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The adaptive significance of the location of the optic disk

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Abstract. Although the 'filling in' of each blind spot by healthy retina in the other eye has long been described as an adaptive property of the spatial arrangement of the optic disks, an explanation of why the disks are specifically located where they are has yet to be proposed. A rationale for their horizontal position in humans is offered that is based on the projections of the blind spots in visual space in relation to fixation distance and to the protrusion of the bony facial occlusion of the nose bridge.

1 Introduction

In man and many animals the optic nerve enters the retina as a structure known as the optic disk or papilla. The disk is not light sensitive and corresponds perceptually to the 'blind spot', a normal scotoma in the visual field. The disk may be quite large, especially in diurnal animals, owing to the many nerve fibers required by the large number of cones present (Walls 1942). In man the blind spot is oval, subtending some 5 deg horizontally and 7 deg vertically, and centered approximately 15 - 16 deg temporally and 1 - 2 deg inferiorly in the visual field[1].

In animals with significant binocular overlap, functional retina in one eye fills the region that corresponds to the blind spot in the other. It is commonly believed that this prevents objects in space from casting images on both blind spots at once, but disparity of location in the two eyes is in fact not sufficient to achieve this (see figure 1). Aside from the requirement that the blind spots fall within the region of binocular overlap, nature's choice of retinal position for the optic disk has until now remained obscure. In this report I present analyses of the projections of the human blind spot in visual space that can account for its horizontal position on the retina, and that provide a rationale for why the blind spot is located (i) on nasal rather than temporal retina (ie, in the temporal visual field), (ii) at least 13 deg eccentric to the fovea, and (iii) at an otherwise minimally eccentric position.

2 Theory

Common to all the analyses presented below is the observation that scotomas in one or both eyes are capable of producing blindness to a volume of visual space. Under some binocular viewing conditions scotomas in both eyes can cause blindness to a finite volume (figure 1a); in other binocular and some monocular cases scotomas can produce blindness to an infinite volume (figure 1b). Scotomas that produce blindness to any volume of space will be called *volume scotomas*. Note that many scotomas are not volume scotomas, because the blindness that is produced in one eye can be compensated for by healthy retina in the other eye. Under most conditions the normal blind spot is an ordinary monocular scotoma. Obviously, those areas of space within which an organism can detect objects define a field of greater functional significance than do the field maps of single retinas that we obtain from ordinary perimetry. It is through analysis of this three-dimensional functional visual field that the adaptive significance of the location of the disk emerges.

In all the examples presented in this paper the blind spot is assumed to be located 15.5 deg in the temporal visual field and to subtend 5 deg horizontally. Ocular dimensions for a schematic eye are taken as follows: radius of curvature of the eye, 1.1 cm; distance between the center of rotation and the nodal point of the eye, 0.6 cm; distance between the centers of rotation of the two eyes, 6.5 cm.

2.1 *Why the disk is located on nasal rather than temporal retina*

Consider what would happen to the functional visual field were the optic disk positioned on temporal rather than nasal retina but at the same eccentricity of 15.5 deg (figure 2b). In this case the functional visual field would have a volume scotoma much closer to the observer than the fixation distance and hence quite hazardously located. Compare this with the actual position of the normal blind spot on nasal retina (ie, in the temporal visual field) (figure 2a). For a wide range of convergence angles there is no volume blindness—all points in space that fall within the region of binocular overlap stimulate functional retina in one or the other eye.

2.2 *Why the disk falls at least 13 deg eccentric to the fovea*

There is a small range of convergence angles for which the blind spot does produce a volume scotoma when fixation is to distances less than 14.1 cm. At the 14.1 cm viewing distance each eye has to rotate inward 13 deg, so that the visual direction of the central boundaries of the blind spots are parallel to each other and to the mid-sagittal plane (figure 3a). Any increase in convergence will produce a volume scotoma farther than the plane of fixation and at a relatively safe distance. It is interesting to note that Mariotte (1717), generally credited with discovery of the blind spot, demonstrated with very close convergence the simultaneous disappearance into the blind spots of two objects fastened to a distant wall.

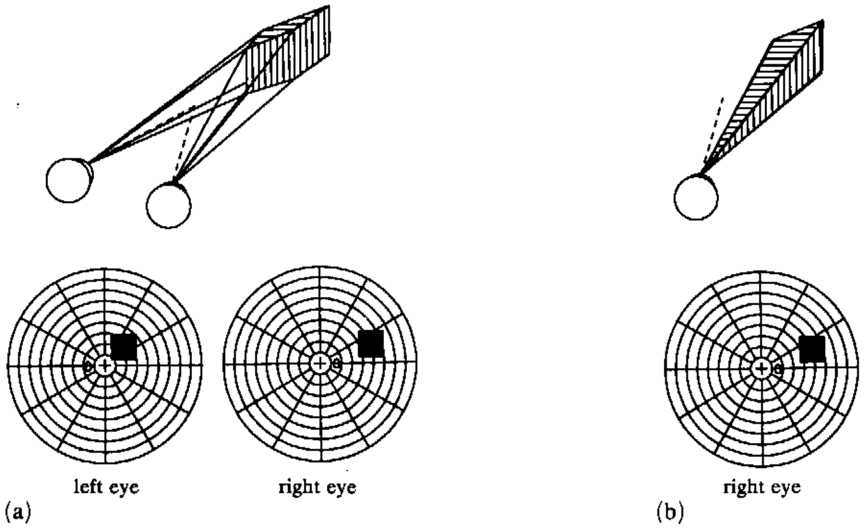

Figure 1. Volume scotomas (hatched areas, upper half of figure) arising from schematic square scotomas of the visual fields (lower half of figure). Dashed lines show projections of the foveas. (a) A volume scotoma arising at the intersection of the projections of scotomas with the same vertical position in the two eyes. Note that the component monocular scotomas need not share horizontal coordinate values, and that the location in depth of points in the volume will be determined by the horizontal retinal disparities among monocular scotomatous points. (b) The volume scotoma that would be produced by the same monocular scotoma of the right eye, were the left eye closed or otherwise occluded. In this case the volume scotoma forms a pyramid with its base at infinity.

This value of 14.1 cm corresponds roughly, by several measures, to the near limit of vision. First, the standard clinically acceptable normal range of the 'near point' of convergence at which one or both normal eyes will break fixation to an approaching stimulus is 8 – 10 cm. This measure, however, is always somewhat of an underestimate owing to the constant errors introduced by both the oculomotor response latency of the patient and the response time of the clinician; observed values are also highly dependent on training (Von Noorden 1980). Second, although the near point of accommodation, which generally determines the near point of simultaneously clear and single vision (Alpern 1969; Hofstetter 1945), declines dramatically with age, subjective clinical measures show it to be about 7 cm at the age of ten years (Turner 1958); objective measurements of the accommodative near point would give a higher value (Hamasaki et al 1956). Finally, note that most individuals cannot comfortably maintain accommodation to less than three times their near point distance for extended periods (Westheimer 1986). Thus although there is high variability for 'near point' measurements across individuals and method of measurement, they are consistent with the positioning of the blind spot at a point sufficiently temporal in the visual field to avoid a volume scotoma under ordinary viewing conditions.

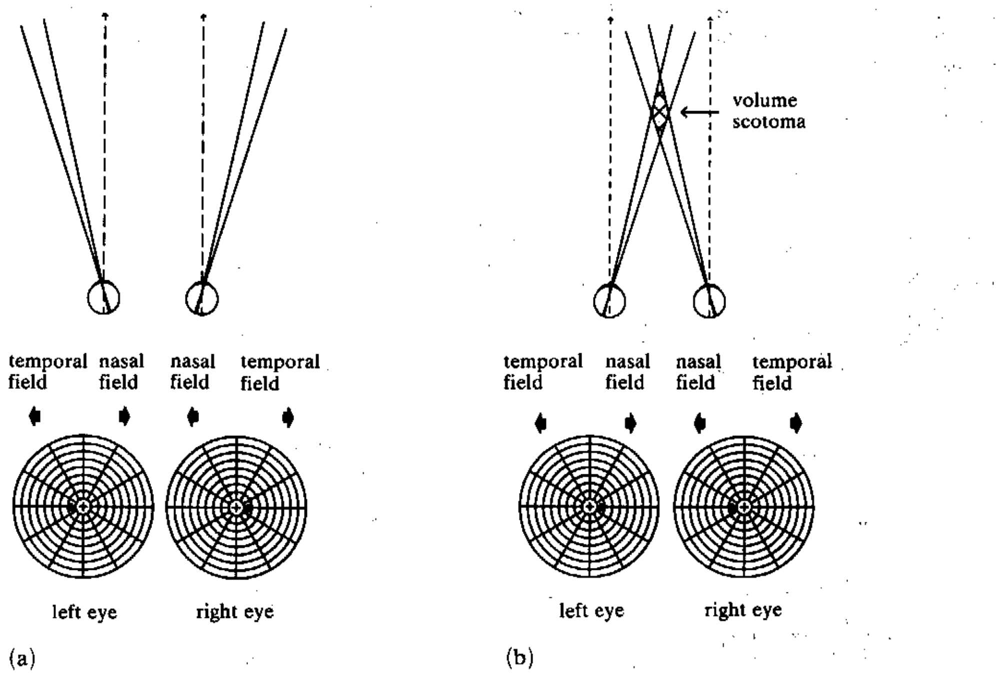

Figure 2. Visual fields (lower half of figure) and top views of projections of blind spots in visual space (upper half of figure) when the eyes have zero convergence with (a) the blind spots located in their normal temporal position in the visual fields, and (b) the blind spots located in the nasal field. If the disks were located at their normal eccentricity but on temporal retina (nasal field), the blind spots would result in a volume scotoma closer to the observer than the fixation distance.

2.3 *Why the disk is otherwise minimally eccentric*

The argument thus far is that the central boundaries of the optic disk are positioned to avoid the functional blindness that would otherwise result from having an optic disk, except that which arises from extremely close viewing. Furthermore, the volume scotoma that arises from close viewing is positioned far from the viewer in visual space.

The question remains, however, as to why the disk is not located even more nasally on the retinas, and more temporally in the visual fields. After all, a more eccentric disk

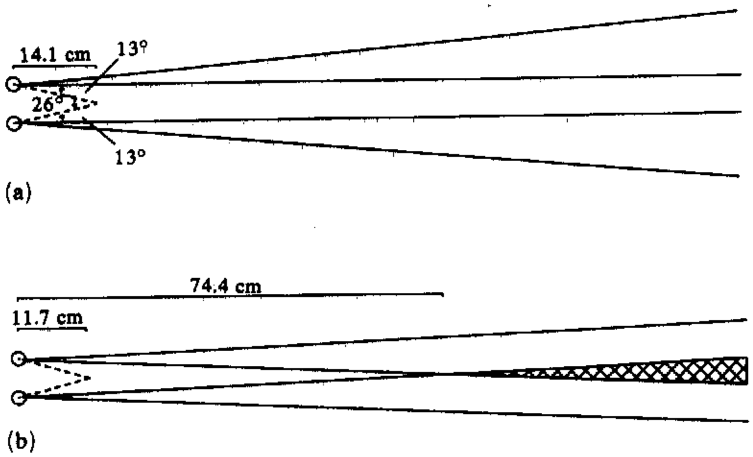

Figure 3. Top viewed projections of blind spots in visual space at different convergence angles. (a) The closest viewing distance (14.1 cm) at which the blind spots do not produce a volume scotoma. This occurs when the projections of their central boundaries are parallel. (b) The volume scotoma that results when the eyes are converged such that the projections of the centers of the blind spots (15.5 deg) are parallel,

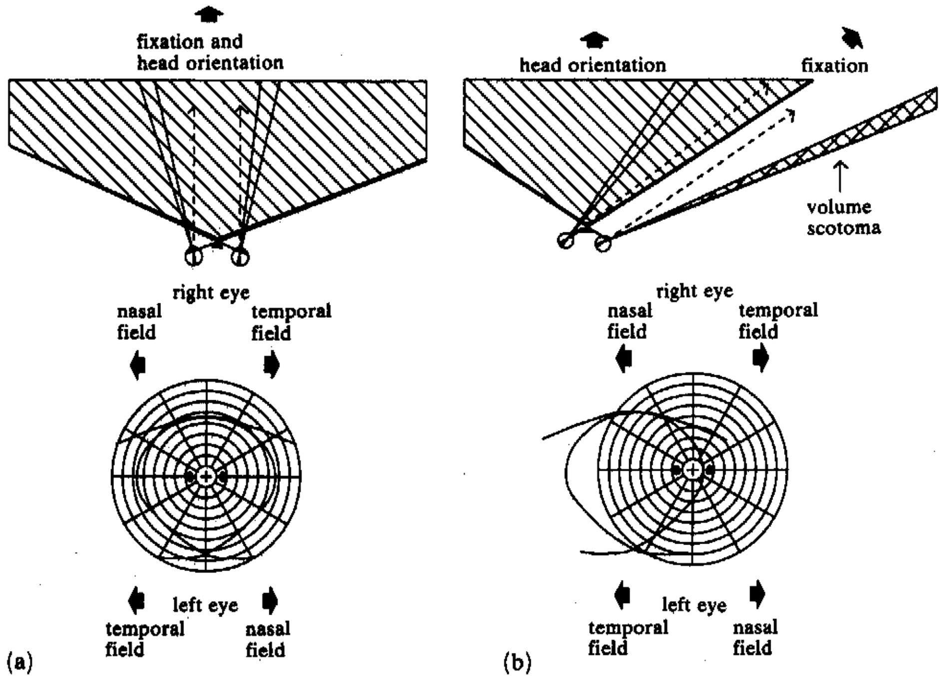

Figure 4. Visual fields with outlines of bony facial occlusions (both eyes superimposed) (lower half of figure) and top views of eyes converged to infinity but gazing (a) straight ahead and (b) to the right with respect to the head (half of figure). Hatched areas indicate the region of binocular overlap, dashed lines the projections of the foveas. In (a) both blind spots fall into the area of binocular overlap and are compensated for by healthy retina in the fellow eye. In (b) the area of the retina in the left eye that would otherwise compensate for the blind spot in the right eye is occluded by the nose. An infinite volume scotoma results. With closer but sufficiently asymmetrical convergence, the resulting volume scotoma may not be of infinite extent.

would eliminate even the volume blindness associated with very close viewing, and, in addition, would fall on a region of even lower acuity than it does.

A reasonable answer is illustrated in figure 4. With the eyes symmetrically converged both blind spots fall well within the region of the visual fields in which one eye can compensate for or 'fill in' the blind spot of the other.(1) Note that the retinal regions that constitute this area of binocular overlap are determined primarily by the positions of the bony facial occlusions on the retinas; along the horizontal meridian of the blind spot, binocular overlap depends on the retinal position of the nose or nose bridge.(2) With our eyes gazing to the right or left, however, one blind spot may fall outside the region of binocular overlap and result in a volume scotoma of infinite extent. Assuming a nose bridge that protrudes 2 cm at the level of the blind spots measured from the centers of rotation of the eyes, an individual can turn the gaze laterally ±48° without producing a scotoma of infinite volume. Were the blind spot located more temporally in the visual field than it is, this range would be further restricted. If it were at 60° in the temporal field, for example, the same individual would be able to turn the eyes only ±6° without loss of field. Given, however, the wide variance in the degree of protrusion of nose bridges, these examples should be taken merely as illustrative. The important point is that increasing temporal eccentricity of the blind spot is accompanied by decreasing range of lateral gaze without loss of functional visual field.

3 Conclusion

There are good reasons, then, for the horizontal location of the blind spot, at least in humans. The optic disks of other animals with front-facing eyes and large areas of binocular overlap seem to be located in approximately the same horizontal position, but the paucity of published perimetric data on animals other than humans makes it difficult to apply the same analysis to them.

Also note that the vertical position of the blind spot cannot be explained by binocular geometry. Prince (1956), however, has noted that in animals whose heads are well off the ground the disk tends to be located in the superior visual field, where few obstructions lie, whereas in small animals it tends to be located in the inferior visual field, leaving the view of larger predators from above unobstructed. If our ancestors lived in the trees, where obstructions abound from both above and below, perhaps neither inferior nor superior location offered any clear advantage.

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Mariotte E, 1717 *Oevres* (Leide)

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(1) Note that regardless of eye position there will always be two tiny finite volume scotomas: those portions of the projections of the blind spots in space that fall so close to the eye that their view by the other eye is occluded by the nose bridge.

(2) The nasal fields of many East Asians and others with small nose bridges are not always limited by the bony occlusions when the gaze is directed straight ahead at effectively infinite distance (Mapp and Ono 1986). However, these occlusions will limit the nasal field of these individuals with inward turning of the eye for near or asymmetric convergence.

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