self-motion (*8*), rather than on the focus (*5*). Our stimulus was designed to dissociate visual sensitivity to flow pattern focus and visual sensitivity to local maxima in magnification rate [also called "local maxima in div **V**" (*13, 14*)]; previous experimental studies have confounded these two factors (*15*). A focus differs from a div **V** maximum in important ways; in particular, focus can be shifted by translational motion (*1*), whereas div **V** is unaffected (*13, 14*). The human visual system is specifically sensitive to div **V** independently of translational motion (*14*), and this sensitivity is adequate to locate the focus of one kind of flow pattern (*16*). However, because computations show that div **V** is not always maximal along the direction of motion [reference 6 in (*1*)], sensitivity to local maxima of div **V** does not provide a sufficient explanation for real-world directional judgments (*4*). The two algorithms discussed so far start with a single sample of a local property of the flow pattern (either focus or div **V**). Alternative kinds of candidate procedure involve several momentary samples of the flow pattern rather than one, and a large-field rather than a local property. Template-matching is one alternative procedure. A suitable template might be a neural mechanism that summed the outputs of many detectors of local radial motion distributed over an extensive area of the visual field (*17*). For some environments, exploratory eye movements would produce the largest response when the fovea was maintained centered on the destination because, for that unique direction of gaze, the retinal flow pattern would correlate most closely with the template [figure 1 in (*1*)]. It remains to be shown, however, that this means of extracting guidance information would be accurate in asymmetric environments.

Torrey (*12*) correctly points out that we leave open the possibility that observers might be able to judge the location of the focus provided that any translational motion is generated by eye movements rather than by moving the physical stimulus pattern as in our experiments; I know of no data to resolve that point.

I do not agree with Priest and Cutting's statement (*3*) that our conclusions (*1*) imply that pilots could not make accurate visual judgments of self-motion. Rather, they imply that a complete explanation for this evident ability is not yet established. Elsewhere we compared quantitative data on pilots' remarkable visual judgments while landing and in other flying tasks in simulators and high-performance jet aircraft (*18*) with visual discrimination of flow patterns. In view of the theoretical interest in the general rotating-eye case, quantitative data on human performance are surprisingly sparse; it has not been experimentally ruled out that a partial or even complete failure of directional judgment might occur when the eye rotates (*19*). Comparisons between different models of extracting guidance information from the optic flow pattern are currently constrained by the shortage of empirical knowledge about human performance.

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4. D. Regan and K. Beverley, in *Sensory Experience, Adaptation and Perception* (Erlbaum, Hillsdale, N.J., 1984), pp. 215–240.
5. "Focus" here means a point at which velocity is locally zero while velocity vectors on opposite sides point in opposite directions.
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7. J. J. Gibson, *Br. J. Psychol.* **49**, 182 (1958).
8. _____, *The Perception of the Visual World* (Houghton Mifflin, Boston, 1950), pp. 117–144.
9. The "optic array" is a theoretical construct that, by definition, is not influenced by eye rotation. Gibson proposed that subjects can use the focus of expansion in the optic array to guide locomotion, implying that ocular rotation can be disregarded in practice. The optic array concept has been discussed elsewhere [R. M. Boynton, in *Handbook of Perception* (Academic Press, New York, 1974), vol. 1, pp. 285–307].
10. K. R. Llewellyn, *J. Exp. Psychol.* **91**, 245 (1971); I. R. Johnson, R. White, R. W. Cumming, *Am. J. Psychol.* **86**, 311 (1973).
11. Torrey (*12*) correctly points out that we unfortunately misquoted Gibson by using the phrase "retinal image" instead of "optic array." However, this should not divert attention from the empirical question whether subjects can or cannot locate the focus of expansion when the eye is rotating.
12. C. C. Torrey, *Science*, **227**, 1064 (1985).
13. For clarity in (*1*), we used the term "local maximum in rate of magnification" rather than "local maxima of div **V**" (vector divergence of the local velocity vector). Flow patterns have been mathematically analyzed in terms of div **V** (*2, 6*). The indifference of div **V** to translational motion can be intuitively understood, because div **V** expresses *relative* motion [see L. Kaufman and D. Regan, in *Handbook of Vision*, in press); (*14*)].
14. D. Regan and K. Beverley, *Vision Res.* **18**, 415 (1978); *J. Opt. Soc. Am.* **70**, 1289 (1980); D. Regan, *Vision Res.* in press.
15. Priest and Cutting [figure 1 in (*3*)] correctly show that our display did not mimic a flat plane. It was not intended to, but rather to dissociate flow pattern focus and div **V**. It is not clear what Priest and Cutting mean by "normal optic flow" because the number of real-world flow patterns is as indefinitely large as the number of different environmental geometries. For that reason we made no attempt to mimic any particular environmental geometry, preferring to search for some general property of the human visual system relevant to a wide range of possible environmental geometries.
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17. Early reports that collicular units respond best to motion away from the center of gaze [M. Straschill and K. P. Hoffman, *Brain Res.* **13**, 274 (1969); P. Sterling and B. G. Wickelgren, *J. Neurophysiol.* **32**, 1 (1969)] have not been confirmed [N. Berman and M. Cynader, *J. Physiol. (London)* **245**, 261 (1975)], but the L.P. nucleus may be radially organized [J. P. Rauschecker, *Perception* **12**, A13 (1983)].
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19. If a movie taken from a camera mounted on an aircraft during landing is projected onto a screen, subjects can judge the point of aim (*8*, p. 130). This might seem to show that eye rotation can be disregarded. If the camera is fixed to the aircraft (even at some arbitrary angle), however, and if the aircraft is traveling in a straight line without pitch or yaw, then by gazing straight at the projection screen the viewer can automatically ensure that the focus of expansion coincides with the destination, thus reducing the problem to the simple nonrotating eye case.
20. Sponsored by the Air Force Office of Scientific Research (grant AFOSR-84-0030) and by the Natural Sciences and Engineering Research Council of Canada (grant A-0323).

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On the Mathematical Structure of the Visuotopic Mapping of Macaque Striate Cortex

Tootell *et al.* (*1*) have published the results of a 2-deoxy-D-glucose (2DG) study of primate striate cortex topographic mapping. In this study, a set of logarithmically spaced rings and equiangular rays was used as a visual stimulus. The rationale for using this particular pattern is that the logarithmic rings and equiangular rays project to an approximately rectangular pattern at the level of the striate cortex (*2, 3*). I have used a pattern of this kind to study human striate cortex topography [using 2DG and positron emission tomography (PETT)] (*4*). Since the data of Tootell *et al.* (*1*) are of much higher spatial resolution than the analogous human PETT data, it is now possible, for the first time, to compare theoretical to experimental cortical map functions directly (Fig. 1). It is thus possible to point out a misinterpretation of the theoretical model of cortical topography (*2*) cited by Tootell *et al.* (*1*) in the analysis of their data.

Tootell *et al.* (*1*) found different values of cortical magnification along the vertical and horizontal meridians (the vertical meridian is longer than the horizontal). They assumed that the cortical map function that I have published (*2, 3*) predicts that the magnification factor should be the same along all meridians. On the contrary, this model predicts differences in cortical magnification at

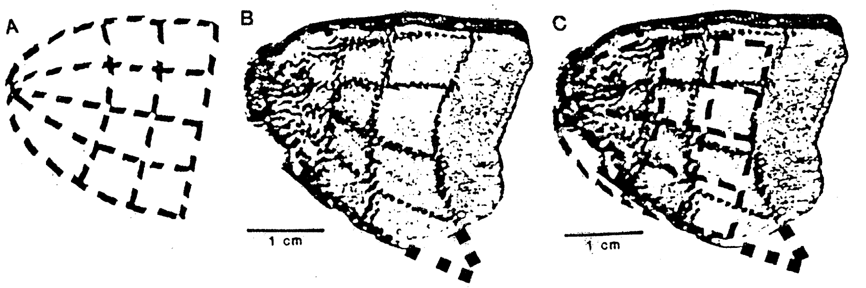

Fig. 1. (A) Theoretical map of three circles at eccentricities of 1°, 2.38°, and 5.66° and rays at −90°, −45°, 0°, 45°, and 90°, generated by the map function $\log (z + 0.3)$. (B) A reproduction of figure 1B in (*1*) for the same visual field pattern. In the lower right corner, the representation of the vertical meridian does not meet the representation of the circle of 5.66° of eccentricity. Solid squares have been linearly interpolated to indicate this missing intersection. (C) A theoretical map (*3*) superimposed on (B). Theory and experiment seem to agree, except for the lower right corner, where the possibility of tissue distortion is suggested by the failure of the vertical meridian to meet the representation of the circular arc of 5.66°. Such distortion may be caused by local curvature of the cortical surface, which is almost flat across most of the operculum, but which seems to become more curved near the representations of the lower and upper vertical meridians (the lunate and inferior occipital sulci).

corresponding points along the vertical and horizontal meridians (*3*), but equal magnification in all directions (locally). In other words, this model states that the cortical map function is conformal (*3*) (locally, but not necessarily globally isotropic). Moreover, these differences are in almost exact agreement with the data presented by Tootell *et al.* (*1*), who found, for example, that the length of the vertical meridian is longer than the length of the horizontal meridian by a factor of 1.25. This may be compared with a factor of 1.22 predicted by the complex log model (*3*). Figure 1 shows this theoretical model superimposed on the data of Tootell *et al.* (*1*).

This work provides an example of a mathematical analysis that has provided not only useful insight to neuroanatomical work, but also an accurate prediction of subsequent data; in addition, it seems to be crucial to the correct interpretation of the data.

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Schwartz (*1*) has correctly described our experiment, but misstated both our findings and our conclusions with respect to anisotropies in the cortical projection. We did not state that the difference in magnification factor along the vertical and horizontal meridians in itself contradicted his theory. Rather we pointed out that this difference [as well as other anisotropies not predicted by Schwartz's logarithmic $(z + a)$ transformation] seems to be related to the direction taken by the ocular dominance strips in various local striate regions. By this model, a small square in the visual field will be represented in a roughly rectangular region of the cortex, with the long axis of the rectangle perpendicular to the long axis of ocular dominance strips. We illustrated some of the evidence for this model in figure 2, C and D in (*2*), which showed a difference in the length of two oblique segments (both at 45° from the retinal horizontal). According to Schwartz's theory, two such oblique segments should be equal in length, but they are not. However, one can account for the difference in length of these two oblique segments on the basis of an ocular dominance–dependent anisotropy, since the ocular dominance strips cross these two oblique ray segments in different directions. Similar results were obtained from comparisons of numerous other segment pairs which should be equal in length according to the $\log (z + a)$ model, but which varied in accordance with an apparent ocular dominance anisotropy. An anisotropy such as this would also account for the global difference in magnification along the vertical and horizontal meridians in the central striate cortex, since here ocular dominance strips tend to run perpendicular to the vertical meridian, but more randomly or parallel to the horizontal meridian. Horton has recently published additional experimental evidence supporting an ocular dominance anisotropy (*3*).

Other features of our 2-deoxy-D-glucose (2DG) autoradiographs also disagree with the strict $\log (z + a)$ conformal map. First, the curvature of the ring segments actually reverses slightly at eccentricities near 5°: this was seen even in the very earliest striate mapping studies (*4*). Second, the labeled rings and rays often do not intersect orthogonally. In order to account for these discrepancies, Schwartz proposes that distortion must have occurred selectively in cortical regions where the 2DG map does not match the log map (but apparently not in areas of agreement). However, the amount of distortion experimentally measured in the flattened tissue is much less than that necessary to account for such a discrepancy (*2*). Finally, another recent study of retinotopic organization (*5*), carried out with different techniques in a different area of the striate cortex, came to conclusions similar to our own: the actual striate maps differ from those predicted by the $\log (z + a)$ model in a number of ways, and the discrepancies are larger than can be accounted for by experimental error.

Despite these discrepancies, we believe the logarithmic conformal map gives a good approximation to the retinotopic mapping in the macaque striate cortex.

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