be exodeviated by the same 30°, which it is not (Nakayama, 1978). Furthermore, there are oblique muscles that can provide the third degree of freedom, and thus there is really no obvious mechanical muscle constraint having sufficient stiffness to ensure Listing's law.

Some analogies might be useful at this point. Consider a soap bubble,

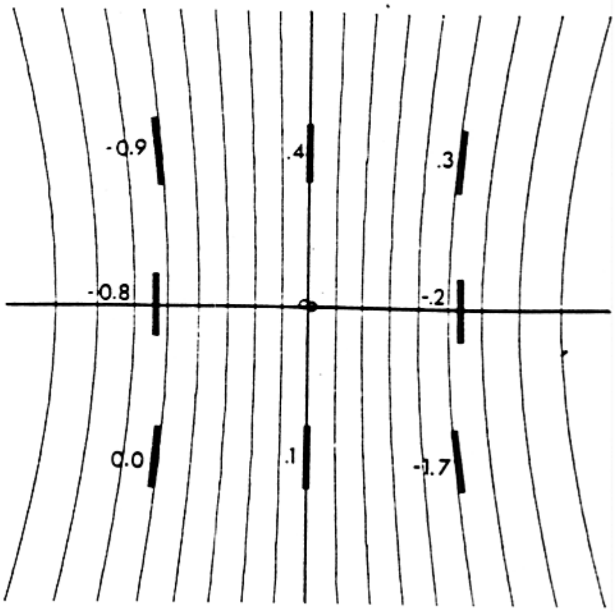

FIGURE 16.4. Experimental confirmation of Listing's law using afterimage alignment. If the law is correct, all afterimages should remain congruent to a family of hyperbolic arcs on a tangent screen. Such arcs are the central projection of vertical direction circles in the spherical field of fixation onto a frontoparallel planar surface (Helmholtz, 1910). Bold lines represent afterimage settings and accompanying numbers show the deviation from Listing's law in degrees. Eye screen distance is denoted by the horizontal line at the bottom of the figure. For more details, see text. From Nakayama K. A new technique to determine the primary position of the eye using Listing's law. American Journal of Optometry and Physiological Optics. Copyright 1978. Reprinted by permission.

a near perfect example of spherical symmetry. Few would ascribe this symmetry to a higher biological purpose, it is simply (though no less miraculously) the "solution" dictated by the classical physical principle of minimal surfaces. Likewise for the behavior of the ball and membrane model. It too has a symmetry (about an axis rather than a point) and this symmetry is the direct result of the constraining rubber membrane forces intrinsic to the model.

On the other hand think of a well-formed meatball. There is no intrinsic force in the meat to aggregate it into a spherical shape. What is required for it to exist is the "purpose" or "goal" of the maker, to ensure that the skillfull hand molds the meat into the desired symmetric form. The same holds for Listing's law. There is no intrinsic mechanical property of the muscles or the fascia in the orbit to dictate the observed radial symmetry seen for the rotational states of the human eye. As with the perfect meatball, it appears that the three-dimensional kinematic behavior of the eye can only be understood by looking beyond its immediate characteristics. One must invoke a higher biological purpose: its behavioral symmetry cannot be understood in terms of physics. Additional evidence to support this conclusion comes from deviations from Listing's law under specific conditions. It is violated with differing amounts of convergence (see below) as well as head tilt, it can be overcome with extensive voluntary effort (Balliet and Nakayama, 1978), and finally, it appears to break down in the state of sleep (Nakayama, 1975).

Because of these conclusions, it is argued elsewhere (Westheimer, 1973; Nakayama, 1975) that Listing's law is upheld by the central nervous system. Not only does it guarantee that the eye is pointed in the proper direction, it precisely apportions the flow of nerve impulses to the muscles so that Listing's law is also maintained. It is clear that many combinations of extraocular muscle innervation that would point the foveal axis in the desired direction are, as it were, forbidden. Only those states that simultaneously point the eye in the right direction and specify its torsional state are "permitted." Because there are essentially only two degrees of rotational freedom (as specified by Listing's law) and because various states of co-contracture during normal versional eye movements have not be observed (Robinson, 1970), the dimensionality of the six-muscle ocular system can be considered as only two, not six.

Several broad hypotheses can be proposed as to how this reduction of dimensionality could be accomplished. First, it should be clear that there must be a system formally equivalent to the model depicted in Figure 16.5, that is, there is a signal of orbital gaze direction expressed as a two-dimensional quantity, formally equivalent to two "command"

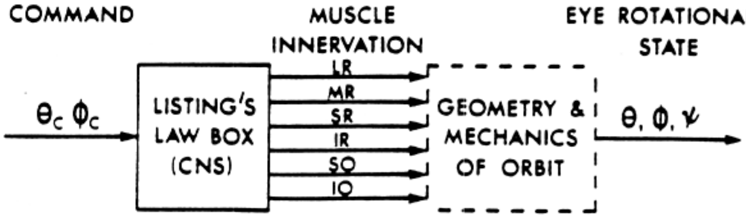

FIGURE 16.5. Block diagram showing that Listing's law is actively determined by the coordinated pattern of nerve impulses to the extraocular muscles. A two-dimensional command signal specifying two spherical angles θ_c, ϕ_c, provides input to the coordinating structure, Listing's law box. Thus in spite of the non-symmetric geometry and elasticities of the muscles and tissues, the torsion ψ is related to θ and ϕ by equation (a). Reprinted with permission from Basic Mechanisms in Ocular Motility and their Clinical Implications. G Lennerstrand, P Bach-y-Rita, eds., Nakayama K, Coordination of extraocular muscles, 1975, Pergamon Press, Ltd.

angles, θ_c, and ϕ_c. These commands go into a neural integrating network. Listing's law box, which then apportions the flow of impulses in such a way that the law is upheld, that is, that equation (*a*) is satisfied. Thus Listing's law is ultimately neurophysiological, and could be explicitly described as a set of synaptic weighting functions transforming a two-dimensional command signal to prescribed amounts of net excitation in the six separate motoneuron pools.

Why Listing's Law

This brings us to the more puzzling question of why, which might be best addressed by asking, how does the nervous system "know" that it is adhering to Listing's law? What feedback is given to the system to ensure this lawfulness? One alternative is that the nervous system is already prewired and precalibrated in its connectivity and strength of synaptic connections so that Listing's law is maintained without feedback. Thus the nervous system does not have to know it is regulating anything; it just happens to be preprogrammed. This seems unlikely because of the great change that occurs during development in the growth of the eye, muscles, and surrounding tissues. Small influences in early life could lead to larger imbalances later on. Furthermore, other open-loop aspects of the oculomotor system are known to be subject to parametric feedback (Ludvigh, 1952). For example, open-loop gains of the saccadic system (Optican and Robinson, 1980; Miller et al., 1980), as well as the vestibuloocular system (Melville Jones and Davies, 1976) can show very large shifts, specifically in terms of the open-loop gains of various subcomponents. Thus the problem of Listing's law becomes especially puzzling when considering the clear answer that has been received regarding the modifiability of saccades as well as the vestibuloocular reflex (VOR). In the case of saccades, there is a retinal position error signal that corrects the size of future saccades. For the VOR, retinal slip velocity can adjust its open-loop gain and phase. Such results suggest that a similar adjustment would be required to fine-tune Listing's law.

Three separable hypotheses have been advanced regarding the goal of Listing's law. The first is a motor hypothesis originally suggested by Helmholtz (1910). He asserted that Listing's law required the eye muscles to exert minimum energy. Such eye rotations require the muscles to do the least work in positions of eccentric gaze. Any other rotational state for a given fixation direction stretches the muscle or tissues beyond the minimum required. The assumptions are several. First is the question of whether eye movements obeying Listing's law actually require the least energy. As specified earlier, this is clearly the case for the rubber membrane model as depicted in Figure 16.1, but whether it holds for the eye is unproved. In fact the position of rest under neuromuscular paralysis changes with age, becoming progressively more divergent (DeGroot et al., 1976). No evidence as yet exists to suggest that the primary direction of regard (the axis of radial symmetry embodied in Listing's law) undergoes a concomitant divergence. In addition to this speculation, the argument assumes that the nervous system can also learn to accomplish the task of eye fixation at minimal energy cost and with great accuracy. It puts the nervous system in the position of performing an ergonometric analysis, measuring the work for each gaze direction and then calculating the rotational state that is associated with the least energy. Thus the hypothesis requires that Listing's law correspond to a set of minimum energy states and furthermore, that differences from the law are sufficiently great in terms of energy consumption that the nervous system can sense and act on them.

A second hypothesis, originally advanced by Hering (1868) and later considered by Westheimer and Blair (1972), is perhaps more ingenious. It is noted that eye movements made according to Listing's law preserve direction congruence for lines passing through the primary direction of regard. To get a modern flavor of this idea, think of a set of Hubel and Wiesel (1962) orientation-sensitive units in cortex. If any straight line is scanned so that it intersects the primary direction of regard, the relative dominance of orientation-tuned units best tuned for the orientation of the line when the eye is in the primary direction will also be the same set of units best tuned for gaze directions on the line in any other scanned portion (Figure 16.6). Thus straight lines will have the property of providing the same stimulation for a given orientation-tuned cell at any fixation along the straight line. In some fashion, therefore, the preponderant existence of straight lines could tune the oculomotor system's behavior so that it conforms to Listing's law.

This approach neglects the potential importance of straight lines that do not intersect the primary direction of regard. Consider the observer facing straight ahead and looking over to the right to scan a telephone pole. A vertically oriented Hubel and Wiesel unit would be optimally stimulated in the primary plane of regard (fixating at the object at eye level), but for points above and below this receptive field would be too extorted or intorted (see Figure 16.6). It might be supposed, however, that fixation of most straight lines of interest intersect the primary direction of regard as the observer can also turn his head for straight ahead frontal viewing. Consequently, off-axis fixations such as that depicted in Figure 16.6 could represent noise to be averaged out.

A third hypothesis suggests that Listing's law serves the cause of binocular vision by keeping the orientation of each eye the same in different directions of parallel gaze. This view suffers because other candidate laws are equally adaptive in this respect, for example, the telescope

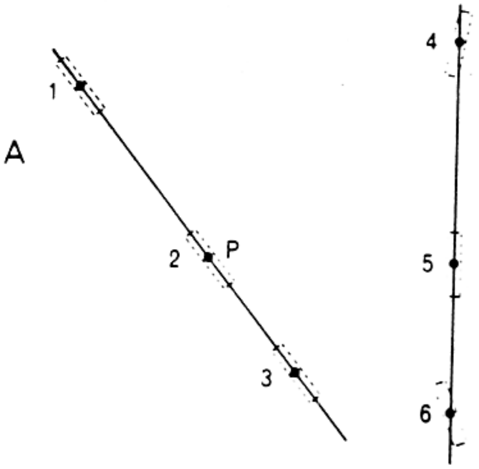

FIGURE 16.6. Preservation and lack of preservation of direction congruence as a consequence of eye rotations made in accordance with Listing's law. The primary direction of regard is designated by P and the sets of dashed rectangles associated with each line are the projection of foveal receptive fields were the eye to look at the various fixation positions (numbers 1-6). A For straight lines that have one point that passes through the primary direction of regard (this requires that the observer look directly at one point of the line), there will be a foveal receptive field orientation that will always line up with the line for other fixations. Thus at fixations 1, 2, and 3 the same class of cells with oriented receptive fields will receive optimal stimulation. B For eye fixations on lines not passing through the primary direction of regard, however, this property does not hold. Thus for fixations 4, 5, and 6 a given foveal receptive field (a vertically oriented one in this case) will not receive optimal stimulation at the different fixations along the line.

law as depicted in Figure 16.2. In this model the torsion of the eye with respect to the vertical would be identical for each direction of parallel gaze. An appropriate test of this binocular view might be to examine the eye kinematics of species having little or no binocular overlap, yet ones that make such large eye movements that adherence to Listing's law could be checked to a sufficient degree of precision. Animals such as the African chameleon may provide such an opportunity.

One might also consider the importance of Listing's law in maintaining binocular correspondence for nonparallel gaze. As it turns out there is some small advantage in this regard. (See below).

VERGENCE EYE MOVEMENTS

In general, versional eye movements obey Listing's law. Therefore as long as the foveal axes are roughly parallel, orientation of the vertical meridian of the eye can be predicted, as in equation (*a*). When the eyes are converged, however, the relation between gaze direction and eye torsion becomes altered, a finding that has been well recognized for more than a century (Hering, 1868).

As an example, consider the following experiment. An observer is placed in a bite apparatus and told to fixate a succession of points (F_1, F_2, F_3 as in Figure 16.7). In each fixation the gaze direction of the right eye is always the same, what varies is the direction of the left eye. This is the case of asymmetric vergence. The torsion of the right eye can be measured very accurately using a camera with telephoto lens as described by Balliet and Nakayama (1978) and this experiment can be repeated for several elevations of gaze. Figure 16.8 shows the change in torsion of the right eye as a function of the amount of asymmetric convergence for these different elevations. Clearly, for level and down gaze there is a large effect of convergence. Even though the right eye is looking in the same direction, the measured value of torsion progressively changes as the angle of convergence increases. This implies that the innervational pattern to a given eye for a given gaze direction will be different depending on the amount of convergence. Thus convergence eye rotations are clearly not mediated through the Listing's law integrating network (as in Figure 16.5), but must have some organization that bypasses this network.

There are several logical possibilities. In one case the vergence signal bypasses Listing's law box and directly innervates a single muscle pair, namely, the horizontal rectus system. This is the most simple conceptually and is in accord with the presumed importance of the horizontal rectus muscles in mediating vergence eye movements. Horizontal rectus muscles clearly must play a role in horizontal vergence movements and an attractive hypothesis is that they are directly innervated to produce vergence eye movements. It is also partially supported by the findings of Keller and Robinson (1971), who have shown that for a given horizontal gaze direction there is a particular discharge rate independent of whether the eye is engaged in versional or vergence movement. A second view is more complex, recognizing that Listing's law box must surely be bypassed

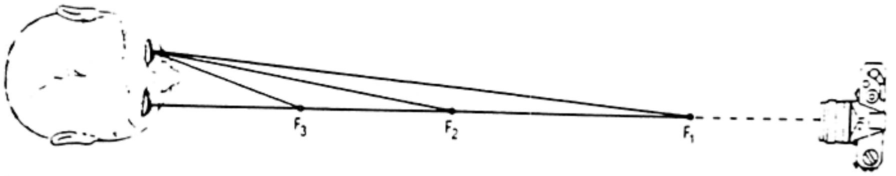

FIGURE 16.7. Schematic diagram of asymmetric convergence paradigm used to measure changes in eye torsion with differing amounts of convergence. Right eye is always in the same gaze direction regardless of the amount of convergence, whereas the left (unmeasured) eye changes fixation. Photographic measurement of torsion is thus confined to the right eye.

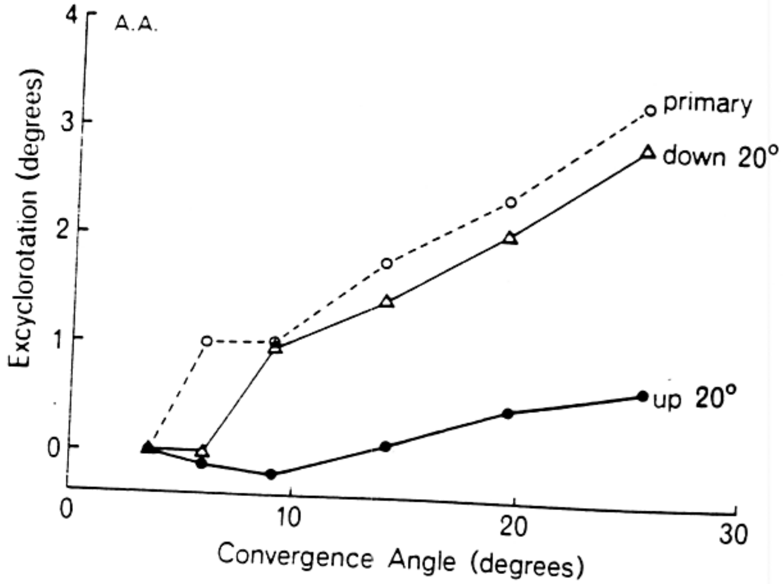

FIGURE 16.8. Torsion measured as a function of convergence for the differing elevations of gaze. Experimental apparatus as in Figure 16.7. Open circles represent level gaze, solid dots represent up gaze (20°), crosses represent down gaze (20°).

to produce the recognized deviations from Listing's Law, acknowledging that the separate contribution from the vergence system is likely to involve more than just the horizontal rectus system.

Experimental results and many other factors favor the second more complex alternative. First is the fact that excyclotorsion tends to increase with increased convergence, and this is especially prominent in horizontal gaze and in down gaze (as in Figure 16.8). From the geometry of the horizontal rectus muscles (they insert on the horizontal meridian of the eye and thus their axis vectors are vertical), one might expect that if there were torsional deviations from Listing's law they would be essentially opposite and of equal amplitude for fixations up versus down with respect to the primary plane of regard. Because the results show an asymmetric deviation from Listing's law, this view seems untenable. It appears that the vertical and the oblique muscles must play a role in vergence movement and furthermore, they must do so in a particular manner, ensuring a relative excyclorotation during convergence in down gaze and in level gaze, but not in up gaze. This participation of vertical and oblique muscles is also supported by some experiments on dark-reared kittens (Cynader, 1979). Such animals show prominent horizontal tropias after a period of dark-rearing during the critical period. Most important to note, however, is a large torsional deviation that accompanies this horizontal deviation.

As the animals recover from the strabismus, both the horizontal and torsional components disappear, demonstrating a strong link between tonic vergence and tonic cyclorotation under these experimental conditions. Both of these results suggest a new set of rules between muscle pairs must occur in vergence movements.

What can be said about vergence muscle coordination within an antagonistic pair? Keller and Robinson (1971) saw no deviation between the motoneuron rate versus position curve during vergence, but they did not measure the motoneuron discharge associated with vertical or oblique muscles. Human vergence appears to be accompanied by a measurable translation of the eye (Enright, 1980). It provides indirect evidence that during vergence various states of co-contracture within a muscle pair are possible, a clear violation of the Sherringtonian principle of reciprocal innervation. Simultaneous measurement of primate oculomotoneurons corresponding to antagonistic muscles during vergence and vergence might help settle the issue.

The functional question of why there should be a deviation from Listing's law in vergence has not received a satisfactory answer, although Hering's position (1868) that it must serve some aspect of binocular vision seems attractive. As one possible approach, consider the horopter in the vertical dimension, those points in space in binocular correspondence. Assuming a geometric model of retinal correspondence, the vertical horopter is a single vertical line through the fixation, at least for symmetric convergence in the horizontal plane (Helmholtz, 1910). In fact, however, the empirical horopter is tilted backward and passes through the feet when a person is viewing targets at infinity (Helmholtz, 1910; Nakayama, 1978; Nakayama et al., 1977), a view that has been collaborated with physiological recordings in cats and owls (Cooper and Pettigrew, 1979). The horopter tilt is a consequence of deviation from strict geometric correspondence between the two retinas, showing a physiological tilt of the vertical meridian in each eye. This very interesting point is discussed in greater detail in Chapter 7.

For parallel axes of the eye that are associated with viewing distant targets straight ahead and on the horizon the horopter line lies in the ground plane, a most convenient place for binocular vision to be optimal. With closer fixations in the primary plane of regard (assuming no violations of Listing's law), the horopter becomes oriented more and more close to the vertical (Figure 16.9).

Of interest is to see whether such torsional deviations from Listing's law might aid in keeping the vertical horopter line in a functionally appropriate orientation with the close viewing associated with convergence. To examine this issue, we note the factors that will determine orientation of the horopter line under these circumstances.

First is the physiological tilt of the vertical meridian of the eye (ψ_H)

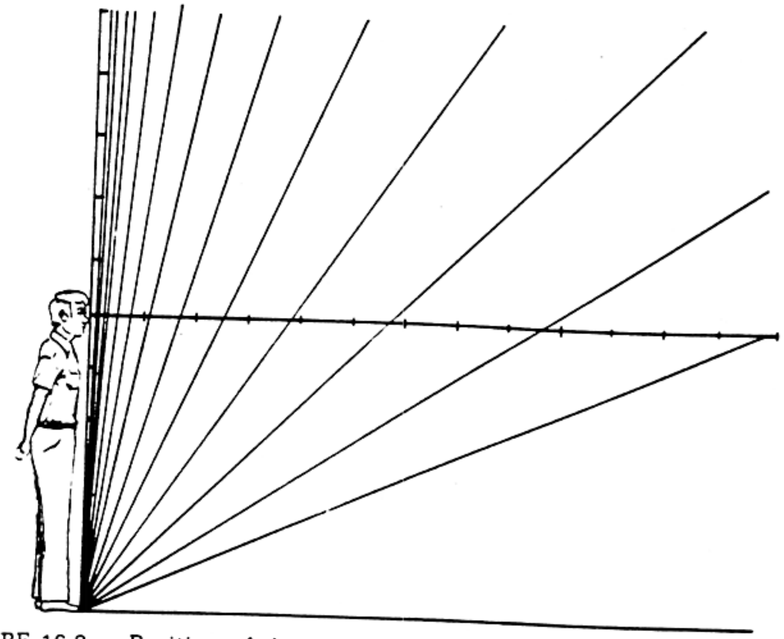

FIGURE 16.9. Position of the vertical horopter line for different distances of symmetric fixation in the horizontal plane of regard. Note that as fixation distance is decreased the horopter changes from a predominantly horizontal to a predominantly vertical orientation.

as originally hypothesized by Helmholtz and subsequently confirmed (Nakayama, 1977). Second is the torsion of the eye with respect to the environmental vertical. This eye movement contribution can be subdivided into two components: "false" torsion due to Listing's law in accordance with equation (a) (ψ_L), and torsion associated with convergence (ψ_C), which can be estimated from the data in Figure 16.8.

Figure 16.10 shows the orientation of the vertical horopter for three elevations of gaze, calculated from estimates of ψ_H, ψ_L, ψ_C. These are represented by the bold lines. In addition, the orientation of the horopter line without ψ_C (torsion changes due exclusively to convergence) is shown as the dashed line. From the figure it should be clear that a very slight advantage can be obtained by ψ_C as it tilts the horopter back by a small angle, at least in down gaze and level gaze. Inasmuch as the horopter line lies within a plane of best correspondence, this additional tilt at near distances may aid in the bincocular inspection of backwardly tilted surfaces. To the extent that such surfaces receive better illumination from overhead sources (presumably the sun or sky) especially in comparison to most vertical surfaces, they will be well placed to ensure optimal binocular stimulation. It must be admitted, however, that the effect is small.

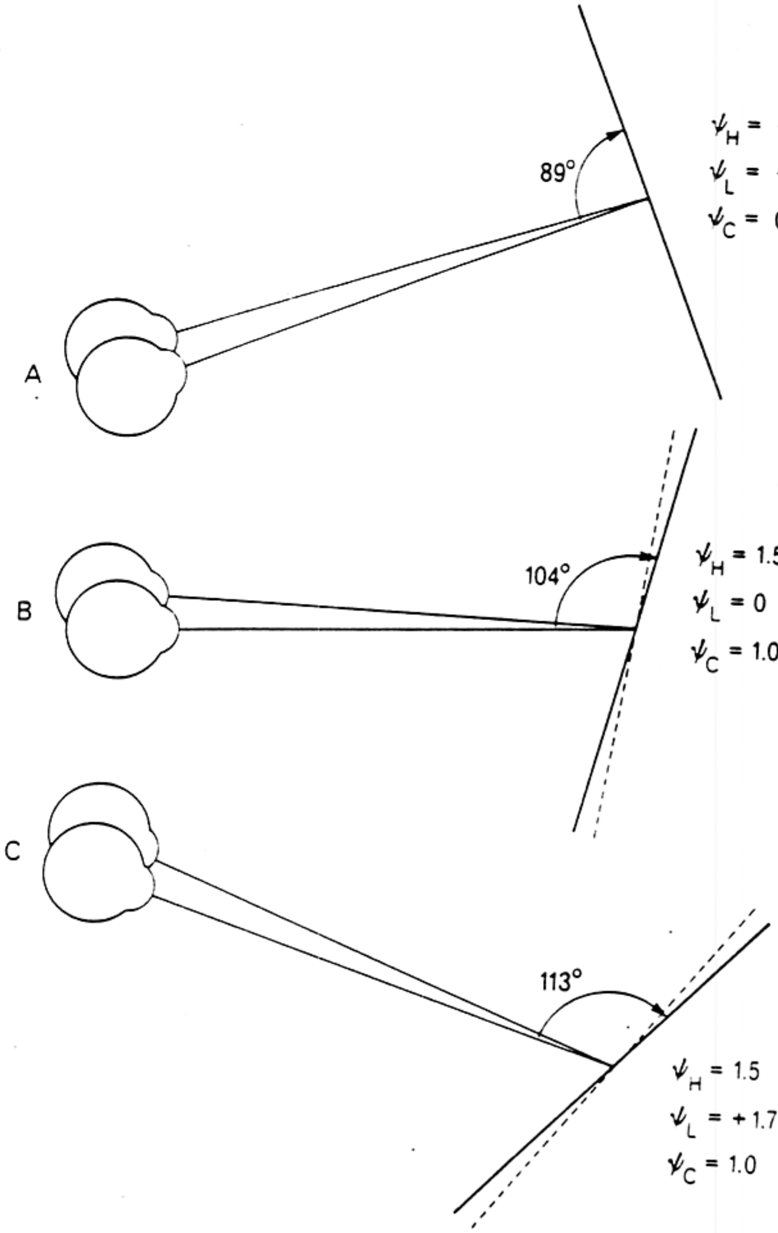

FIGURE 16.10. Orientation of the vertical horopter at a close viewing distance (19.3 cm) for three elevations of gaze: 20° elevation, level, and 20° depression. Bold solid lines in each case reflect the best estimate of the vertical horopter line orientation based on ψ_H (the physiological tilt of the vertical meridian as originally suggested by Helmholtz), ψ_L (eye extorsion introduced by Listing's law),

As the final note, it should be clear that the torsion associated with Listing's law during inward and downward gaze contributes an even greater tilt to the vertical horopter in the close viewing situation, much more so than the convergence-induced violation of Listing's law. Whether this is a cause or a byproduct of the law remains unanswered.

CLINICAL APPLICATIONS OF EYE KINEMATICS

Earlier sections of this chapter established the view that the relation between torsion and gaze direction was fixed by the nervous system. Thus whenever the eye is to make a saccade to a particular position in the orbit specifiable in terms of two angles, the brain allocates the innervation to the six muscles in a very stereotyped manner, ensuring that the third degree of freedom, torsion, is fixed.

The question to be considered is the degree to which this neurologic stereotypy can be used to assist in understanding disorders of the oculomotor system, especially those concerning the peripheral muscular pathology. At the outset, it must be noted that a similar type of reasoning based on neuronal stereotypy already exists as a cornerstone in the diagnosis of strabismus, namely, reliance on Hering's law of equal innervation. With Hering's law, the two eyes are assumed to be yoked neurologically and any changes in their conjugacy is attributed to peripheral factors, not to the possibility that Hering's law itself might be violated. Hering's law provides the scientific basis of the cover test, one of the most widely used tools in the diagnosis of strabismus.

Using analogous reasoning, one might also deduce pathological features of the peripheral oculomotor apparatus using Listing's law instead of Hering's law. One could assume that the neurologic machinery to maintain Listing's law is essentially intact at least over the short run and that any given deviation must be due to some form of mechanical abnormality of the oculomotor system. What is attractive is that such reasoning is based on the data from a single eye, and this could enable one more accurately to pin-point the abnormality especially in comparison to a test that simply compares the difference in rotation between the two eyes.

The variation with tropia as a function of gaze direction using the cover test, for example, can often localize the problem to four muscles: the four horizontal muscles for horizontal tropias or two pairs of oblique

---

and ψ_C (extorsion produced by convergence). Estimates of these parameters are set to the right of each condition. Dotted line represents tilt of the horopter without the extorsion produced by convergence. Numbers represent the angle of the horopter with respect to the line of sight. Note that it is larger in level and in down gaze.

and verticals for vertical deviations. Thus with a monocular test it may be possible to narrow the ambiguity by a factor of two. As yet the usefulness of this approach has still to be examined with a varied clinical population. It remains to be seen whether it will significantly add to our understanding of peripheral motor mechanisms associated with version or vergence, and as a separate issue, whether it will have peculiar advantages in the differential diagnosis of strabismus.

In this regard, it would seem that disorders involving vertical gaze would be most clarified through monocular kinematic analysis. In contrast to horizontal eye rotations, vertical eye rotations more obviously require the cooperation of several muscle groups, in particular, vertical rectus and oblique muscles. Figure 16.11 shows a cutaway view of the extraocular motor system with the axis of the vertical and oblique systems labeled. Each group acting independently will rotate the eye about an axis of rotation that is not in Listing's plane. The vertical rectus muscles will rotate the eye about an axis that makes an angle of 30° with Listing's

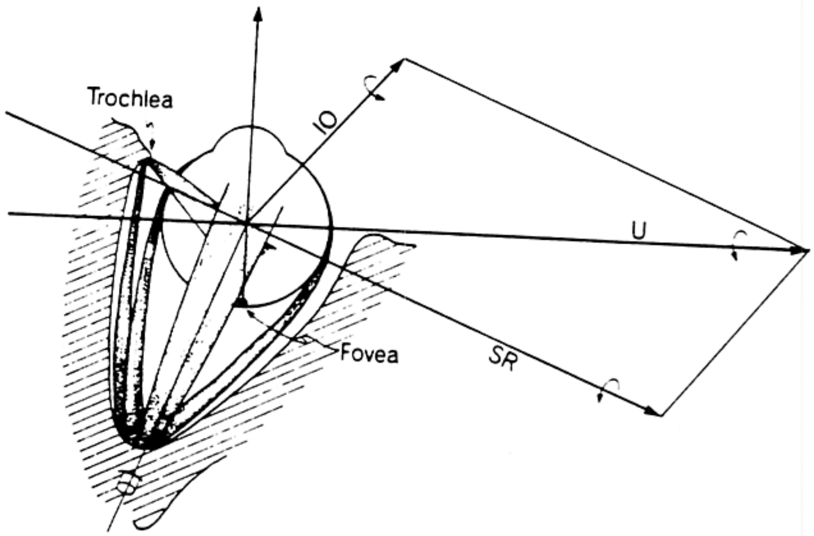

FIGURE 16.11. Partial schematic view of the extraocular muscle system showing that the action of the vertical and oblique muscles is far from being symmetrically arranged around the primary direction of regard. The action vector of the superior rectus muscle is denoted by $\hat{SR}$. Its direction represents the axis about which the eye would move if this muscle were activated alone and its length represents its relative torque for an infinitessimally small ocular elevation. $\hat{IO}$ represents the same for the inferior oblique muscle. Thus the vector sum of these torque vectors represents the resulting torque required for a vertical eye movement. This is labeled as the vector $\hat{U}$. Note that it must lie in Listing's plane so that the rotation is in accordance with Listing's law.

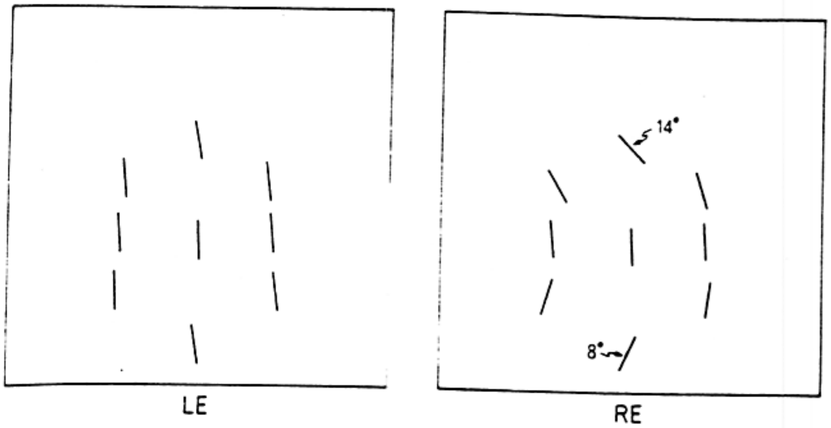

FIGURE 16.12. Normal and abnormal eye rotations. Torsional states of the eye (expressed as an angle that is three times the deviation from Listing's law) for different directions of gaze. Note that in the left eye there appears to be no marked deviation from Listing's law, whereas for the right eye there is a marked deviation. Right eye of this patient shows marked Brown's syndrome (see text).

plane and the oblique muscles will rotate the eye about an angle that deviates by about 51° in the opposite direction. From the geometry of the situation and knowledge of Listing's law one can deduce that each muscle group must contribute a certain rotational component (as depicted by the lengths of the rotational axis vectors) so that the resultant vector lies in Listing's plane. For example, in making a small elevation from the primary plane of regard it should require about twice as much torque from the superior rectus muscle as compared to the inferior oblique, otherwise vertical rotations from the primary direction of regard would not be in accordance with Listing's law. This can be most clearly seen by noting that only this ratio of torque vectors between the vertical and oblique systems can summate to give a resultant torque vector in Listing's plane (see Figure 16.11).

To give an example of how a monocular kinematic analysis might clarify a rather complex clinical case involving these muscles, following are data on one patient with Brown's syndrome. The patient has great difficulty in looking downward or upward. In particular, he had about 1 prism of right hypertropia in left, primary, and right gaze; 16 to 18 prisms of right hypertropia and 5 prisms of exotropia in up gaze; and 10 prisms of right hypotropia and 5 prisms of esotropia in down gaze. Independent evidence established that the cause of the motility disorder in the right eye was an adhesion of the superior oblique tendon in the trochlea, a side effect of nasal surgery.

Figure 16.12 shows a set of torsional measurements for different positions of gaze, obtained separately for each eye by measuring the orientation of a vertical afterimage at different locations on a tangent screen using a method described by Nakayama and Balliet (1977). The torsion is calculated as deviation from Listing's law and is represented by a line in each gaze position such that the torsional deviation is magnified by a factor of three. As expected, the normal left eye conforms to Listing's law. In contrast, there is a marked deviation for the right eye in the opposite direction in up gaze and down gaze.

To obtain a more intuitively satisfying spatial picture of this disordered set of torsional states, the orientation of the "equivalent" axis of rotation was calculated using an algorithm based on orthogonal matrices (Nakayama, 1974). This equivalent axis is the one about which the eye would rotate if it were to move directly to the measured fixation position with the measured amount of torsion. Thus it provides an analytical summary of how the eye can move from the primary position to any other measured rotational state by defining the axis of a shortest path rotation linking the two rotational states.

From the previous definition of Listing's law it should be clear that the axis vectors for all fixations of a normal eye should lie in Listing's

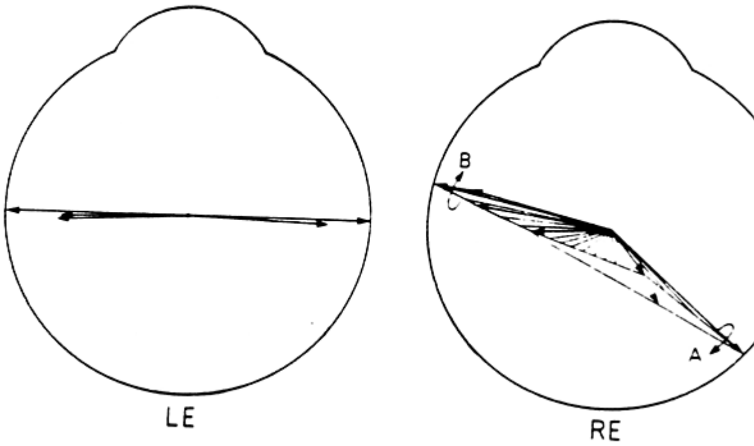

FIGURE 16.13. Top view of equivalent axes of rotation calculated for eye positions depicted in Figure 16.12. For each eye position away from the primary position (described in terms of three angles) it is possible to calculate an "equivalent axis of rotation" that will take the eye from the primary position to the measured fixation by the most direct rotation. If Listing's law is true, it is predicted that such axes will lie in Listing's plane, the frontoparallel plane passing through the center of rotation of the eye. It should be noted that such is the case for the normal left eye. For the right eye, however, such axes are clearly not in Listing's plane, deviating in the direction of the action of the vertical rectus system. As a comparison, note the similarity of the orientation of calculated axes of rotation and those of the vertical rectus system (as shown in Figure 16.11).

plane, that is the frontal parallel plane passing through the center of the eye. Figure 16.13 shows that this is definitely the case for the normal left eye and this congruence provides a nice confirmation of Listing's law.

For the right eye, however, the set of equivalent axis vectors is clearly outside Listing's plane. Note the orientation of arrows A and B, which describe the equivalent axes of rotation of pure up gaze and pure down gaze, respectively. They define an orientation that is very close to the axis of rotation of the vertical rectus muscles as shown in Figure 16.11.

Comparison of the measured equivalent axes and the known axes of the extraocular muscles, therefore, suggests an intelligible picture, one that does not immediately emerge from a consideration of the disordered torsional states as shown in Figure 16.12. The restriction at the trochlea prevents rotations in the axis of rotation of the oblique system, thereby leaving the rotation of the eye to be determined largely by the vertical rectus system. This can be seen by noting that the measured equivalent axes of rotation become tilted out of Listing's plane and are very close to those axes defined by the vertical rectus system.

The foregoing results offer a hypothesis that may be of some use in understanding complex muscle pathology. It suggests that if there is a restriction in any muscle system, in particular those movements requiring the cooperation of vertical and oblique muscles, the equivalent axis of rotation will shift out of Listing's plane toward the axis of rotation of the synergistic muscle system. Such a view if confirmed could conceivably aid in the diagnosis of vertical muscle disorders.

REFERENCES

Allen MJ. Dependence of cyclophoria on convergence, elevation and the system of axes. Am J Optom Arch Am Acad Optom 1954;31:297.

Alpern M. Kinematics of the eye. In: Davson H, ed. Vol. 3. New York: Academic Press, 1969.

Balliet R, Nakayama K. Training of voluntary torsion. Invest Ophthalmol Visual Sci 1978;17:303–14.

Cooper M, Pettigrew JD. A neurophysiological determination of the vertical horopter in the cat and owl. J Comp Neurol 1979;184:1–24.

Cynader M. Interocular alignment following visual deprivation in the cat. Invest Ophthalmol Visual Sci 1979;18:726–41.

De Groot J, Scott AB, Sindon A, Authier L. The human ocular anatomic position of rest: a quantitative study. In: Fells P, ed. Transactions of the Second Congress of the International Strabismological Association, Marseilles, May 1974. Marseilles: Diffusion Generale de Libraire, 1976:408–14.

Enright JT. Ocular translation and cyclotorsion due to changes in fixation distance. Vision Res 1980;20:595–601.

Helmholtz H. Treatise on physiological optics. Southall JPC, ed. New York: Dover, 1910.

Hering E. The theory of binocular vision (1868). Bridgeman B, Stark L, eds. trans New York: Plenum Press, 1977.

Hering E. Der Raumsinn und die Bewegungen des Auges. In: Hermann L, ed Handbook der Physiologie. Vol. 3. Leipzig: FCW Vogel, 1879:343–601.

Hubel DH, Wiesel TN. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J Physiol 1962;160:106–54.

Keller EL, Robinson DA. Abducens unit behavior in the monkey during vergenc eye movements. Vision Res 1971;12:369–82.

Ludvigh E. Control of ocular movements and visual interpretation of environment Arch Ophthalmol 1952;48:442–48.

Melville Jones G, Davies P. Adaptation of cat vestibulo-ocular reflex to 200 day of optically reversed vision. Brain Res 1976;103:554–55.

Miller J, Anstis T, Templeton WB. Saccadic plasticity: parametric adaptive contro by retinal feedback. J Exp Psychol Hum Percept Perform 1980;2:356–66.

Nakayama K. Photographic determination of the rotational state of the eye usin matrices. Am J Optom Physiol Opt 1974;51:736–42.

Nakayama K. Coordination of extraocular muscles. In: Lennerstrand G, Bach-y Rita P, eds. Basic Mechanisms in ocular motility and their clinical implications. New York: Pergamon Press, 1975:193–207.

Nakayama K. Geometrical and physiological aspects of depth perception. In: Benton S, ed. 3-D image processing. Society of Photo-Optical Instrumentatio Engineers Proceedings, 1977:1–8.

Nakayama K. A new technique to determine the primary position of the eye usin Listing's law. Am J Optom Physiol Opt 1978;55:331–36.

Nakayama K, Balliet R. Listing's law, eye position sense, and perception of th vertical. Vision Res 1977;17:453–57.

Nakayama K, Tyler CW, Appelman J. A new angle on the vertical horopter. Inves Ophthalmol 1977;(Suppl):82.

Optican LM, Robinson DA. Cerebellar dependent adaptive control of primat saccadic system. J Neurophysiol 1980;44:1058–76.

Robinson DA. The oculomotor control system: a review. Proc IEEE 1968 56:1032–49.

Robinson DA. Oculomotor unit behavior in the monkey. J Neurophysio 1970;33:393–404.

Robinson DA. A quantitative analysis of extraocular muscle coordination an squint. Invest Ophthalmol 1975;14:801.

Southall JPC. Introduction to physiological optics. New York: Dover 1961.

Westheimer G. Saccadic eye movements. In: Zikmund V, ed. The oculomoto system and brain function. Bratislava, Czechoslovakia: Publishing House o the Slovak Academy of Science, 1973.

Westheimer G, Blair S. Mapping the visual sensory onto the visual motor system 1972;12:490–96.