A Clinician-Friendly Approach to Understanding Listing's Law

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Objectives

At the conclusion of this program, participants will be able to:

1. Explain what Listing's law is.
2. Describe the functional significance of Listing's law.
3. Discuss the implications of Listing's law for ocular motor control, as well as the clinical implications of Listing's law.

CME Questions

1. Which of the following statements about Listing's law is FALSE?
   a. Listing's law states that when the head is fixed, the eye assumes only those orientations that can be reached from primary position by a single rotation about an axis in a plane called Listing's plane
   b. Listing's half-angle rule applies when the eye starts its rotation from an eccentric position
   c. Binocular extension of Listing's law applies during convergence
   d. Fixation, saccades, smooth pursuit and the vestibulo-ocular reflex all obey Listing's law

2. Which of the following statements is FALSE?
   a. The "primary position" defined in Listing's law is the same primary position used clinically
   b. Listing's law can be expressed using different coordinate systems, such as Fick coordinates, Helmholtz coordinates, rotation vectors and quaternions
   c. Listing's law represents an optimization strategy for motor efficiency
   d. The binocular extension of Listing's law represents an optimization strategy for both motor efficiency and binocular visual function

3. True or False: Ocular motor control for torsion can be implemented entirely by the mechanical properties of the orbit and extraocular muscles (ocular motor plant) for all classes of eye movements.

I. Introduction

The last ten years have brought a renewed interest in Listing's law, a kinematic principle that governs three-dimensional (horizontal, vertical and torsional) eye movements. While confusion abounds because of the advanced mathematical language used in the literature, a fundamental understanding of Listing's law is of great importance to clinicians. Here, I attempt to explain Listing's law using a non-mathematical approach. I will discuss what Listing's law is, how it is implemented, what its functional significance is and whether it is adaptive. I will also discuss its implications for ocular motor control, as well as its clinical significance.

II. Listing's Law

The eye rotates with three degrees of freedom. This means that the eye can rotate about: (1) a vertical axis to generate horizontal eye movements (abduction and adduction), (2) a horizontal axis to generate vertical eye movements (elevation and depression), and (3) the line of sight to generate torsional eye movements (excyclotorsion and incyclotorsion). In theory, the eye could assume an infinite number of torsional positions for any gaze direction (Figure 1). Figure 1A is a schematic of an eye directed straight ahead at the reader, and the thick black vertical (solid) line represents its superior pole, which is at 12 o'clock. Figures 1B to 1D show that there are many different torsional positions that the eye can adopt when it looks straight ahead: at 1 o'clock, 2 o'clock, 3 o'clock, etc.

If there are an infinite number of possible torsional positions for each gaze direction, does the eye adopt one or multiple torsional position(s) for a particular gaze direction? The answer to this question was provided by Listing's law. It states that, when the head is fixed, there is an eye position called *primary position*, and that the eye assumes only those orientations that can be reached from primary position by a single rotation about an axis in a plane called Listing's plane.[1] This plane is *orthogonal* to the line of sight when the eye is in primary position.

Listing's law is illustrated in Figure 2. The eye at the center is in primary position and the plane of the paper is Listing's plane, which is orthogonal to the line of sight. All the eye orientations drawn with solid lines accord with Listing's law, because they can be reached from primary position by rotating about axes (thick black solid lines) in Listing's plane. But the position drawn with dashed lines at the top center violates Listing's law, because the rotation to that orientation from primary position has its axis (thick dotted line) tilted out of Listing's plane.

III. Coordinate System

Listing's law can be expressed using different coordinate systems, such as Fick coordinates, Helmholtz coordinates, rotation vectors and quaternions. All have relative strengths and weaknesses, so which coordinate system to use depends on the problem at hand. The Helmholtz coordinate system is perhaps the most intuitively appealing to clinicians, and it is especially useful in presenting binocular data.[2] In Helmholtz's system, an eye position is subdivided into a series of three subrotations. Starting from primary position, the eye first undergoes a torsional rotation through angle T about the line of sight, then a horizontal rotation through angle H about a headfixed vertical axis, and finally a vertical rotation through angle V about the interaural axis. Expressed mathematically in Helmholtz coordinates, Listing's law says:

$$T = - HV / 2 \qquad (1)$$

where T represents torsional, H horizontal and V vertical angles in radians (not degrees). Positive directions for angles T, H and V are defined as clockwise, right and up, respectively, all from the subject's point of view.

As equation (1) makes clear, Listing's law requires that the Helmholtz-torsional angle of the eye varies as a function of horizontal and vertical eye position. Figure 3 depicts the torsional positions of the eye, represented by thin black lines with respect to the vertical meridian (dashed line), in different combinations of horizontal and vertical eye positions, as viewed by the examiner. If the eye is 30E down and 30E left (bottom right panel), then the eye (thin black line) rotates 7.9E (0.14 rad) counterclockwise from the subject's point of view (and clockwise from the examiner's point of view), with respect to the vertical meridian (dashed line). In other words, Listing's law specifies quantitatively the degree of ocular torsion for any given horizontal and vertical eye position. Any torsion that differs from that specified by equation (1) means that Listing's law is violated.

Listing, by the way, was a mathematician, and taught engineering in Hannover before he was appointed professor of physics at Göttingen University. He apparently formulated his law based on pure geometrical aesthetics. He never produced any formal publication about this law, and it was unclear whether he did any measurements at all. The significance of the law was not fully appreciated until Helmholtz verified it using afterimages and named it after Listing.[1]

The "primary position" defined in Listing's law (Listing's primary position) is not synonymous with the primary position used clinically. Listing's primary position is defined as the reference eye position from which all other eye positions can be reached by a single rotation about an axis that lies in Listing's plane, whereas the primary position used clinically refers to the straight ahead gaze position and roughly corresponds to the center of the ocular motor range.

IV. Listing's Half-Angle Rule

Listing's law holds during fixation, saccades and smooth pursuit.[3-5] It defines Listing's plane as orthogonal to the line of sight when the eye is in *primary* position. But what if the eye starts its rotation from an *eccentric eye position*? In this situation, the orientation of the eye is still determined by rotation about axes that lie in a plane, but this plane is no longer orthogonal to the line of sight; instead it is tilted in the same direction as the line of sight but only half as much.[3, 4] This relationship of Listing's plane to gaze angle is called *Listing's half-angle rule*.

Figure 4 illustrates Listing's half-angle rule. The dashed horizontal line represents the line of sight when the eye is in Listing's primary position, and the dashed vertical line represents Listing's plane, which is orthogonal to the line of sight. When the eye is *not* in primary position (i.e., in an eccentric position), say when it is looking up at angle α (solid arrow), then the new plane is rotated in the same direction, but only half as much as the line of sight, that is $\alpha/2$. For example, when the eye looks 30° up (α), then the new plane is rotated 15° up ($\alpha/2$), such that the angle between the new plane and the line of sight is now 75° (instead of 90°). Note that this new plane is now called the *velocity plane*, and that Listing's plane is a special name given to a unique velocity plane when it is *orthogonal* to the line of sight when the eye is in primary position.

V. Binocular Extension of Listing's Law

Listing's law applies when the eye fixates a target at optical infinity. However, the torsional position of the eye changes when the eyes converge on near object. During convergence, the orientation of each eye is still determined by rotation about axes that lie in a plane; however, this velocity plane is rotated temporally and roughly symmetrically in each eye [6-8], through about a quarter of the vergence angle (Figure 5).[9] These convergence-dependent changes of torsional position (that is, orientation of Listing's plane) have been referred to as the *binocular extension of Listing's law* or *L2*.[2, 7, 10] Note that L2 is a generalization of Listing's original, monocular law, and reduces it to when the vergence angle is zero, as when the eye fixates a distant object. The more the convergence, the more the temporal rotation of the plane, meaning that during convergence, there is a relative excyclotorsion on upgaze, and a relative incyclotorsion on downgaze, when one expresses torsion in Helmholtz coordinates.

VI. Half-Listing's Law Strategy for the VOR

An eye movement system that does not obey Listing's law is the vestibulo-ocular reflex (VOR). Listing's law only applies to eye rotation when the head is fixed, while the VOR generates compensatory eye movements when the head moves. By counter-rotating the eye at about the same speed as the head but in opposite direction, the VOR stabilizes the retinal image during head rotation. An ideal VOR that stabilizes the *entire* retinal image therefore requires the eye to rotate about the head's rotation axis, independent of the direction of the gaze line. However, empirical human data showed that when the head turns, the VOR does not counter-rotate the eye about exactly the same axis as the head, as one might expect for optimal retinal image stabilization. Nor does it tilt the eye's velocity plane by half as much as the gaze line, as required for full compliance to Listing's half-angle rule. Rather, during horizontal (about an earth-vertical axis) and vertical (about an earth-horizontal axis) head rotation, the eye's rotation axes tilt in the same direction but only about a quarter to a third as much as the gaze line [11-15], whereas during head roll, they tilt as far as the gaze line but in the *opposite* direction.[11, 12, 15] This characteristic behavior of the human VOR reflects a compromise strategy *halfway* between optimal retinal image stabilization (no tilting of eye's rotation axes with gaze line) and perfect compliance with Listing's law (tilting of eye's rotation axes half as much as the gaze line, i.e., half-angle rule). It is therefore referred to as the *half-Listing's law strategy* (Figure 6). Some authors have used the term "*quarter-angle rule*" to describe this VOR behavior. This term is confusing and should be avoided because it implies that the behavior of VOR represents another consequence of Listing's law, when, in fact, it does not.

To illustrate how the VOR breaks Listing's law, let us consider the torsional VOR when the head rolls between the right and left shoulders while looking straight ahead. In humans, the normal dynamic torsional VOR gain, defined as the ratio of the speed of eye rotation to the speed of head rotation, is about 0.7.[16] For example, *with the eye looking straight ahead*, when the head rolls at 10°/s, the eye counterrolls at about 7°/s; when the head rolls at 20°/s, it counterrolls at about 14°/s; when the head rolls at 30°/s, it counterrolls at about 21°/s, and so on. Thus without changing the gaze direction, the eye can roll into many different torsional positions depending on the amplitude of the head roll, and so VOR does not follow Listing's law.

VII. Implementation of Listing's Law

Listing's law holds during fixation, saccades and smooth pursuit, but fails during sleep [17, 18] and the vestibulo-ocular reflex (VOR).[19] This failure shows that the eye muscles are capable of violating Listing's law, so it is not the orbital plant but the neural commands driving fixation, saccades and pursuit that constrain the eye to obey the law.[4, 20] The muscles may, however, be arranged in a way that simplifies the brain's work in implementing Listing's law, [21-27] as in the "active-pulley hypothesis,"[26] where contraction of the *global* layer of the rectus muscle rotates the globe, while contraction of the *orbital* layer displaces the connective-tissue sleeves, or "pulleys," which direct the paths of the muscles.

The brain circuitry responsible for implementing Listing's law has not been identified. A major neural pathway underlying saccadic eye movements involves the superior colliculus,[28-30] which sends saccadic signals to the medium-lead burst neurons in the pontine paramedian reticular formation (PPRF) and the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF).[31, 32] These burst neurons, in turn, project to the extraocular motoneurons, the final common pathway for all eye movements.[31, 32] Electrical stimulation and three-dimensional recordings in alert monkeys have shown that the superior colliculus generates saccades that conform to Listing's law.[33] Stimulation of the medium-lead burst neurons in the caudal PPRF and riMLF evokes abnormal saccades that violate Listing's law.[34] These findings suggest that the circuitry implementing Listing's law is downstream from the superior colliculus and upstream from the medium-lead burst neurons.

VIII. Functional Significance of Listing's Law

Why does the brain go through the trouble of maintaining Listing's law, and why do different ocular motor systems implement the law differently?

Both Helmholtz[1] and Hering[35] felt that the purpose of Listing's law is to optimize visual processing. Hering [35] proposed that Listing's law optimizes certain aspects of image flow across the retina, thereby simplifying the neural processing of visual information. Assume, for example, that the eye begins in primary position and looks at the center of a pattern of radiating lines. As the eye follows any of the lines outward, the retinal image of the line will continue to fall along the same set of receptors as long as the eye follows Listing's law. This steady retinal image flow may simplify the brain's work in identifying and locating lines in space. Helmholtz's theory [1, 36] was more complex, but it too essentially proposed that Listing's law optimizes certain aspects of retinal image flow.

As retinal image flow depends on the eye's motion relative to space, both Hering and Helmholtz assumed that the eye rotates relative to *space* in the way dictated by Listing's law. In fact, it is only eye rotation relative to *head* that follows Listing's law. Owing to head movement, eye rotation relative to *space* does not.[37-39] This reference frame problem undermines any "visual" explanations of Listing's law that are based on retinal image flow.

Listing's law – an optimization strategy for motor efficiency. Fick and Wundt proposed that Listing's law enhances motor efficiency by minimizing the rotational eccentricity of the eye.[1, 40] Minimizing eccentricity may reduce the elastic recoiling force, and thereby minimize the work load on the eye muscles to maintain the globe in an eccentric position. It may also allow the eye to respond to incoming stimuli swiftly and flexibly. Just as a squash player tries to stay near center court so that no corner is unguarded, Listing's law keeps the eye near the center of its torsional range so it can quickly respond to unpredictable targets that may appear from any direction.

Binocular extension of Listing's law (L2) – an optimization strategy for both motor efficiency and binocular visual function. Recent evidence suggests that L2 may represent an optimization strategy that combines motor efficiency with stereo vision.[41-43] To achieve stereoscopic vision, the brain must search for corresponding image features on the two retinas. Stereo matching is a very complex task. For example, in a random-dot stereogram that presents 5000 dots to each eye, there are 5000^2 (i.e., 2.5×10^7) possible pairings between the right and left images, with only 5000 of them being correct. Yet, the brain can solve this type of random-dot stereogram within a few hundred milliseconds. How can the brain perform such a complex task within such a short time? The answer lies in the fact that, instead of searching the entire retina of each eye for matching features, the brain narrows its search by searching retina-fixed zones that are large enough to cover all the usual locations of the features in question.[43]

The smaller the search zone, the more efficient the stereo matching and the lighter the computational load on the brain. As discussed above, during monocular viewing of a distant object, Listing's law enhances motor efficiency by minimizing the rotational eccentricity of the eye. Unfortunately, optimizing motor efficiency does not also minimize the area of the search zone. Schreiber et al.[43] proposed that L2 represents a compromise strategy between the motor program that minimizes the rotational eccentricity of the eye (i.e., Listing's law), and the motor program that would minimize the size of the retinal search zones for stereo matching. In other words, the brain utilizes a strategy that strikes a balance between the motor, monocular advantages of Listing's law and the optimization of stereoscopic search.

IX. Listing's Law Is Adaptive

Recent studies in normal subjects using different stimuli paradigms[41, 42, 44, 45] and in patients with strabismus and ocular motor nerve palsy[46-50] have shown that Listing's law is adaptive.

We[49] investigated the effects of unilateral sixth nerve palsy on Listing's law by dividing patients into three groups: those with (1) *acute peripheral* palsy caused by a presumed ischemic lesion; (2) *chronic peripheral* palsy caused by a presumed ischemic lesion; and (3) *central* fascicular palsy caused by brainstem lesions. We found that, during fixation and saccades, Listing's law was violated in the paretic eye in patients with *acute peripheral* palsy, presumably because the lateral rectus muscle was paretic. In contrast, both the paretic and non-paretic eyes obeyed Listing's law in *chronic peripheral* palsy, even though the lateral rectus was still markedly weak, as evidenced by limited abduction and persistent esotropia. This recovery shows that the neural circuitry underlying Listing's law is adaptive, restoring the law despite a palsied muscle and possibly a mismatched pulley system. Neural adaptation must work by readjusting the innervations to the remaining extraocular muscles; it may also adjust their pulleys, though theoretically Listing's law could be restored with or without a new pattern of pulley placement and motion. In addition, we [49] found that patients with *central* fascicular palsy had abnormal ocular torsion in both the paretic and non-paretic eyes, regardless of the duration and severity of their palsy. This finding indicates that the neural adaptive mechanisms underlying Listing's law cannot restore it after certain brainstem lesions.

In another study, we [48] investigated patients with acute versus chronic unilateral fourth nerve palsy. We found that patients with acute palsy violated Listing's law, while those with chronic palsy obeyed it, providing further evidence that Listing's law is adaptive.

What is the functional advantage of reestablishing Listing's law after neural injury? As discussed, Listing's law permits quick responses to unpredictable targets that may appear from any direction by ensuring that the eye stays near the center of its torsional range. These motor advantages may be regained when patients with chronic ocular motor nerve palsy reestablish Listing's law.

X. Implications of Listing's Law for Ocular Motor Control

To appreciate the significance of Listing's law for ocular motor control, it is important to recognize that rotations are non-commutative. Non-commutativity means that the order of rotations affects the final orientation. This is illustrated in Figure 7. Starting from the same orientation, the schematic heads undergo identical rotations in different orders. In Figure 7A, the head first rotates 90° right and then 90° up, whereas in Figure 7B, it rotates first 90° up and then 90° right. As shown, the final orientations of the heads clearly differ.

Because rotations are non-commutative, traditional ocular motor concepts that were well established for the horizontal (one dimensional) system needed to be reevaluated. Let us take the velocity-to-position neural integrator as an example. During conjugate eye movements, the command that *moves* the eye to a new position is a velocity signal that is encoded by premotor neurons. During the motion, the neural integrator uses the velocity signal to compute a position signal. Once the eye reaches its desired position, the signal from the neural integrator holds the eye in its new position. In one dimension (1D), a *linear* velocity-to-position neural integrator could simply mathematically integrate the eye velocity into an eye position signal. In three dimensions (3D), however, because of non-commutativity, angular velocity is not the derivative of 3D eye position. Thus, in order to extend the neural integration concept from 1D to 3D, one hypothesis suggests that premotor neurons encode 3D angular velocity and that a *nonlinear* (multiplicative) neural integrator transforms the 3D angular velocity into 3D eye position signal.[4, 51] The computation is therefore more complex in 3D than in 1D.

However, this hypothesis has been challenged. Attempts to identify a clear neural representation of 3D angular velocity in the premotor pathway for saccades have been unsuccessful.[33, 52-55] This has prompted an alternate hypothesis which proposes that kinematically appropriate eye movements could be generated from the ocular motor plant itself. According to this hypothesis,[26, 27, 56] the rectus extraocular muscles run through adjustable connective tissue sheaths or "pulleys," which shift position on different gaze. With mobile "pulleys," a two-dimensional (2D) derivative of eye orientation (instead of 3D angular velocity) could be encoded by premotor neurons, and the neural integrator could then be linear, thereby simplifying the brain's work. In fact, a theoretical study has shown that appropriately placed pulleys can generate physiologically realistic *saccades* and implement the half-angle rule without a need for a nonlinear neural integrator.[24]

This latter hypothesis is viable in theory for saccades and pursuit but not for the VOR. In the VOR, semicircular canal afferents are known to encode 3D angular velocity rather than 2D derivative of eye orientation.[57, 58] In the pursuit system, recent evidence indicates that premotor pathways encode 3D angular velocity.[59] Thus, nonlinear mathematical operations, in addition to appropriately placed pulleys, are likely required for pursuit and the VOR.[15, 60] These issues of 3D eye control show that the study of Listing's law is not only relevant to our understanding of torsional control, but it also provides important insights into the fundamental neural and mechanical organization of the ocular motor system.

XI. Clinical Implications of Listing's Law

Because rotations in different orders produce different 3D orientation (non-commutativity), there is no *a priori* reason why a specific torsional orientation should be defined for each position of gaze, as required by Listing's law. If the brain and the ocular motor plant orchestrate to control torsional eye position with such precision, there must be strong benefits in doing so. Traditionally, the clinical evaluations of strabismus and strabismus surgery have mainly focused on horizontal and vertical alignment; little is known about the relationship between torsion, motor efficiency and stereo vision. To date, a few studies[47, 61-65] have used a three-dimensional approach to investigate the effects of strabismus and strabismus surgery. However, because these studies examined a heterogeneous group of patients who had different forms of strabismus and different types of operations, it is difficult to draw any conclusion at the present time. Several questions remain unanswered. For example, what are the effects of strabismus and strabismus surgery on 3D orientation of the eye? What are the consequences of surgery for torsion despite good eye realignment? How do neural commands and orbital mechanical factors (including pulleys) interact to control 3D eye movements during normal and diseased states? What type of surgery would best optimize ocular alignment, motor efficiency and stereo vision? The answers to these questions will have important clinical implications for the optimal management of strabismus.

Answers to CME Questions

1. d
2. a
3. False

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Figure 1

The eye can theoretically assume an infinite number of torsional positions for any position of gaze. (A) A schematic of an eye directed straight ahead at the reader, with the thick black vertical (solid) line represents its superior pole, which is at 12 o'clock. (B) to (D) There are many different torsional positions that the eye can adopt when it looks straight ahead: (B) at 1 o'clock, (C) 2 o'clock, (D) 3 o'clock, and so on.

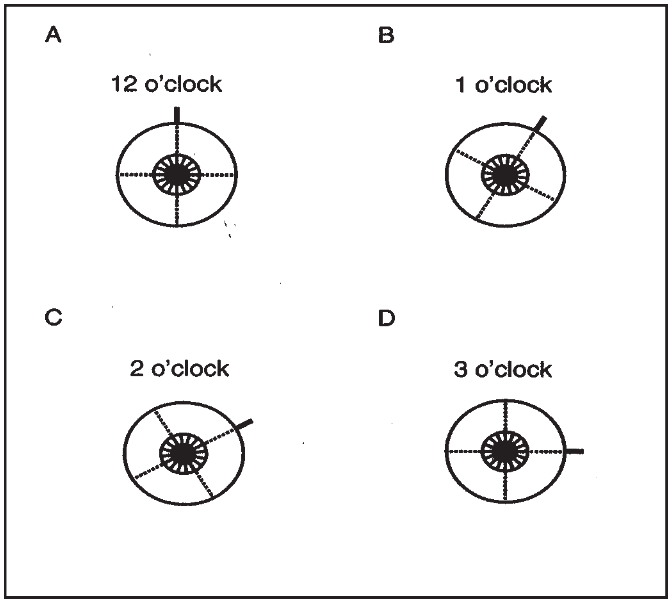


Figure 2

The nine orientations drawn in solid lines accord with Listing's law, because they are attainable by rotating from primary position (center) about axes (thick black solid lines) lying in Listing's plane (the plane of the paper). The position drawn in dashed lines at top center does not fit Listing's law because the rotation to this position from primary position occurs about an axis (thick dotted line) that is tilted out of primary position. (Redrawn from Wong AM, Sharpe JA, Tweed D: Adaptive neural mechanism for Listing's law revealed in patients with fourth nerve palsy. *Invest Ophthalmol Vis Sci* 2002; 43: 1796-803.)

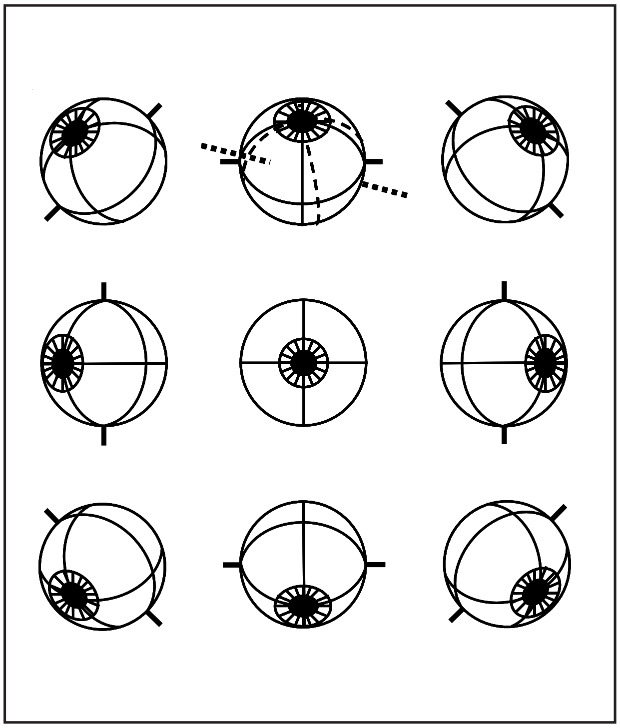


Figure 3

Torsional positions of the eye, as represented by thin black lines with respect to the vertical meridian (dashed line), in different combinations of horizontal and vertical eye positions, as viewed by the examiner. If the eye is 30E down and 30E left (bottom right panel), then the eye (thin black line) rotates 7.9E (0.14 rad) counterclockwise from the subject's point of view (and clockwise from the examiner's point of view), with respect to the vertical meridian (dashed line). CW, clockwise from the subject's reference; CCW, counterclockwise from the subject's reference. Note that the crosses represent the torsional positions of the subject's eye, not afterimages viewed by the subject. (Redrawn from Wong AM, Tweed D, Sharpe JA: Adaptive neural mechanism for Listing's law revealed in patients with sixth nerve palsy. *Invest Ophthalmol Vis Sci* 2002; 43: 112-9.)

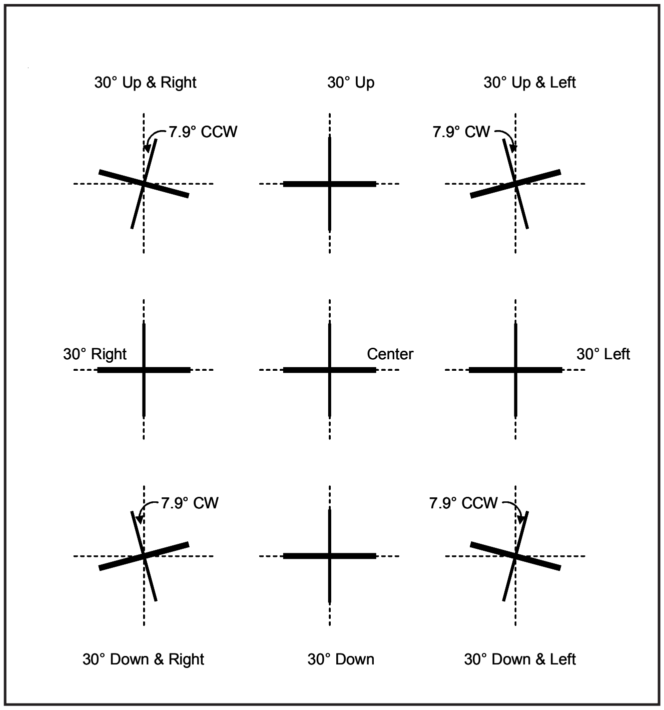


Figure 4

Listing's half-angle rule for saccades and smooth pursuit. The dashed horizontal line represents the line of sight when the eye is in primary position, and the dashed vertical line represents Listing's plane, which is orthogonal to the line of sight. When the eye starts from an eccentric position (angle α, solid arrow), the orientation of the eye is determined by rotation about axes that lie in a plane. This plane is rotated in the same direction, but only half as much as the line of sight, that is $\alpha/2$.

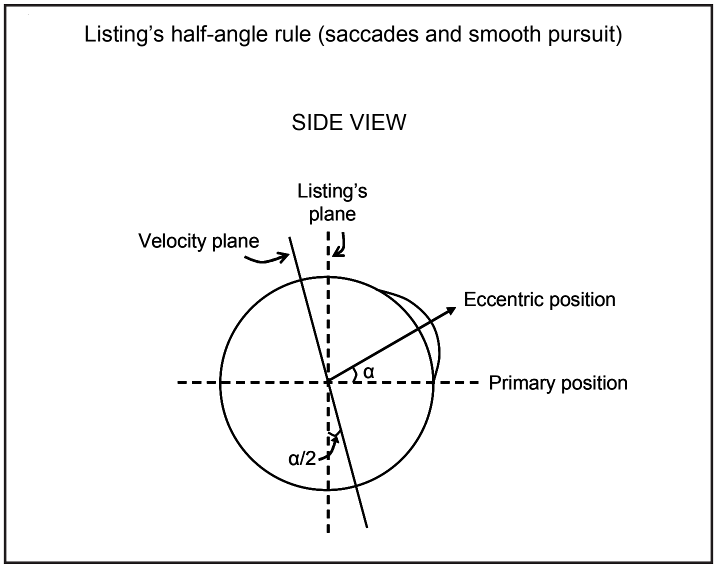
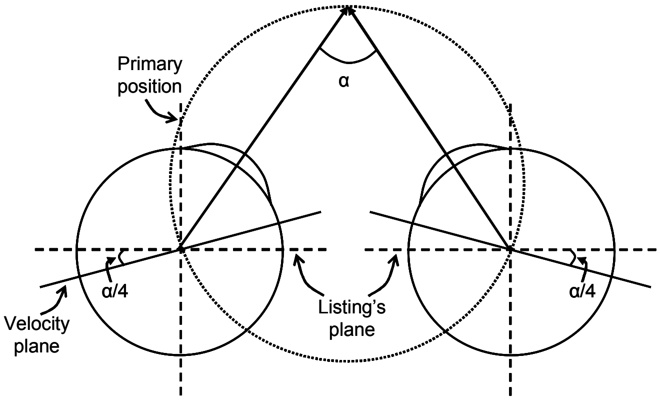


Figure 5

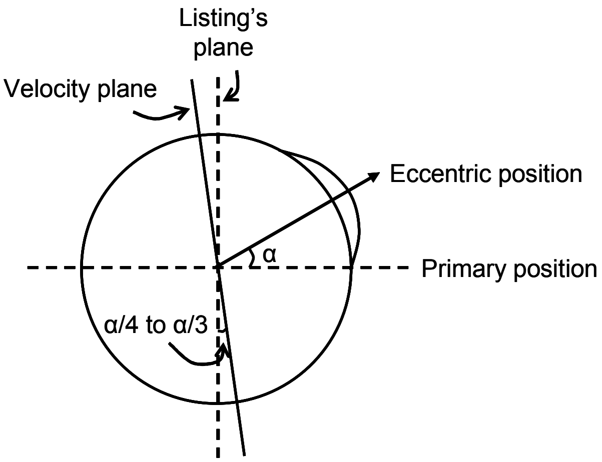
Binocular extension of Listing's law (vergence)

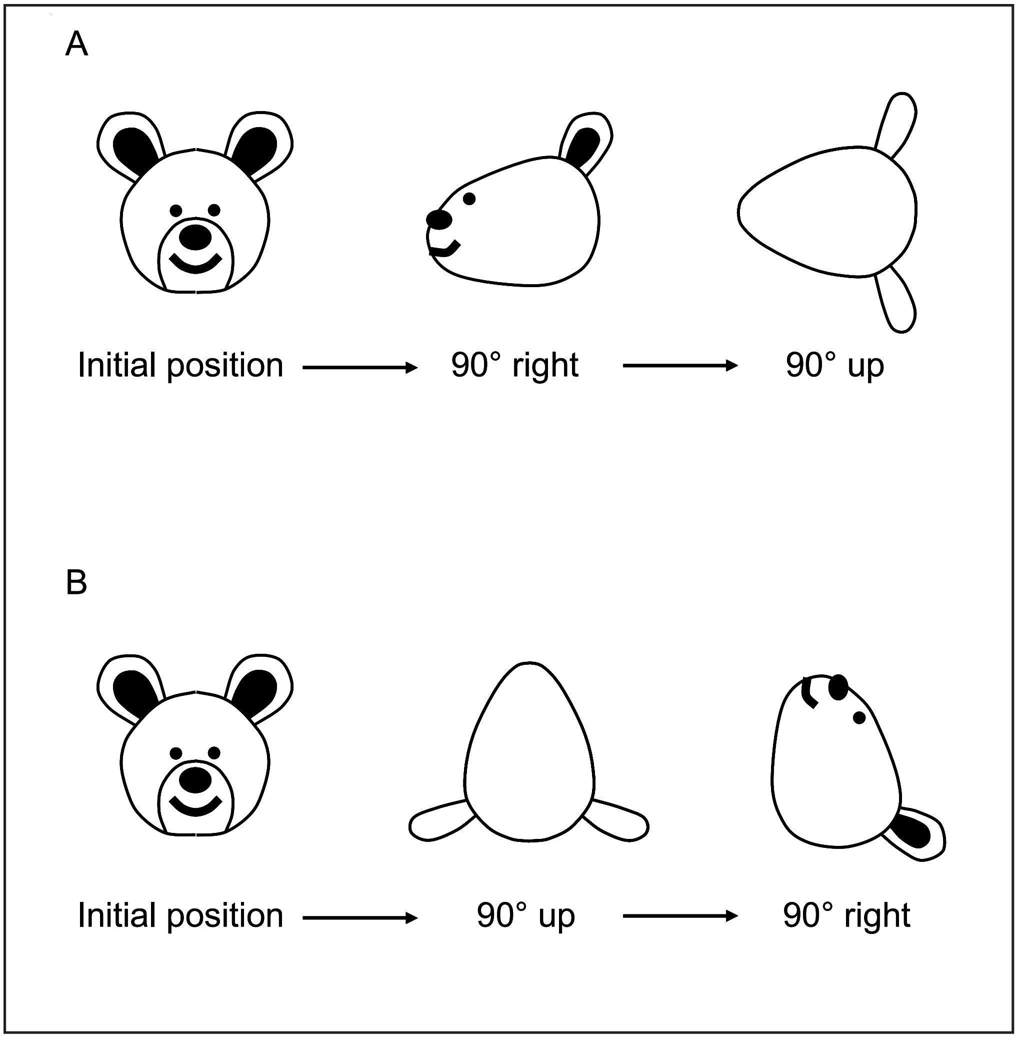
TOP VIEW



Half Listing's law strategy (VOR)

SIDE VIEW




A
Initial position → 90° right → 90° up
B
Initial position → 90° up → 90° right