Vision Res. Vol. 17, pp. 453 to 457. Pergamon Press 1977. Printed in Great Britain.

LISTING'S LAW, EYE POSITION SENSE, AND PERCEPTION OF THE VERTICAL

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(*Received* 16 *June* 1976; *in revised form* 30 *August* 1976)

Abstract—The vertical meridian of the eye does not remain vertical as the eye moves into oblique positions of gaze, but is tilted according to Listing's Law. In order to measure the relation between eye torsion and the apparent vertical, observers sat in darkness and set a luminous line to vertical for different positions of gaze. The responses of the subjects were not veridical, but deviated by an amount which was proportional to the torsion of the eye. Two conclusions were drawn: (1) there exists an extraretinal eye position signal which varies linearly with the torsion of the eye, (2) the gain of the signal is much less than 1.0 and is thus insufficient to insure a correct perception of the vertical.

INTRODUCTION

As we turn our head and eyes, vertical lines in the environment do not always remain vertical on the retina, yet ordinarily we experience little noticeable change in the apparent vertical. Thus, in spite of the changing retinotopic array, we preserve a sense of the objective vertical. Many studies indicate that both visual and body position information play a role in maintaining this perceptual invariance, although the exact relation between the various factors remains a subject of dispute (Witkin and Asch, 1948a,b; Howard and Templeton, 1966).

With respect to studying the role of body position sense, investigators have removed visual context cues for judgments of vertical for different spatial orientations of the head and body. The results of such experiments are often complex and are difficult to interpret (Howard and Templeton, 1966) due in part to the fact that gravity receptors (otoliths), neck proprioceptors and eye position sense are all potential sources of information or misinformation. Therefore an experimental outcome can be due to the operation of many sub-systems operating simultaneously.

The experiment to be described in this paper has the advantage of simplicity inasmuch as we were able to assess the perception of the vertical when *only* eye position is altered. Under these circumstances the results have a particularly simple form.

METHOD

The logic of the experiment rests on the fact that as the eye moves into oblique gaze directions, the vertical meridian of the eye does not remain vertical but is rotated by an amount described by Listing's Law (Helmholtz, 1910; Southall, 1937; Nakayama, 1974). This law states that the angular orientation of the vertical meridian of the eye (ψ) will be a single-valued function of the direction of gaze. For example, if we choose the angles θ and ϕ to be horizontal and vertical rotations in a Fick system of axes, the torsion of the vertical retinal meridian can be expressed by (Southall, 1937; Robinson, 1963):

$$\psi = \sin^{-1}\frac{\sin\theta\sin\phi}{(1+\cos\theta\cos\phi)}. \qquad (1)$$

Thus, for our purposes we can vary ψ, the orientation of the vertical, simply by having the observer make fixations into different oblique directions of gaze. Then we can measure the relation between eye orientation and the perception of the vertical.

Measurement of eye orientation

In order to quantify eye orientation for any position of gaze, we utilized an afterimage matching technique (Helmholtz, 1910). Under monocular conditions, the observer was placed on a bite-bar in front of a tangent screen viewed at 89 cm. The observer fixated the center of the screen and received a thin vertical flash (1/8° × 3°). This led to a vivid and crisp foveal afterimage. Sometimes an overhead light was flashed at approx 1 Hz to aid in the continuous visibility of the afterimage (Magnussen and Torjussan, 1974). A rotatable servo-driven vertical line was placed at various positions on the tangent screen and the observer rotated the line by a potentiometer control until the afterimage was parallel to the comparison line.

The angle of afterimage on the tangent screen was read out directly by a digital voltmeter from the servomotor potentiometer. The accuracy of this reading was better than 4′.

To calculate the torsion of the eye, one must take account of the fact that the angle of the projected afterimage or comparison line on the tangent screen is not the same as the angle of torsion of the eye. This discrepancy is due to perspective distortion and can be readily corrected by an expression [equation (A6)] which is derived in the Appendix.

Measurements of perceived vertical

The procedure to measure the orientation of an observer's perceived vertical was a variation of our procedure to measure eye torsion. In this case, only an electroluminescent target line was visible against a background of complete darkness and there was no afterimage. The readout of the perceived vertical was obtained on the same digital voltmeter and the same correction for perspective distortion [equation (A6)] was applied. For the selected gaze directions, the observer was instructed to set the luminous line to vertical. At no time during this procedure was the observer allowed to see whether the judgments were correct. This precaution was taken to eliminate opportunities for a sensory recalibration by the observer.

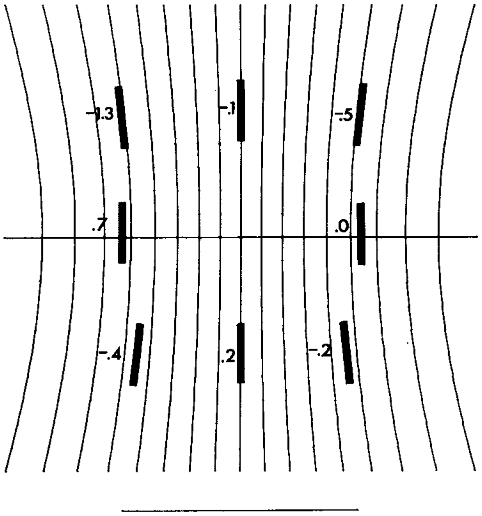

Fig. 1. Dark bars represent afterimage alignments of subject FM as they appear on the tangent screet. If Listing's Law is correct, these afterimage settings should be tangent to one of a family of hyperbolic curves described by Helmholtz. Numbers represent measured deviations from Listing's Law in degrees. Bottom horizontal calibration represents the eye–screen distance (89 cm), and thus subtends 45° if one end is placed on the screen center. In terms of the angles θ and ϕ, they correspond to 26.8 and 24.2°, respectively, for the upper right setting.

RESULTS

The data were obtained from three observers (age range 30–35), none of whom knew the purposes of the experiment. It was relatively easy to match the afterimage to the target line and as a consequence, the standard errors for such judgments were low, in the range of approximately 0.1–0.3° for 10 settings. Comparing the orientation of the afterimage with that of Listing's Law, we find a close fit. As an example, in Fig. 1 we have plotted the orientation of the afterimage for nine selected positions of gaze as they actually appear on the tangent screen. If the eye obeys Listing's Law, these afterimage settings should be tangent to a family of hyperbolas which are projections of vertical direction circles in a spherical field of fixation (Helmholtz, 1910; Southall, 1937). The judged orientations of these afterimages fall very close to these theoretical curves.

The setting of a line to the vertical in a dark room was more difficult for the observers but could be obtained with sufficient accuracy (S.E. for 10 observations = 0.4°) for our purposes. In addition, there was often a small but consistent error in judging the vertical in the primary position (looking straight ahead). Figure 2 depicts the appearance of the afterimage on the tangent screen in different positions of gaze superimposed with the setting of subjective vertical in the darkened room. For the purpose of better visualization, all orientation deviations from the vertical have been magnified by a factor of three.

Qualitatively, the results are in the same direction as Listing's Law, i.e. the judgments of the vertical become rotated clockwise in the upper right and lower left fixation fields and the reverse is true for the remaining quadrants. Quantitatively, however, there is less deviation for the perceived vertical than for the objective torsion.

In order to obtain a better description of how the judgment of the vertical varied with eye torsion, we needed to vary eye torsion systematically over a range. This was accomplished by selecting a number of gaze directions all along a horizontal line 27° above the primary plane of regard. θ ranged from $-24°$ to $+24°$ for SH and FM, $-18°$ to $+18°$ for AA. In this case Listing's Law [equation (1)] predicts that the vertical meridan of the retina will rotate from negative to positive as the eye proceeds from left to right. Eye torsion and the perception of the vertical were obtained for these gaze directions and in addition, measurements were also taken in the primary position to measure the constant error of the judgment of the vertical. This constant error was subtracted from all angular values of the perceived vertical.[1]

In Fig. 3 we show that the objective orientation of a line which is perceived to be vertical is a function of the torsion of the eye for the three observers. If

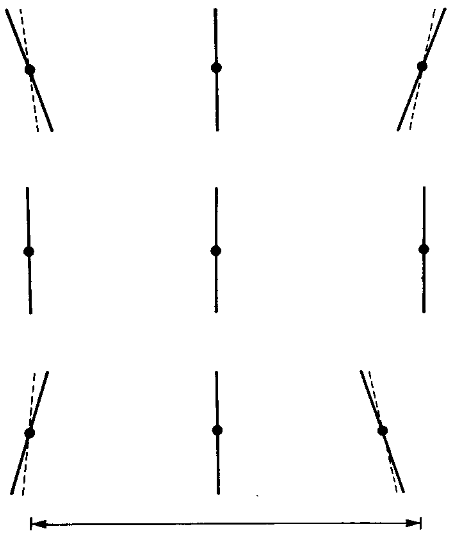

Fig. 2. Superposition of afterimage settings (solid lines) with the settings of the perceived vertical (dashed lines). For purposes of visualization, all angular deviations from the vertical have been magnified by a factor of three. For secondary gaze directions (pure horizontal or pure vertical rotations) these settings are virtually indistinguishable. Bottom horizontal calibration represents the eye–screen distance (89 cm).

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[1] Theoretically it might seem more appropriate to subtract the constant error of the vertical judgment when the eye was looking directly up (in a secondary position of gaze) on the elevated horizontal line; for in this case, equation (1) would predict that the torsion of the eye would be zero. In practice, however, this assumes that the center of the screen is exactly coincident with the primary direction of regard; otherwise the eye torsion in this elevated secondary position would deviate slightly from zero. With this in mind it was considered to be more reasonable to use the judgment of the vertical at the screen center as the indication of the constant error, as it is in this position that the eye torsion is most likely to be closest to zero.

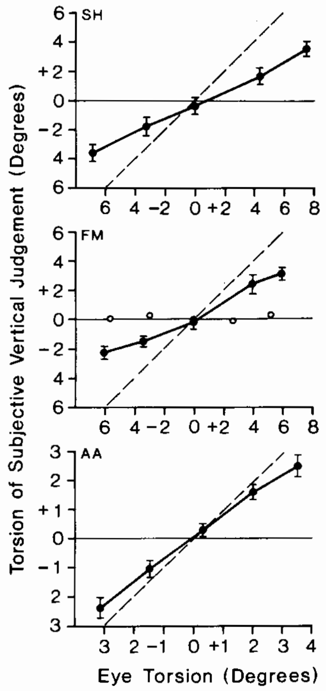

Fig. 3. Solid dots represent the relationship between the perceived vertical and eye torsion for three observers in the absence of visual context cues. For observer FM the open circles are for the same judgement *with* the presence of visual context cues. Error bars indicate 1 S.E.

the judgments were veridical, one would expect to see no change in the orientation of this vertical judgment and thus the results would fall on a straight line with zero slope (solid line). On the other hand, if the observer were to utilize only the retinotopic orientation of the stimulus, one would expect the data to fall on a line with a slope of one (dashed line). For all observers neither is the case but the results are of an intermediate form. In two cases (SH and FM), the result is approximately halfway between the two, whereas in a third case (AA) the results are close to but very definitely fall short of a slope of one, the retinotopic prediction.

Thus, the results do not follow either rule but there is a linearity in the manner in which the judgement of the vertical deviates from either prediction, and it is clear that this deviation is proportional to the amount of eye torsion. If we assume the retinotopic signal to be scaled correctly in the registration of the line orientation on the retina, the deviation from the retinotopic prediction (dashed line with a slope of one) can be plotted (Fig. 4) and this deviation can be interpreted as a measure of the oculomotor contribution signal (in degrees) for different amounts of eye torsion.

In one control experiment, the observer made judgments of the vertical but in this case the room lights were left on, providing the observer with all the natural everyday cues, including the vertical borders of the screen. Under these circumstances, the judgment of the vertical was very close to veridical (Fig. 3, open circles), indicating the importance of visual context cues under ordinary viewing conditions.

DISCUSSION

In the absence of contextual cues, only two sources of information are available for the subject to make a judgment of the vertical for an isolated line segment: retinotopic and eye position information. Furthermore, in cases where the physiological vertical meridian of the eye does not remain objectively vertical, both sources of information are required.

The results of the present experiments indicate that the sense of the vertical is not veridical when the eye rotates, and this implies an improper utilization of eye position information. The lack of appropriate compensation for oculomotor action is of interest because, in order to execute eye movements with the specificity of Listing's and Donders' Law, the oculomotor system must have an exact signal regarding eye position in the orbit (Westheimer, 1973; Nakayama, 1975). Thus, a precise position sense of the eye (either via proprioception or efference copy) must be available to the nervous system at least at the level of motor control. The data of the present experiment indicate the existence of an additional extra-retinal eye position signal which is available to a perceptual system as well. For although the judgments of the vertical are not veridical, they clearly do not conform to a retinotopic prediction and hence imply the utilization of a compensatory signal of eye torsion. The gain of this signal is not sufficient, however, to insure veridicality. For example, if we assume the retinotopic orientation signal to be correctly proportional to retinal stimulus orientation, we can take the slope of the deviation curve of Fig. 4 as the gain of the extra-retinal position signal when it is subtracted from the retinal signal itself. The gain ranges from 0.25 to 0.53 and is clearly less than the gain of 1.0 necessary to provide an appropriate compensation.

The results of this experiment may be taken as yet another example of the tendency of oculomotor information to assist but not be sufficient to insure the

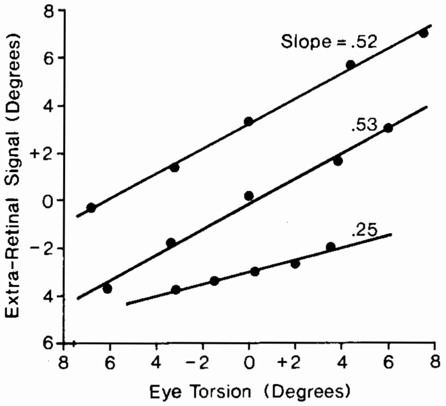

Fig. 4. The extra-retinal position signal as a function of eye torsion. Deviation of the judgement of the vertical from a retinotopic prediction (i.e. extraretinal contribution) is plotted against eye torsion for three subjects (from top to bottom: SH, FM and AA). Upper and lower curves have been displaced by 3°. Numbers represent the slope of the best fit linear regression and are taken as the gain of the extra-retinal signal for each subject.

veridicality of perception. Other examples include the role of convergence in determining depth (Gogel, 1961; Foley and Richards, 1972) and the role of eye versions to determine perceived visual direction (Matin, 1972). Such results taken together underline the importance of additional visual information in maintaining the perceptual invariances of orientation, depth and direction during eye movements.

Acknowledgements—We wish to thank Dr. C. W. Tyler for a critical reading of the paper and Mrs. Eleanor Lidolf for typing the manuscript.

This research was supported by National Institutes of Health grants No. EY-01582, No. EY-00299 and the Smith-Kettlewell Eye Research Foundation.

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APPENDIX

DETERMINATION OF EYE TORSION AND GAZE DIRECTIONS FROM AFTERIMAGE PROJECTIONS ON A TANGENT SCREEN

Below we describe the relationship between the rotation of the eyes (in spherical angles) and the position of an afterimage projected onto the surface of a frontal tangent screen. We define a right-handed coordinate system centered in the right eye and which is fixed in the head. The horizontal and vertical axes are formed by X and Z, respectively, and the Y-axis forms the fixation direction when the eye is looking straight ahead and fixating the vertical afterimage target (Fig. 5).

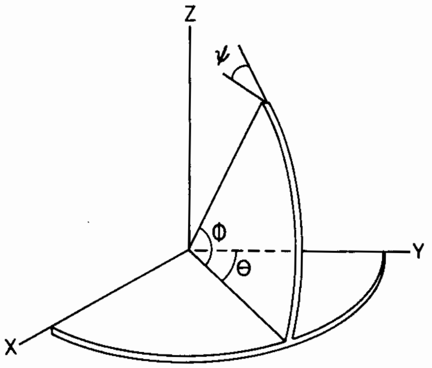

Fig. 5. Fick system of axes to describe eye rotations from the primary position. Three angles θ, ϕ and ψ are necessary to uniquely define the rotation of the eye. X and Z represent the horizontal and vertical orbital axes, respectively. Y represents the primary direction of regard.

In addition, we define a set of axes X', Y', Z' which rotate *with* the eye and which coincide with the head based axes when the eye is looking straight ahead. Three spherical angles are chosen to describe the eye's rotation from this reference position. The angle θ is a left-handed horizontal rotation about Z', ϕ is a right-handed vertical rotation about X' and ψ is a right-handed torsional rotation about Y'.

Scaling the distance of the tangent screen to the eye to be one, the equation of the screen is simply $Y = 1$ and the position of the center of the projected afterimage on the screen can be defined by the position of the matching target and specified as X_a, 1, Z_a (see Fig. 6). The angle the projected afterimage makes with the vertical on the screen is designated ψ'. By trigonometry, the determination of θ and ϕ, can be observed to be:

$$\theta = \tan^{-1} X_a \tag{A1}$$

$$\phi = \tan^{-1} (Z_a \cos \theta). \tag{A2}$$

The relationship between ψ' (the orientation of the afterimage) and ψ (the eye orientation) can be appreciated by considering two planes: a vertical plane passing through the visual axis and an afterimage plane passing through

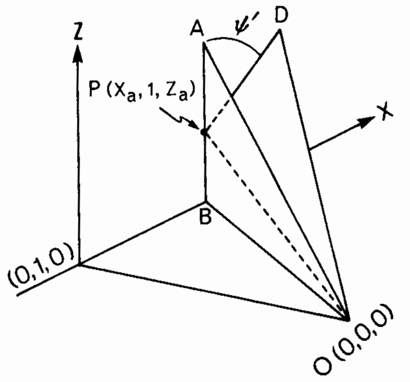

Fig. 6. Pictorial description relating the projection of an afterimage on a screen with the torsion of the eye. The eye is fixing on point P and thus the afterimage is centered on P. The vertical plane through the line of fixation is formed by OBA. The afterimage plane is formed by OPD. The torsion of the eye ψ is equivalent to the dihedral angle between these two planes.

the center of the eye and the projected afterimage on the screen. It should be clear that the torsion of the eye ψ is equivalent to the dihedral angle between these two planes (Fig. 6). The equation for the vertical plane is:

$$X - X_a Y = 0. \tag{A3}$$

The equation of the afterimage plane is defined by three points: the eye center (0, 0, 0), the fixation position on the tangent screen $(X_a, 1, Z_a)$ and a point on the screen on the projected afterimage line $(X_a + \sin\psi', 1, Z_a + \cos\psi')$. In determinant form, the equation of the afterimage plane is:

$$\begin{vmatrix} X & Y & Z & 1 \\ 0 & 0 & 0 & 1 \\ X_a & 1 & Z_a & 1 \\ X_a + \sin\psi' & 1 & Z_a + \cos\psi' & 1 \end{vmatrix} = 0, \tag{A4}$$

which is equivalent to:

$$\cos\psi' X + (X_a\cos\psi' - Z_a\sin\psi')Y + \sin\psi' Z = 0. \tag{A5}$$

Equations (A3) and (A5) represent the vertical and afterimage planes, respectively, and the angle between these two planes, the torsion of the eye, is identical to the angle between vectors which are perpendicular to these respective planes. Since the coefficients of equations of (A3) and (A5) form vectors normal to each plane, the angle between these two planes can be determined from the angle between these two vectors. This angle can be expressed in terms of their vector scalar product (dot product). Thus:

$$\cos\psi = \frac{\cos\psi' - X_a(X_a\cos\psi' - Z_a\sin\psi')}{\sqrt{(1 + X_a^2)}\sqrt{[1 + (X_a\cos\psi' - Z_a\sin\psi')^2]}} \tag{A6}$$

is the expression relating the torsion of the eye ψ to the position and orientation of an afterimage projected on a tangent screen.